DISSERTATION

IMPACTS OF WILDFIRE ON BENTHIC INSECTS IN BURNED STREAMS: COMMUNITY AND POPULATION RESPONSES AT MULTIPLE SCALES

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the degree of Doctor of Philosophy

Colorado State University

Fort Collins, CO

Summer, 2003

COLORADO STATE UNIVERSITY

July 1, 2003

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY NICOLE KATHLEEN MACRURY VIEIRA ENTITLED "IMPACTS OF WILDFIRE ON BENTHIC INSECTS IN BURNED STREAMS: COMMUNITY AND POPULATION RESPONSES AT MULTIPLE-SCALES" BE ACCEPTED AS FULLFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Advisor

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ABSTRACT OF DISSERTATION

IMPACTS OF WILDFIRE ON BENTHIC INSECTS IN BURNED STREAMS: COMMUNITY AND POPULATION RESPONSES AT MULTIPLE SCALES

This research combines several approaches, spanning a range of spatial and temporal scales and biological organization, to document the impacts of wildfire on stream insects of the Pajarito Plateau, near Los Alamos, New Mexico. I present results of an eight-year monitoring study to describe physicochemical and insect population and community responses to the 1996 Dome fire in a burned stream (Chapter 1). To better understand mechanisms behind community resistance and resilience in this long-term study, I explored how insect population attributes (i.e. life-history, morphological, and behavioral traits) were associated with recovery time and environmental conditions after the Dome fire (Chapter 2). Fortuitously, I was able to conduct these studies with a before-after-impact-control design, where benthic insect responses and trait-environment associations were compared between a burned stream and an unburned stream for two years before and six years after the wildfire. I also conducted a short-term *in situ* experiment at the microhabitat level, where I compared community colonization patterns on cobbles in six watersheds across a gradient of wildfire history (Chapter 3). Specifically, I measured community resilience in two streams burned in the 1996 Dome fire, in two streams burned in the 1977 La Mesa fire, and in two unburned streams.

I also compared representation of population attributes shown to convey community resilience after the Dome fire (Chapter 2) across these six streams. Finally, after documenting low resilience of shredder populations to both wildfire and experimental disturbance, I conducted experiments to investigate colonization and growth of stonefly shredders, *Pteronarcella badia* Hagen, on two types of burned detritus (deciduous and coniferous) (Appendix A).

The 1996 Dome fire had moderate to severe impacts on physical, chemical, and hydrological stream characteristics in the burned stream, which resulted in strong negative impacts on stream insect communities (Chapter 1). Insect communities showed low resistance to a 100-year flash flood following the fire in 1996, where insect densities and taxa richness were reduced to near zero. Total insect density showed high resilience and recovered within a year of the fire. This was largely due to the colonization of disturbance-tolerant and strong-dispersing taxa such as *Simulium* sp. blackflies, *Baetis tricaudatus* Dodds mayflies, and Chironomidae. Taxa richness was less resilient and recovered after 3 years, while taxa composition remained markedly different from pre-fire composition in the burned stream. Several stonefly taxa and elmid beetles common in pre-fire years were greatly reduced or absent at the end of the study. In contrast, dramatic changes in total insect density, taxa richness, and community composition were not observed in a nearby and geomorphically similar unburned stream.

Relationships between insect population attributes and environmental conditions explained patterns of community resistance and resilience in the burned stream (Chapter

2). Specifically, taxa with traits conveying high resilience (i.e. strong larval and adult dispersal, multi-voltinism, resource generalists) colonized earlier and were positively associated with higher peakflows after the Dome fire. Traits conveying high resistance (i.e. ability to avoid or tolerate high flows through swimming, attachment to substrate, or burrowing; low drag forces) were also strongly represented in early post-fire years with floods in the burned stream. These relationships made sense in light of strong colonization barriers presented to both larval and adult insects in streams of the Pajarito Plateau. Specifically, these streams lack tributaries, have upper and lower ephemeral reaches, and are embedded in a harsh canyon-mesa landscape. Despite common landscape factors, the unburned stream did not show the same relationships between resistant and resilient traits and environmental conditions as the unburned stream.

Patterns of resilience to a small-scale experimental disturbance corresponded to a gradient of wildfire history, where insect communities in recently burned streams were more resilient than communities in unburned streams (Chapter 3). Taxa with attributes that convey resilience (multi-voltinism, strong larval dispersal, generalist-feeding strategies) dominated recently burned streams. For instance, Chironomidae and Baetidae recolonized quickly via drift. In contrast, taxa dominating unburned streams had poorly resilient attributes, such as weak larval dispersal, specialist feeding strategies, and semi-voltine life-cycles (i.e. grazing heptageniids, shredder stoneflies). This study demonstrated that wildfire and post-fire flooding can have lasting effects on community composition, and suggests that post-disturbance communities are more resilient to local scale disturbances. In a separate set of experiments, I found that *P. badia* were able

colonize and grow on burned detritus, regardless of lower microbial conditioning and nutrition (Appendix A). These results suggest that low resistance and resilience of shredders in burned streams, as well as on experimentally-disturbed cobbles, may have been due to reductions in quantity rather than quality of detritus.

A multiple-level approach, including monitoring studies and experiments across different spatial and temporal scales, and endpoints spanning levels of biological organization, was necessary to understand impacts of wildfire on stream insect communities. Further, I demonstrated the utility of adopting a trait-based perspective to reveal mechanisms behind stream insect community responses to disturbance. Linking species traits with environmental conditions in burned streams, and interpreting relationships in light of colonization barriers of the landscape, revealed distinct post-fire succession patterns. In general, trait-based approaches are both ecologically and evolutionarily relevant since real-time trait-environment interactions determine species persistence, while traits are a result of natural selection. Traits also reflect functional significance (i.e. foodweb position and productivity) of insect species. Finally, trait representation in communities can be compared across regions with different species pools, allowing for broader tests of ecological theory.

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ACKNOWLEDGEMENTS

It has been an exhilarating (and often exhausting!) experience working in streams of Bandelier National Monument, New Mexico. My canyons are located in wilderness areas that are only accessible by strenuous hiking, or in Adolph Bandelier's own words "...by dint of toilsome climbing and clambering". Without the tough skin (especially tough feet) and minds of my field helpers, I never would have been able to conduct this project. One of my most enthusiastic (and physically fit, I might add) field helper was also my advisor, Dr. Will Clements. I feel very fortunate to have been offered this Ph.D. project, and my sincerest gratitude goes to Will for entrusting me with it and also for his support/advice along the way. Considerately, Will encouraged me to "reduce and focus" my dissertation work, and I learned the hard way that your advisor is always right! I would also like to thank the rest of my committee for their support, and for pushing me to higher heights (albeit against my will sometimes– haha!). The energetic team consisted of Dr. LeRoy Poff, Dr. Boris Kondratieff, Dr. Jennifer Hoeting, and Dr. Nancy DuTeau. LeRoy put a good deal of effort into helping me think on a more theoretical level. Because of this, the "light at the end of the tunnel" was not finishing the dissertation; it was truly seeing stream ecology in a whole new "light". Special thanks go to my National Park Service contact at Bandelier National Monument, Brian Jacobs, for his excellent ideas, for always being one step ahead of me, and for his patience. Brian's savvy acquired the funding for this project through National Park Service and the Southwest Parks and Monuments Association.

I deeply appreciate the many people who helped me pull this project off: Lynette Stevens, Katharine Mitchell, Adam Craig and Tom Cady, Richard Thorp, Tiffany Barnes, Laura Dunham, Lisa Courtney, Bob Kuhl, Blair Prusha, Jeff Clark, Diana Hammerdorfer, Maria Carreon, the two Kristis (Walski and Neptun), Dr. Ken Poppe, Erik Tate-Boldt, Lance Everette, Michelle Cummer, Mike Morrow, Sarah Converse, and my husband Mark. Daren Carlisle, Elizabeth Harrahy, Bob Zuellig, the Craig's, and the Lytle-Vieira's provided additional moral support along the way. Special thanks and love to my family for encouraging me to pursue science. Dr. Thomas MacRury (otherwise known as Dad!) served as the primary inspiration for me in both childhood and adulthood to attain high academic heights and to *apply my mind.* When I was a very young girl, we took a walk one night and he observed that the streetlights were on, even though no wires were to be seen. He asked "Nicky, how can this be?" I can still remember the awesome feeling when the light bulb of deductive logic clicked on... "they are underground!", I shouted. Science was a natural pursuit from that point forward. Thanks also to Carole MacRury (Mum) for providing her friendship, moral support, and her "joie de vivre" (oh, and the occasional finances for new clothing as I shrunk a size in the field, gained a size at the scope, shrunk a size, etc, etc...ha ha)! My brother Morgan helped me "keep it real" by telling me to enjoy playing a few jazz licks once in awhile.... Last but not least, my love and gratitude to my husband Mark Vieira for his infinite patience, unwavering support, and devotion. This dissertation is dedicated to you, Mark, for being Mr. Majyck!

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CHAPTER 1

STREAM INSECT COMMUNITY RECOVERY CORRESPONDS TO MULTIPLE HYDROLOGIC DISTURBANCES AFTER A WILDFIRE IN BANDELIER NATIONAL MONUMENT, NEW MEXICO

Small white fairies dance
on the Rio Grande. Usually they swim
Deep through their days and nights
Hiding from our eyes, but when the white
Sun pulls them up, up
They leap about, tiny shimmering stars.

The desert says: feel the sun
Luring you from your dark, sad waters,
Burst through the surface

Dance

- Pat Mora from *Chants* (1984)

ABSTRACT

Stream insect communities in burned watersheds are subjected to multiple hydrologic and chemical disturbances associated with wildfire. I had the unique opportunity to document community resistance and resilience to a series of post-fire flash floods with a before-after-control-impact (BACI) design. Insect communities in a burned and an unburned stream were sampled two years before, and six years after, the 1996 Dome fire in Bandelier National Monument, New Mexico. In the year of the fire, multiple 100-year flood events reduced total insect density and taxa richness to near zero in the burned stream. Despite low resistance, density returned to pre-fire densities within a year of the fire due to the successful colonization of *Simulium* sp. black flies, *Baetis tricaudatus* Dodds mayflies, and chironomid midges. These disturbance-tolerant taxa recolonized despite repeated moderate flash floods in the second and third post-fire years. Taxa richness was less resilient and corresponded to post-fire hydrologic disturbance, where recovery to pre-fire richness did not occur until flash floods abated. Community composition in the burned stream, measured as changes in both presence and densities of taxa, did not recover by six years after the fire and unique post-fire communities were established. Inter-annual changes in composition corresponded to post-fire flash flooding. Similar changes in total insect densities, taxa richness, and composition were not found in the unburned stream, strongly suggesting that multiple post-fire hydrologic disturbances shaped community responses in the burned stream.

INTRODUCTION

Disturbance is a key factor shaping insect communities in stream ecosystems (Resh et al. 1988; Reice et al. 1990). Natural disturbances in streams are typically characterized by changes in intensity, frequency, duration and predictability of hydrologic events (Poff and Ward 1989; Poff and Ward 1990); flood magnitude (Quinn and Hickey 1990); and substrate stability (Death and Winterbourn 1995; Townsend et al. 1997a). Community resistance (magnitude of change compared to pre-disturbance communities) to disturbance depends on how insect populations withstand mortality and displacement, given species attributes (i.e. life history tactics, morphology, and behavior) and availability of refugia (Lake 2000). Resilience (rate of "recovery" to pre-disturbance communities) depends on persistence of survivors and recolonization given proximity of colonist sources and insect dispersal abilities (Gray and Fisher 1981; Cushing and Gaines 1989; Boulton et al. 1992).

Community resilience also depends on how spatiotemporal scales of a disturbance correspond to scales within which population recovery mechanisms operate (Fisher 1990). Insect communities are typically resilient to spates, which are characterized by short-term and spatially patchy substrate movement, because drifting insects quickly recolonize from upstream refugia (Resh 1988; Wallace 1990; Lake 2000; but see Cushing and Gaines 1989). In contrast, slow recovery has been observed after landscape-level

disturbances that alter physical habitat (Niemi et al. 1990; Mackay 1992) such that in-stream refugia and colonist sources are reduced (Yount and Niemi 1990). Community resilience may also be low after disturbances that occur infrequently or unpredictably compared to the historical disturbance regime (Poff and Ward 1990; Poff 1992). Species with necessary attributes to recover after an atypical event have not been previously "selected for" in the community (Poff 1997). Multiple disturbances that are rapidly compounded in time may also overwhelm population recovery mechanisms, resulting in "ecologically surprising" changes in community state (Paine et al. 1998).

Multiple disturbances associated with wildfire hold potential to yield "ecological surprises" (sensu Paine et al. 1998) in stream insect communities. Wildfires alter both terrestrial and aquatic environments of a watershed, resulting in direct disturbances (i.e. heat, ashfall) and a suite of post-fire disturbances in burned streams. Post-fire disturbances in burned streams vary in severity, spatial extent, and persistence (see review in Gresswell 1999). Changes in temperature (Royer and Minshall 1997), water chemistry (Spencer and Hauer 1991), sediment transport (Troendle and Bevenger 1996; White 1996), flooding (Novak and White 1989; Scott and Van Wyk 1990; Lavabre et al. 1993), and organic material (McIntyre and Minshall 1996) have been documented for days up to decades after wildfires. Negative impacts on insect communities have been noted after fires that also resulted in post-fire flooding (La Point et al. 1983; Rinne 1996; see review in Gresswell 1999). However, most studies lacked pre-fire data and were too short-term to relate recovery to post-fire disturbances.

I had the unique opportunity to examine recovery of stream insect communities after a wildfire and multiple post-fire hydrologic disturbances with a before-after-impact-control (BACI) approach (Stewart-Oaten et al. 1986). In 1996, a severe canopy fire (the Dome fire) burned over 65 km^2 of the Pajarito Plateau, including Capulin canyon in Bandelier National Monument, near Los Alamos, NM. Post-fire hydrologic disturbances in Capulin canyon included multiple 100-year flood events in the year of the fire (Veenhuis 2002). Debris flows associated with these floods moved even the largest substrate (i.e. boulders and logs; Cannon and Reneau 2000), resulting in major alterations in stream morphology and bed substrate (Reneau et al. 1999). Moderate (one order of magnitude above pre-fire peakflows) but progressively dampening floods continued for up to three years after the fire (Veenhuis 2002). Similar hydrologic events were not observed in Rito de los Frijoles (herein referred to as Frijoles), a nearby and geomorphically similar canyon that was not burned in the Dome fire (Veenhuis 2002).

Fortuitously, both water chemistry and insect communities were documented in the streams in Capulin and Frijoles canyons before the Dome fire (Stevens 1996). Therefore, I was able to compare water chemistry and insect communities in these streams for two years before (1994-1995) and six years after (1996-2001) the Dome fire. Specifically, I investigated community resistance and recovery patterns after post-fire flooding. I expected the severity of the first 100-year post-fire flood, compounded with direct effects of fire, to result in low community resistance. Thus, I expected to find significant reductions in density and taxa richness in Capulin in the year of the fire. To determine impacts of flash floods independent of direct fire effects, I investigated

resistance of insect communities to moderate post-fire floods in the second and third post-fire years. Similarly, I tested whether community resilience in Capulin, or the rate of recovery to pre-fire taxa richness and total density, corresponded to post-fire flooding. I also explored how these responses were associated with post-fire changes in water chemistry and peakflow magnitude.

Insect community composition typically shows slower recovery than total insect densities and taxa richness after large-scale disturbances (Yount and Niemi 1990) such as wildfires (see review in Gresswell 1999). Therefore, I expected changes in composition to hold the greatest potential for yielding the ecological surprises described by Paine et al. (1998). Quantitative measures of composition, or changes in relative densities of insect taxa, reflect responses to a disturbance event at a specific location (Poff and Ward 1990). Numerically dominant species possess attributes that allow them optimize population growth under local post-disturbance conditions. However, these attributes may become less suitable as local environmental conditions change, resulting in temporal peaks in population densities (Poff and Allan 1995). In contrast, qualitative measures of community composition based on species presence are less sensitive to temporal fluctuations in the environment, and also account for which species "selected" under the historical disturbance regime can persist after a disturbance (Poff and Allan 1995). In this study, I investigated recovery trajectories of both quantitative and qualitative measures of composition to determine how post-fire hydrologic disturbances altered insect communities in Capulin.

STUDY SITE DESCRIPTION

This study was conducted in streams located in Capulin and Frijoles canyons of Bandelier National Monument, New Mexico (Figure 1.1). The Monument is located on the eastern slopes of the Sierra de los Valles range and Pajarito Plateau, and ranges in elevation from 3111 m at the Caldera rim of Cerro Grande to 1590 m at the Rio Grande River valley. The Pajarito Plateau was created when pyroclastic ashflows from pre-historic volcanic eruptions left tuff deposits up to 300 m thick along the east flank of the Sierra de los Valles. Currently, the Plateau slopes towards the Rio Grande River in a series of canyons and mesas that have been carved into the rheolitic tuff by erosion. Capulin and Frijoles watersheds are similar in drainage area (approximately 50 km^2), stream order (spring-fed first-order streams with no permanently-wetted tributaries), flow permanency (perennial reaches between 1600-3000 m), gradient (3-4% at lower elevation and 6-7% at higher elevations), and baseflow (0.04 - 0.06 m^3/s). Riparian vegetation in both canyons consists primarily of Western box elder (*Acer negundo*), narrowleaf cottonwood (*Populus angustifolia*), alder (*Alnus oblongifolia*), and ponderosa pine (*Pinus ponderosa*).

The Pajarito Plateau has a semiarid mountain climate, with mean annual precipitation ranging from 33-46 cm. Annual hydrographs for all Plateau streams are snowmelt driven in mid-spring and show flashy responses to monsoonal precipitation events in summer. Localized and intense convectional thunderstorms occur from July through September and contribute more than half of the annual rainfall (Purtymun and

Adams 1980). These storms can result in flash floods in one canyon but not in adjacent canyons. Flash floods occur when in-stream sediment dams are created from erosion during intense rain events and then break, releasing large volumes of stored water downstream. While the monsoon season creates spatial and intra-seasonal variation in peakflows among Pajarito streams, inter-annual differences in flow are driven by winter snowmelt and spring precipitation from large-scale frontal storms. Changes in baseflow across years are more similar among streams, where cyclic El Niño climate events bring increased spring and summer precipitation approximately every four years (Andrade and Sellers 1988).

Wildfire has played a central role in the Pajarito Plateau ecosystem. High-frequency, low-intensity ground fires have been replaced by low-frequency, high-intensity canopy fires due to increases in fuel load through fire suppression and grazing (Touchan et al. 1996). Two canopy wildfires have burned most of Capulin and Frijoles watersheds in the last thirty years (Figure 1.1). In June 1977, the La Mesa Fire burned 65 km^2 and the eastern half of Bandelier National Monument (including 58% of the Frijoles watershed). The majority of the burned area (57%) experienced moderate burn intensities, while 33% experienced high intensity (i.e. 100 % tree mortality) burn (Veenhuis 2002). In April 1996, the Dome Fire burned 66.8 km^2 and the western half of the Monument (including approximately 90% of the Capulin watershed). High-intensity burn occurred in 27% of the Capulin canyon watershed, while moderate burn occurred in 28% of the canyon (Cannon and Reneau 2000). Despite differences in burn intensities between the La Mesa and Dome fires, post-fire hydrologic responses in Frijoles and

Capulin streams were very similar (Figure 1.2). Peakflows increased by two orders of magnitude and then dampened over several years post-fire (Veenhuis 2002). Historical (prior to 1900) severe flood events in Plateau canyons have also been found to correspond to wildfires (McCord 1996).

METHODS

I compared water chemistry and stream insect communities between Frijoles and Capulin streams for two years prior to (1994 - 1995) and six years after (1996 - 2001) the 1996 Dome fire. Three 50-m reaches, at least 100 m apart and at approximately 2000 m elevation, were sampled in each stream during 1994-1995 as part of a previous study (Stevens 1996). I sampled these reaches in post-fire years with the same sampling schedules, techniques, and equipment that were used in pre-fire sampling. Post-fire sampling was conducted in spring (April-May), summer (July-August), and fall (October) to capture intra-annual variation in water chemistry, hydrology, and insect communities. Seasonal sampling allowed me to compare communities before and after known post-fire flash flood events, and also better accounted for differences in life-history schedules (and thus capture probability at a given sample date) of insect taxa. Hazardous conditions in 1996 restricted sampling in Capulin to only one sampling period after the first post-fire flash flood event. Thus, I was unable to collect samples between the fire and the first flood.

On each sampling date, water temperature (°C), conductivity (μS), pH, and dissolved oxygen (Winkler Titration kit; mg/L) were measured in each reach (n = 3 per

stream). Water samples (1 L) were also collected, chilled on ice, and transported to the laboratory. I analyzed water hardness with EDTA titrimetric Method 130.2 (US EPA 1983) and alkalinity with pH 4.5 titrimetric Method 310.1 (US EPA 1983). Water samples were also analyzed for total dissolved solid (TDS) concentrations (anion plus cations) at the Rocky Mountain Forest and Range Experiment Station, USFS, Fort Collins, CO. After filtration through a 0.45-μm filter, cation concentrations were determined with atomic absorption Method 3111 and inductively-coupled plasma Method 3120 (APHA 1989). Anions were determined with ion chromatography Method 4110 (APHA 1989).

To determine how sample periods corresponded to hydrologic events in Capulin and Frijoles, data on timing and magnitude of peakflow events in both canyons were obtained from publications (Veenhuis 2002) and USGS data archives (USGS stream gauge #08313350). Discharge data were somewhat limited for Capulin because only partial gauges were functional and peakflows (but not daily flows) were only recorded with these gauges through 1998. Thus, qualitative information on peakflows for years 1999-2001 was obtained from measuring post-flood debris lines (indicative of flood stage) and movement of painted cobbles between sample periods (indicative of discharge). For instance, flows less than 0.5 m^3/s did not move cobbles and remained below bankfull levels, while flows above 1.5 m^3/s moved all cobbles and exceeded bankfull levels (N.K.M. Vieira, Colorado State University, unpublished data).

On each sample event, I collected three standard-sized (0.093 m^2 area) 750-μm mesh Surber samples per reach (n = 9 per stream) to document stream insects. This mesh size, while coarser than the 500-μm typically used to sample macroinvertebrates, was used to keep post-fire samples consistent with samples collected in 1994-1995 (Stevens 1996). Samples were collected in three randomly selected riffles within each reach. Potential sample riffles were restricted in that they could not contain boulders or coarse woody debris (logs) and had to consist of at least 25% fist-sized cobble substrate. Insects were preserved in 80% ethanol in the field, transported to the laboratory, and sorted and identified with a dissection microscope to taxonomic levels reported for pre-fire samples (Stevens 1996). I calculated total insect density and taxa richness, as well as community composition expressed as both taxa-specific densities and presence of taxa (hereafter referred to as persistence).

Statistical Analysis

All statistical analyses were conducted with use of SAS/STAT statistical software (SAS Institute 1996). Descriptive statistics were generated to compare water chemistry parameters among sample periods in each stream (n=3 per sample period). Temporal changes in concentrations of TDS (ueq/L) and dominant ions (mg/L) in Capulin and Frijoles were investigated graphically with means and standard errors (Ott 1993). I also compared temporal changes in total insect density (# insects/0.09 m^2) and taxa richness between Capulin and Frijoles with graphs of means and standard errors for each sample period (n = 9 per sample period).

I constructed *a priori* linear contrasts (Ott 1993) to investigate community resistance and resilience to post-fire flash floods. I employed two-way analysis of variance (ANOVA) to determine whether total insect density and taxa richness were significantly related to main effects of canyon, time (sample period), and their interaction. Sample reaches were included in both models as a random effect nested within canyons. Linear contrasts were constructed for statistically significant canyon*time interactions (alpha <0.05) to compare temporal changes in community responses between Capulin and Frijoles over specific sample periods. Total insect densities were natural log-transformed and taxa richness was square root transformed to meet parametric assumptions of ANOVA and Student t-tests used in linear contrasts (Ott 1993).

To determine community resistance, I tested whether changes in insect density and taxa richness between samples taken pre-fire (1995) and in the year of the fire (1996) differed between Capulin and Frijoles. This contrast tested resistance to both the Dome fire and the first 100-year flood event after the fire. I also compared changes in both responses between streams before and after moderate flood events (2-5 year recurrence interval; Veenhuis 2002) that occurred in late summer of 1997 and 1998 (July versus October sample periods in both years). To determine resilience, I compared mean pre-fire (1994-1995) insect density and taxa richness to mean levels observed in post-fire years with moderate flash floods (1997 and 1998), and in the first year when flash floods

in Capulin were the same order of magnitude as pre-fire floods (1999). Since individual Surber samples within reaches were often spatially close (i.e. 10 m), stream reaches (n = 3 per stream per sample period) were considered replicates to meet parametric assumptions of independence of errors (Ott 1993).

I investigated how total insect densities and taxa richness were correlated with peakflow and TDS concentrations with Pearson product-moment correlation coefficients. To better understand factors related to resilience after the fire in Capulin, data from pre-fire sample periods and the year of the fire were removed from the analyses (all 1997-2001 sample periods included; n = 15). Correlations using the same sample periods (n = 15) were conducted for Frijoles to compare these relationships between streams. Peakflows were expressed as a semi-quantitative natural log-based index to account for qualitative data from 1999-2001. Peakflow values were natural-log transformed and then rounded up to the nearest whole number (e.g. a peakflow of 85 m^3/s was log-converted to 4.45 and then rounded up to an index value of 5). Index values represented the highest magnitude flood event that occurred between sampling periods.

I employed canonical discriminant analysis (CDA) to investigate quantitative changes in community composition before and after the Dome fire in Capulin and Frijoles. This descriptive, dimension-reducing multivariate technique constructs linear combinations of independent measurement variables (taxa-specific densities) to maximize separation between pre-assigned groups (years 1994-2001) based on a set of observations (Surber samples). Taxa-specific densities were log-transformed to meet

assumptions of multivariate normality for measurement variables (Ott 1993). When densities of individual taxa populations were still not normally distributed after transformations, these taxa were combined by Family or Order until assumptions were met. For a qualitative assessment of community composition, I also employed CDA to maximize separation between sample years based on taxa presence/absence (coded as 1/0 binary data for each Surber sample). Multivariate analyses for Capulin and Frijoles were conducted separately. Correlations between taxa and canonical variables constructed in CDA (total canonical coefficients), were interpreted in light of inter-annual changes in densities and persistence of taxa in both streams.

RESULTS

Dissolved oxygen was above 8 mg/L for all sample periods in both streams. Variation in temperature and pH among post-fire years in Capulin was similar to variation in mean levels recorded in pre-fire years and in Frijoles (Table 1.1). In contrast, hardness, alkalinity, and conductivity in Capulin were three times higher after the fire and first 100-year flood (July 1996) compared to pre-fire and Frijoles levels, and remained elevated until May 2001 (Table 1.1). TDS concentrations in Capulin also increased dramatically in July 1996, but dampened significantly by May 1997 (Figure 1.3). Thereafter, TDS remained slightly elevated until May 2001, and showed little correspondence to moderate flood events (see Figure 1.3 for flood dates). Increases in alkalinity and hardness, and moderate increases in Ca^{+}, Mg^{+}, K^{+}, and SO_4^{-} were responsible for increased TDS concentrations in post-fire Capulin samples (Figure 1.4;

also see Appendix 1.1). In contrast, only slight fluctuations in these water chemistry parameters were observed in Frijoles, despite the occurrence of a moderate flood event in August 1998 (Figures 1.3 and 1.4).

Total insect densities were similar between Capulin and Frijoles in the two years prior to the Dome Fire (Figure 1.5). However, after the fire and first post-fire flood in July 1996, Capulin densities were reduced to only a few individuals, whereas Frijoles densities increased. Capulin densities recovered to pre-fire levels by May 1997 due to colonization of *Simulium* sp. (56% of total density), Orthocladiinae (22% of total density), and *Baetis tricaudatus* Dodds (17% of total density). These taxa were unevenly distributed spatially and thus contributed to high variation among Surber samples. Capulin densities were severely reduced again by October 1997 following flash floods in late August and early September of 1997. Frijoles densities were also slightly reduced in October 1997 despite lack of moderate flood events. Capulin densities remained similar to (or higher than) pre-fire and Frijoles densities in most sample periods between May 1998 through October 2001. A notable exception was July 2001, where densities in Capulin were reduced although no above-average peakflows occurred.

Similar to temporal patterns in insect density, taxa richness in Capulin was greatly reduced in July 1996 to a mean of two taxa (Figure 1.6). However, taxa richness remained lower than pre-fire Capulin and post-fire Frijoles richness until October 1999. By October 2001, taxa richness in Capulin was higher than richness in Frijoles and also exceeded pre-fire levels. Compared to Capulin, richness in Frijoles did not decrease

dramatically in July 1996 and generally showed similar seasonal fluctuations across years (Figure 1.6).

Linear contrasts revealed that community resistance to post-fire flooding in Capulin was similar for total insect density and taxa richness. Canyon*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 taxa richness ($F = 11.55$, $P < 0.0001$). Linear contrasts comparing insect densities and taxa richness between pre-fire samples and 1996 samples showed that reductions in Capulin were significantly greater than changes observed in Frijoles (Table 1.2). Similarly, densities and taxa richness were reduced to a greater degree in Capulin compared to Frijoles after moderate floods in the second post-fire year. Temporal changes in insect density and taxa richness were similar between Capulin and Frijoles in the third post-fire year after moderate (but lower magnitude) floods in both streams.

Linear contrasts revealed that resilience was lower for taxa richness compared to insect density in Capulin (Table 1.2). Differences between mean annual pre-fire and post-fire densities in Capulin were similar to those observed in Frijoles as early as 1997, whereas differences in taxa richness were not similar between streams until 1999. Associations between community responses and hydrologic or chemical variables did not explain resilience patterns in Capulin between 1997-2001. Both taxa richness and insect densities in Capulin and Frijoles were negatively correlated with peakflow index, although relationships were stronger for taxa richness in Capulin (Table 1.3). TDS

concentrations were also negatively correlated with taxa richness in Capulin and Frijoles, while insect densities were not significantly related to TDS concentrations in either stream. Peakflow index and TDS concentrations were positively correlated in both streams (Capulin: $r = 0.6921$, $P = 0.0043$; Frijoles: $r = 0.5403$, $P = 0.0376$).

CDA conducted with taxa densities revealed significant changes in community composition among sample years in Capulin (Wilks' Lambda: $F_{df=149} = 18.27$; $p<0.0001$). The first two canonical variables explained 82.2 % of the variation in quantitative composition among years. Annual changes in densities of taxa were considered to interpret canonical axes (see Appendix 1.2a). The first canonical variable (CAN1) explained 51.0 % of the total variation among years ($F_{df=149} = 18.27$; $p<0.0001$) and generally distinguished all post-fire Capulin samples from pre-fire samples (Figure 1.7). Densities of elmid beetles, *Amphinemura banksi* Baumann and Gaufin, heptageniids, and *Lepidostoma* sp. were lower in post-fire years compared to pre-fire years and thus were negatively correlated with CAN1 (Table 1.4). Taxa densities that were positively correlated with CAN1, including other Ephemeroptera (primarily *Tricorythodes minutus* Traver), other Trichoptera (primarily *Hesperophylax* sp.), Chironomidae, and Glossosomatidae were higher in most post-fire samples (1998- 2001) (Table 1.4).

Canonical variable-2 (CAN2) explained 31.2% of the total variation among years ($F_{df=122} = 12.77$; $p<0.0001$) and separated samples in post-fire years with moderate to severe flash floods (1996-1998) from samples in late post-fire years with more typical peakflows (1999-2001) (Figure 1.7). CAN2 separated early post-fire flood years (1996-

1998) from pre-fire years (1994-1995). Densities of *Simulium* sp., and to a lesser degree densities of Baetidae (primarily *B. tricaudatus*), other Diptera (primarily *Chelifera* sp.), and *Agabus* sp., were higher in early post-fire flood years and were negatively correlated with CAN2 (Table 1.4). Densities of Glossosomatidae, Odonata (*Oplonaeschna armata* Hagen and *Argia* sp.), *Ceratopsyche* sp., *Hesperophylax* sp. (other Trichoptera), and *Isoperla* sp. were higher in later post-fire years (1999-2001) compared to pre-fire and early post-fire years and were positively correlated with CAN2 (Table 1.4).

CDA with quantitative changes in community composition revealed different temporal patterns in Frijoles. Significant trends in insect densities across years were found (Wilks' Lambda: $F_{df=161} = 6.17$; $p<0.0001$) and the first two canonical variables explained 62.1 % of the variation among years. Annual changes in densities of taxa were considered to interpret canonical axes (see Appendix 1.2b). CAN1 explained 32.1 % of the total variation ($F_{df=161} = 6.17$; $p<0.0001$) and generally distinguished 1994-1995 from 1996- 2001 (Figure 1. 8). However, taxa patterns that separated these years were different or opposite to patterns observed in Capulin (Table 1.5). CAN2 explained 30% of the variation ($F_{df=132} = 5.20$; $p<0.0001$) and separated samples collected in 1999-2001 from samples in other years (Figure 1.8). With the exception of the importance of *Ceratopsyche* sp. in 1999-2001 samples, taxa that separated these years differed between Frijoles and Capulin (Table 1.5). Inter-annual changes in densities of taxa further distinguished composition trends in Capulin from trends in Frijoles (Figure 1.9). Patterns in densities of *Simulium* sp., elmids, *A. banksi*, *Lepidostoma* sp., *Isoperl*a sp., and heptageniids were different between streams, while patterns for Chironomidae, Baetidae

(*B. tricaudatus* and *Fallceon quilleri* Dodds), other Diptera (i.e. *Chelifera* sp.), and *Ceratopsyche* sp. were more similar.

CDA conducted with taxa presence/absence showed inter-annual differences in community composition in Capulin (Wilks' Lambda: $F_{df=149} = 18.27$; $p<0.0001$). These differences were similar to those observed with quantitative composition data. The first two canonical axes (CAN1 and CAN2) explained 73.9% of the variation in qualitative composition among years. Annual changes in persistence of taxa were considered to interpret canonical axes (Appendix 1.2c). CAN1 explained 54.9 % of the total variation ($F_{df=149} = 12.5$; $p<0.0001$) and generally distinguished samples in post-fire years with moderate to severe flash floods (1996-1998) from pre-fire and late post-fire years (1999-2001) (Figure 1.10). Presence of *Simulium* sp. increased in samples collected in early post-fire years and was negatively correlated with CAN1 (Table 1.6). Glossosomatids, *Ceratopsyche* sp., Odonata (primarily *O. armata*), *Isoperla* sp., and heptageniids were positively correlated with CAN1 and represented taxa that were often found in samples collected in pre-fire and late post-fire years (Table 1.6).

CAN2 explained 19.0% of the total variation in composition among years ($F_{df=122} = 8.66$; $p<0.0001$) and separated pre-fire years (1994-1995) and samples in the year of the fire (1996) from all later years (1997-2001) (Figure 1.10). Elmid beetles, *A. banksi*, heptageniids, and *Lepidostoma* sp. were negatively correlated with CAN2 and were more often found in samples collected in pre-fire samples (Table 1.6). However, a few elmid individuals survived the fire and first post-fire flood event, and were thus also present in

1996 samples. Taxa that were positively correlated with CAN2 represented both early and late post-fire taxa. Presence of *T. minutus* and *Hesperophylax* sp. increased between 1999-2001, while Chironomidae, Baetidae (primarily *B. tricaudatus*), and other Diptera (primarily *Chelifera* sp.) persisted in post-fire flood years with moderate floods (1997-1998) (Table 1.6).

Similar to CDA with insect densities, changes in taxa persistence in Frijoles were different compared to temporal patterns observed in Capulin. Significant trends in insect persistence across years were found (Wilks' Lambda: $F_{df=154} = 3.33$; $p<0.0001$) and the first two canonical variables explained 54.7 % of the variation among years. Annual changes in persistence of taxa were considered to interpret canonical axes (Appendix 1.2d). The first canonical variable explained 33.4 % of the total variation ($F_{df=154} = 3.33$; $p < 0.0001$), and distinguished 1999 samples from 1996-1997 samples (Figure 1.11). CAN2 explained 21.3% of the variation ($F_{df=126} = 2.79$; $p < 0.0001$) and distinguished samples in 1998 versus 2000-2001 (Figure 1.11). Taxa that were important in separating years were different or opposite to taxa that differentiated years in Capulin (Table 1.7). Between 1996-1998, *O. armata*, *Lepidostoma* sp., and *A. banksi* were present in Frijoles samples more often in Capulin samples. Also, *Simulium* sp. was highly persistent in Capulin in 1996, but was found more often in 1999 samples in Frijoles.

DISCUSSION

Insect community resistance to and recovery after a wildfire corresponded to post-fire hydrologic disturbances in a burned stream. Multiple 100-year flood events severely altered stream morphology and bed substrate in the year of the Dome fire, and hydrologic and physical attributes did not approach pre-fire conditions until four years after the fire (Cannon and Reneau 1999; Reneau et al. 2000; Veenhuis 2002). Insect communities showed low resistance to post-fire floods, where total insect density and taxa richness decreased dramatically after the first severe flash flood and following repeated moderate flash floods in the second post-fire year. Insect density recovered to pre-fire levels after these moderate floods, whereas taxa richness did not recover until the fourth post-fire year when flash floods had dampened to pre-fire peakflow magnitudes. Similar flooding and dramatic community responses were not observed in a geomorphically similar unburned stream, strongly suggesting that post-fire flash floods influenced community resistance and recovery in the burned stream.

Heat and ashfall from the Dome fire likely had minimal influence on insect community responses in the burned stream. First, direct effects of fire on stream insects have been shown to be negligible (Minshall et al. 1997; see review in Gresswell 1999). For example, insect communities in another Pajarito Plateau stream burned in the 2000 Cerro Grande fire were highly resistant to direct effects of fire (Vieira and Clements 2003). Second, my study reaches in the burned stream only experienced low-intensity

burn; severe burning occurred primarily on the mesa portion of the watershed. Not surprisingly, I did not observe dramatic increases in dissolved concentrations of ions (i.e. nitrogen, phosphorous) typically associated with ashfall and higher intensity burns (Spencer and Hauer 1991; Brass et al. 1996). Instead, increases in stream buffering capacity and calcium were probably associated with soil erosion and scouring during post-fire floods, as evidenced by the strong correlation between peakflow and total dissolved solids. Severe post-fire floods after both the Dome and Cerro Grande fires nearly eliminated insect communities (Vieira and Clements 2003), supporting the idea that post-fire hydrological disturbances are the primary factor shaping insect communities.

Others have also found that hydrologic disturbances associated with wildfires negatively impact insect communities in burned streams. For instance, Rinne (1996) found severe reductions in insect densities and diversity in first-order, southwestern streams due to post-fire sediment-laden floods. Episodic, substrate-moving storm events after wildfire in Idaho were linked with low resistance and slow recovery of taxa richness and diversity in low-order burned streams (La Point et al. 1983). Following the Greater Yellowstone Area fires in 1988, recovery of insect density and taxa richness was slower in high-gradient burned streams that were physically altered by runoff events (Minshall et al. 1997). These studies in combination with my research show repeatable patterns in community responses to post-fire hydrologic disturbance, even though hydroclimatology differed among studies. For instance, Pajarito Plateau streams are flashy due to intense monsoonal rainfall in conjunction with steep and highly erodible hillslopes. Thus, flash

floods in my burned stream were more sudden and severe in magnitude compared to post-fire runoff events in streams burned in the Yellowstone fires, which are snowmelt-driven and are hydrologically more stable. Similar community responses between studies fit predictions of Minshall et al. (1989) that post-fire hydrologic events that result in bed scouring or channel alteration can "reset" recovery trajectories in burned streams.

Temporal patterns of community composition in the burned stream corresponded to the occurrence of flash floods after the Dome fire, lending further evidence that post-fire hydrologic disturbances may have "reset" recovery trajectories. Taxa-specific persistence and densities changed dramatically after the first 100-year flood in the year of the fire, and continued to diverge during post-fire years with moderate floods. After flash floods abated, taxa persistence showed only limited movement towards pre-fire composition and did not recover. Changes in taxa densities were more dramatic; composition continued to diverge after floods abated to reach a post-fire community that differed substantially from pre-fire communities. Shifts in persistence and densities in an unburned stream differed from those in the burned stream and diverged less from pre-fire communities. Inter-annual changes in composition in the unburned stream corresponded to changes in annual precipitation, where composition in dry years (1994, 1995, and 2001) differed from composition in wet years (1996, 1999) (NCDC; data published on www.ncdc.noaa.gov). Thus, taxa-specific responses in the burned stream were related to post-fire disturbances, while responses in the unburned stream were more related to natural variation in environmental conditions (also see Chapter 2).

Post-fire changes in community composition in the burned stream were consistent with changes observed after other large-scale disturbances, where tolerant taxa dominate newly disturbed systems (see reviews in Niemi et al. 1990; Yount and Niemi 1990). For instance, *Simulium* sp., Chironomidae, and *B. tricaudatus* recolonized rapidly and dominated the burned stream during post-fire years with moderate to severe floods. In contrast, common pre-fire taxa such as heptageniid mayflies, nemourid stoneflies, and elmid beetles were greatly reduced. Once flash floods abated, *O. armata*, Glossosomatidae, and *Ceratopsyche* sp. recolonized to high densities, while elmids and *A. banksi* recolonized but remained rare. Similar changes in taxa composition were documented in streams burned in the 1988 Greater Yellowstone Area fires. Baetid mayflies and Chironomidae densities increased in early post-fire years, while elmid beetles, heptageniid and *Ephemerella* sp. mayflies, glossosomatid caddisflies, and *Isoperla* sp. stoneflies were still reduced in lower-order burned streams for up to four years (Mihuc et al. 1996; Minshall et al. 1997).

Recolonization and survival of insects after large-scale disturbances depends on population attributes such as functional feeding strategies, voltinism and egg diapause, drift capability, and adult dispersal (Wallace 1990). Attributes conveying resistance (i.e. hydrodynamic body shape, small size, attachment to substrate) and resilience (i.e. strong dispersal, multi-voltinism, and generalist resource use) allow certain taxa to pass through environmental "filters" associated with disturbance (Poff 1997; Townsend et al. 1997b). In my study, taxa with both resistant and resilient traits were important in recovery during post-fire years. Multivoltine taxa with high larval drift propensities and streamlined

bodies (Baetidae), small size and low drag (Chironomidae), or the ability to attach to substrate (*Simulium* sp.) recolonized quickly and survived moderate post-fire flash floods. Once floods abated and the strength of flood "filters" were reduced, taxa (i.e. several dragonfly, damselfly, and caddisfly taxa) with low resistance but with strong adult dispersal recolonized to establish unique post-fire communities. Taxa with weaker adult dispersal ability (i.e. elmid beetles, *A. banksi*) showed slower recolonization and did not recover to pre-fire densities. In Chapter 2, I further show that representation of resistant and resilient attributes in the burned stream were explained by post-fire peakflows and recovery time since the Dome fire. In contrast, population attributes in the unburned stream were typically associated with seasons.

Patterns of community recovery in the burned stream, and population attributes driving these patterns, reflect in-stream refugia and colonization barriers. Survivors after the first post-fire flood (primarily elmids) lacked resistant and resilient attributes (Chapter 2) and probably arrived via catastrophic drift during flooding. These taxa were numerically dominant in pre-fire years. However, low densities of these survivors and dramatic decreases in taxa richness indicated that few refuges existed near study reaches in the year of the fire and most individuals were lost. First, multiple 100-year flood events moved large substrates (i.e. boulders, woody debris) along the entire perennial segment of the burned stream, indicating greatly reduced flow refugia at the microhabitat scale (Lancaster and Hildrew 1993). Also, shallow bedrock underlying Pajarito Plateau streams, and scouring to this bedrock layer during flash floods, precluded hyporheic refugia (sensu Palmer et al. 1992). Given the lack of refuges in study reaches, survivors

of the first post-fire flood were eliminated in subsequent floods in 1996 and did not contribute to community recovery. Instead, insects with resistant and resilient attributes likely recolonized from headwater reaches within the burned stream. These upper reaches only experienced moderate flooding in 1996. *Simulium* sp. and baetid mayflies typically dominate these ephemeral upper reaches (N. K. M. Vieira, Colorado State University, unpublished data) and likely recolonized via larval drift in early post-fire years. Recolonization from small upstream spring sources has been noted in other montane desert streams following severe flash floods (Molles 1985).

Townsend (1989) predicted that insect drift would be of minimal importance following large-scale disturbances that also denude upstream reaches of biota. Others have found that recolonization by aerial adults may be more important to community recovery after scouring flash floods in desert streams (Gray and Fisher 1981; Fisher et al. 1982; Lytle 2002). While early colonists likely recolonized my burned stream from upper headwaters, larval drift from these intermittent reaches was not the primary recolonization mechanism for most insect taxa. Taxa that recolonized study reaches in later post-fire years were not found in headwater communities (N. K. M. Vieira, Colorado State University, unpublished data) and were also not survivors of the first post-fire flash flood, suggesting that they recolonized as aerial adults from nearby streams or the Rio Grande River. The extreme topography of the Pajarito Plateau presents numerous colonization barriers to dispersing adults, including long distances (2-6 km) across arid mesas, and uni-directional winds within deep canyons. Not surprisingly, most taxa that recolonized to establish a new stable post-fire community were large-bodied, longer-lived

adults with moderate to strong flying ability (Chapter 2). Taxa with weaker adult dispersal potential were still absent or were only found in low densities six years after the fire, despite the fact that they dominate communities in nearby Pajarito streams (Chapter 3).

Did a wildfire and compounded post-fire hydrologic disturbances result in "ecologically surprising" (sensu Paine et al. 1998) changes in stream insect communities? The answer to this question depended on how community recovery was assessed. Despite low resistance to floods, total insect density and taxa richness both recovered within four post-fire years. However, recovery trajectories of community composition revealed that post-fire hydrologic disturbances had lasting impacts on insect communities. Changes in taxa persistence, which is more indicative of long-term adjustments to community composition (Poff and Allan 1995), were most "surprising" for several reasons. First, insect species in other flashy desert streams have been shown to be adapted (i.e. development time, emergence schedules) to severe (i.e. >90% larval insects removed) and predictable monsoonal floods (Lytle 2001; Lytle 2002). In this study, post-fire flash floods also occurred during the monsoon season, and were thus predictably timed compared to the historical disturbance regime. Second, flood frequencies only increased three-fold and quickly dampened to pre-fire frequencies within several post-fire years (Veenhuis 2002). My study indicates that dramatic increases in flood magnitudes and the spatial extent of the flooding overwhelmed recovery mechanisms of many insect taxa.

Evolutionary constraints on the resistance and resilience of insects in the regional species pool may prevent full community recovery in the burned stream. In support of this idea, I found that insect community composition, as well as resilience of these communities to further disturbance, varied along a gradient of fire disturbance history in Pajarito Plateau streams (Chapter 3). Specifically, streams that experienced severe post-fire flooding over 25 years ago are more diverse than recently burned streams, but still differ from unburned streams due to the persistence of disturbance-tolerant insect taxa. Continued long-term monitoring of streams along this wildfire gradient will ultimately reveal whether "ecological surprises" associated with post-fire hydrologic disturbances are temporary or permanent. Comparing recovery of different community responses (Gore et al. 1990) in light of ecological and evolutionary expectations (Poff and Ward 1990; Poff 1992) will be crucial in ultimately assessing how stream insect communities respond to canopy wildfires on the Pajarito Plateau.

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Table 1.1. Mean (n=3) water chemistry measures before and after the 1996 Dome fire, near Los Alamos, NM in a burned (Capulin) and unburned (Frijoles) stream.

FIRE	DATE	CANYON	PH	TEMPERATURE (C)	CONDUCTIVITY	HARDNESS	ALKALINITY
BEFORE	Jul-94	FRIJOLES	7.3	18	100	43	34
		CAPULIN	7.8	16	113	53	46
	Aug-94	FRIJOLES	7.6	17	110	33	47
		CAPULIN	8.2	17	137	46	66
	May-95	FRIJOLES	6.9	11	87	28	36
		CAPULIN	7.4	12	130	36	54
	Jun-95	FRIJOLES	7.1	11	110	24	44
		CAPULIN	7.4	12	130	24	54
	Aug-95	FRIJOLES	7.4	20	117	31	49
		CAPULIN	7.7	17	140	42	61
AFTER	Jul-96	FRIJOLES	8.2	17	113	32	50
		CAPULIN	8.4	21	420	185	203
	May-97	FRIJOLES	8.0	13	108	30	42
		CAPULIN	8.2	13	162	57	67
	Jul-97	FRIJOLES	7.8	21	80	33	48
		CAPULIN	7.9	18	130	61	81
	Oct-97	FRIJOLES	7.7	14	116	33	50
		CAPULIN	8.0	14	147	58	72
	May-98	FRIJOLES	7.6	18	113	35	46
		CAPULIN	8.2	17	170	53	66
	Jul-98	FRIJOLES	8.1	18	147	36	47
		CAPULIN	8.2	17	207	57	67
	Oct-98	FRIJOLES	7.6	15	90	33	52
		CAPULIN	7.8	14	141	51	72
	May-99	FRIJOLES	8.3	11	130	34	50
		CAPULIN	8.4	12	170	46	61
	Jul-99	FRIJOLES	8.0	17	130	33	50
		CAPULIN	8.2	22	193	59	72
	Oct-99	FRIJOLES	7.0	9	137	47	54
		CAPULIN	7.5	11	160	55	71
	Apr-00	FRIJOLES	7.5	11	113	31	52
		CAPULIN	7.6	14	143	50	68
	Jul-00	FRIJOLES	7.6	19	150	35	51
		CAPULIN	8.0	17	197	53	72
	Oct-00	FRIJOLES	7.5	10	143	39	50
		CAPULIN	7.5	9	147	51	67
	May-01	FRIJOLES	7.1	13	113	37	45
		CAPULIN	7.4	13	108	50	53
	Jul-01	FRIJOLES	7.5	16	130	31	48
		CAPULIN	8.1	17	140	51	60
	Oct-01	FRIJOLES	7.5	12	127	31	49
		CAPULIN	7.5	12	130	50	61

Table 1.2. *A priori* linear contrasts testing differences in total insect density and taxa richness over specific time periods reflecting resistance and resilience to post-fire flash flooding. Temporal changes in a stream burned in the 1996 Dome fire, near Los Alamos, NM (Capulin) were compared to changes observed in a nearby unburned stream (Frijoles). Student t-test values and associated significance levels are presented. A positive sign for t-statistics indicates a greater reduction in Capulin.

Linear Contrasts	Total Insect Density		Taxa Richness	
	t	P	t	P
Resistance				
Pre-fire vs. year of the fire (after the first severe flood)	10.21	<0.0001	8.64	<0.0001
Before vs. after moderate floods in second post-fire year	6.68	<0.0001	2.46	<0.0157
Before vs. after moderate floods in third post-fire year	-0.55	0.5832	-0.07	0.9466
Resilience				
Pre-fire vs. second post-fire year	1.31	0.1935	4.65	<0.0001
Pre-fire vs. third post-fire year	-0.79	0.4341	3.83	0.0002
Pre-fire vs. fourth post-fire year (first year without a moderate flood event)	-0.80	0.4275	-0.73	0.4672

Table 1.3. Pearson product moment correlation coefficients (r) and corresponding P-values for associations between community responses (taxa richness and total insect density) and stream characteristics (natural-log based index of peakflow and total dissolved solid concentrations; see text for further details) in a stream burned in the 1996 Dome fire, near Los Alamos, NM (Capulin) and a nearby unburned stream (Frijoles). Only post-fire sample periods between 1997-2001 were used for analysis (n=15 each stream).

		CAPULIN		FRIJOLES	
Variable	Statistic	Insect Density	Taxa Richness	Insect Density	Taxa Richness
Insect Density	r	-	0.6185	-	0.6683
	P	-	0.0140	-	0.0065
Taxa Richness	r	0.6185	-	0.6683	-
	P	0.0140	-	0.0065	-
Peakflow Index	r	-0.5566	-0.7901	-0.5656	-0.5870
	P	0.0312	0.0005	0.0280	0.0214
Total Dissolved Solids	r	-0.1113	-0.6074	-0.3769	-0.5366
	P	0.6929	0.0163	0.1662	0.0392

Table 1.4. Summary of canonical discriminant analysis for eight sample years in a stream burned in the 1996 Dome fire (Capulin), Bandelier National Monument, near Los Alamos, NM, defined in terms of relative densities of stream insect taxa. Correlations with the first two canonical variables (CAN1 and CAN2), and univariate F-statistics and significance levels indicating whether densities of individual taxa were different among years, are presented.

TAXA	CAN1	CAN2	F	P-value
Baetidae (*Baetis tricaudatus, Fallceon quilleri*)	0.01	-0.10	18.04	<0.0001
Ephemerella sp.	0.10	0.50	11.51	<0.0001
Heptageniidae (*Nixe* sp., *Cinygmula* sp., and *Epeorus* sp.)	-0.50	0.41	20.63	<0.0001
Paraleptophlebia sp.	0.21	0.44	8.75	<0.0001
Other Ephemeroptera (*Drunella* sp., *Ameletus* sp., *Tricorythodes minutus*)	0.42	0.42	15.60	<0.0001
Amphinemura banksi	-0.76	0.27	47.65	<0.0001
Isoperla sp.	0.21	0.52	14.30	<0.0001
Other Plecoptera (*Capnia* sp., *Triznaka* sp., *Sweltsa* sp.)	-0.10	0.12	5.15	<0.0001
Ceratopsyche sp.	0.02	0.65	34.36	<0.0001
Lepidostoma sp.	-0.49	0.27	20.15	<0.0001
Other Trichoptera (*Hesperophylax* sp., *Ochrotrichia* sp., *Oecetis* sp., *Polycentropus* sp., *Rhyacophila* sp.)	0.36	0.57	19.47	<0.0001
Glossosomatidae (*Agapetus* sp. and *Glossosoma* sp.)	0.32	0.85	85.39	<0.0001
Chironomidae (Tanytarsini, Tanypodinae, Orthocladiinae, Chironominae)	0.34	0.10	17.10	<0.0001
Dicranota sp.	0.01	0.12	6.21	<0.0001
Other Tipulidae (*Antocha* sp., *Hexatoma* sp., *Pedicia* sp., *Tipula* sp.)	0.28	0.43	9.53	<0.0001
Maruina sp.	0.19	0.04	17.26	<0.0001
Simulium sp.	0.23	-0.61	28.41	<0.0001
Other Diptera (*Caloparyphus* sp., *Chelifera* sp., *Dixa* sp., *Hemerodromia* sp. *Limnophora aequifrons*, *Oreogeton* sp., *Palpomyia* sp., *Pericoma* sp.)	0.30	-0.09	7.61	<0.0001
Elmidae (*Optioservus* sp., *Zaitzevia parvula*)	-0.90	0.35	203.83	<0.0001
Odonata (*Oplonaeschna armata*, *Argia* sp.)	0.17	0.78	42.53	<0.0001
Coleoptera and other (*Agabus* sp., *Helichus striatus*, Hemiptera, *Petrophila* sp.)	0.02	-0.08	2.13	0.0430

Table 1.5. Summary of canonical discriminant analysis for eight sample years in an unburned stream (Frijoles), Bandelier National Monument, near Los Alamos, NM defined in terms of densities of stream insect taxa. Correlations with the first two canonical variables (CAN1 and CAN2), and univariate F-statistics and significance levels indicating whether densities of individual taxa were different among years, are presented.

TAXA	CAN1	CAN2	F	P-value
Baetidae (*Baetis tricaudatus* and *Fallceon quilleri*)	0.42	0.27	8.10	<0.0001
Ephemerella sp.	-0.10	0.26	5.70	<0.0001
Heptageniidae (*Nixe* sp., *Cinygmula* sp., and *Epeorus* sp.)	-0.02	-0.02	1.68	0.1162
Paraleptophlebia sp.	-0.25	0.42	7.65	<0.0001
Other Ephemeroptera (*Drunella* sp., *Ameletus* sp., *Tricorythodes minutus*)	-0.07	0.06	4.27	0.0002
Amphinemura banksi	-0.02	-0.36	9.80	<0.0001
Isoperla sp.	-0.04	0.15	2.83	0.0008
Pteronarcella badia	0.05	-0.16	5.62	<0.0001
Other Plecoptera (*Capnia* sp., *Triznaka* sp., *Sweltsa* sp., *Hesperoperla pacifica*)	-0.25	0.59	14.41	<0.0001
Brachycentrus sp.	-0.01	-0.54	10.03	<0.0001
Ceratopsyche sp.	0.43	0.31	7.54	<0.0001
Lepidostoma sp.	0.02	-0.30	5.50	<0.0001
Other Trichoptera (*Hesperophylax* sp., *Ochrotrichia* sp., *Oecetis* sp., *Polycentropus* sp., *Rhyacophila* sp.)	0.64	-0.06	12.24	<0.0001
Glossosomatidae (*Agapetus* sp. and *Glossosoma* sp.)	0.15	0.24	4.16	0.0003
Chironomidae (Tanytarsini, Tanypodinae, Orthocladiinae, Chironominae)	0.22	0.11	5.29	<0.0001
Dicranota sp.	-0.01	0.35	3.37	0.0021
Other Tipulidae (*Antocha* sp., *Hexatoma* sp., *Pedicia* sp., *Tipula* sp.)	0.36	0.18	4.44	<0.0001
Maruina sp.	-0.12	0.25	3.44	0.0018
Simulium sp.	0.18	0.54	12.56	<0.0001
Other Diptera (*Caloparyphus* sp., *Chelifera* sp., *Dixa* sp., *Hemerodromia* sp., *Limnophora aequifrons*, *Oreogeton* sp., *Palpomyia* sp., *Pericoma* sp.)	0.06	0.27	2.45	0.0203
Elmidae (*Optioservus* sp., *Zaitzevia parvula*)	-0.60	-0.08	2.67	<0.0001
Odonata (*Oplonaeschna armata*, *Argia* sp.)	-0.07	-0.34	2.12	0.0118
Coleoptera and other (*Agabus* sp., *Helichus striatus*, Hemiptera, *Petrophila* sp.)	0.20	-0.06	1.02	0.0439

Table 1.6. Summary of canonical discriminant analysis for eight sample years in a stream burned in the 1996 Dome fire (Capulin), Bandelier National Monument, near Los Alamos, NM defined in terms of presence of stream insect taxa. Correlations with the first two canonical variables (CAN1 and CAN2), and univariate F-statistics and significance levels indicating whether densities of individual taxa were different among years, are presented.

TAXA	CAN1	CAN2	F	P-value
Baetis tricaudatus and *Fallceon quilleri*	0.39	0.36	34.67	<0.0001
Ephemerella sp.	0.52	0.16	11.23	<0.0001
Heptageniidae (*Nixe* sp., *Cynigmula* sp., and *Epeorus* sp.)	0.64	-0.39	28.00	<0.0001
Paraleptophlebia sp.	0.38	0.26	9.04	<0.0001
Other Ephemeroptera (*Drunella* sp., *Ameletus* sp., *Tricorythodes minutus*)	0.22	0.58	13.60	<0.0001
Amphinemura banksi	0.53	-0.54	29.97	<0.0001
Isoperla sp.	0.65	0.12	18.42	<0.0001
Other Plecoptera (*Capnia* sp., *Triznaka* sp., *Sweltza* sp.)	0.30	-0.19	4.41	0.0002
Ceratopsyche sp.	0.78	0.18	44.91	<0.0001
Lepidostoma sp.	0.45	-0.49	18.45	<0.0001
Other Trichoptera (*Hesperophylax* sp., *Ochotrichia* sp., *Ocetis* sp., *Polycentropus* sp., *Rhyacophila* sp.)	0.39	0.40	14.12	<0.0001
Glossosomatidae (*Agapetus* sp. and *Glossosoma* sp.)	0.81	0.34	66.62	<0.0001
Chironomidae (Tanytarsinae, Tanypodinae, Orthocladinae, Chironominae)	0.39	0.37	23.76	<0.0001
Dicranota sp.	0.19	0.10	7.73	<0.0001
Other Tipulidae (*Antocha* sp., *Hexatoma* sp., *Pedicia* sp., *Tipula* sp.)	0.34	0.31	6.78	<0.0001
Maruina sp.	0.20	0.23	17.19	<0.0001
Simulium sp.	-0.08	0.25	10.13	<0.0001
Other Diptera (*Calopharus* sp., *Chelifera* sp., *Dixa* sp., *Hemerodromia* sp. *Limnophorus aequifrons*, *Oreogeton* sp., *Palypomia* sp., *Pericoma* sp.)	0.06	0.36	8.86	<0.0001
Elmidae (*Optioservus* sp., *Zaitzevia parvula*)	0.57	-0.39	21.16	<0.0001
Odonata (*Oplonaeshna armata*, *Argia* sp.)	0.76	0.09	35.04	<0.0001
Coleoptera and other (*Agabus* sp., *Helichus striatus*, Hemiptera, Petrophilidae)	0.08	0.01	0.69	0.6841

Table 1.7. Summary of canonical discriminant analysis for eight sample years in an unburned stream (Frijoles), Bandelier National Monument, near Los Alamos, NM defined in terms of presence of stream insect taxa. Correlations with the first two canonical variables (and univariate F-statistics and significance levels indicating whether densities of individual taxa were different among years) are presented. NA indicates that taxa were present in all samples collected in that year (no variation and thus no correlation with canonical variables).

TAXA	CAN1	CAN2	F	P-value
Baetidae (*Baetis tricaudatus* and *Fallceon quilleri*)	0.11	0.06	1.77	0.096
Ephemerella sp.	0.23	-0.17	4.77	<0.0001
Heptageniidae (*Nixe* sp., *Cinygmula* sp., and *Epeorus* sp.)	-0.07	0.12	2.66	0.0121
Paraleptophlebia sp.	0.40	0.28	6.17	<0.0001
Other Ephemeroptera (*Drunella* sp., *Ameletus* sp., *Tricorythodes minutus*)	0.02	0.42	4.02	0.0004
Amphinemura banksi	0.03	-0.34	4.36	0.0002
Isoperla sp.	0.12	0.15	3.33	0.0023
Pteronarcella badia	0.00	0.01	1.07	0.3869
Other Plecoptera (*Capnia* sp., *Triznaka* sp., *Sweltsa* sp., *Hesperoperla pacifica*)	0.39	0.30	5.62	<0.0001
Brachycentrus sp.	-0.59	0.15	8.30	<0.0001
Ceratopsyche sp.	0.03	0.43	2.47	0.019
Lepidostoma sp.	-0.28	0.21	3.38	0.0021
Other Trichoptera (*Hesperophylax* sp., *Ochrotrichia* sp., *Oecetis* sp., *Polycentropus* sp., *Rhyacophila* sp.)	-0.30	0.22	5.23	<0.0001
Glossosomatidae (*Agapetus* sp. and *Glossosoma* sp.)	0.00	-0.05	3.63	0.0011
Chironomidae (Tanytarsini, Tanypodinae, Orthocladiinae, Chironominae)	0.07	0.20	1.48	0.1763
Dicranota sp.	0.31	0.09	1.63	0.1297
Other Tipulidae (*Antocha* sp., *Hexatoma* sp., *Pedicia* sp., *Tipula* sp.)	0.13	0.48	4.36	0.0002
Maruina sp.	0.33	-0.26	2.81	0.0084
Simulium sp.	0.31	0.27	6.16	<0.0001
Other Diptera (*Caloparyphus* sp., *Chelifera* sp., *Dixa* sp., *Hemerodromia* sp., *Limnophora aequifrons*, *Oreogeton* sp., *Palpomyia* sp., *Pericoma* sp.)	0.21	0.00	1.42	0.1998
Elmidae (*Optioservus* sp., *Zaitzevia parvula*)	0.00	0.00	na	na
Odonata (*Oplonaeschna armata*, *Argia* sp.)	-0.26	-0.16	2.20	0.0358
Coleoptera and other (*Agabus* sp., *Helichus striatus*, Hemiptera, *Petrophila* sp.)	-0.11	0.10	1.87	0.0776

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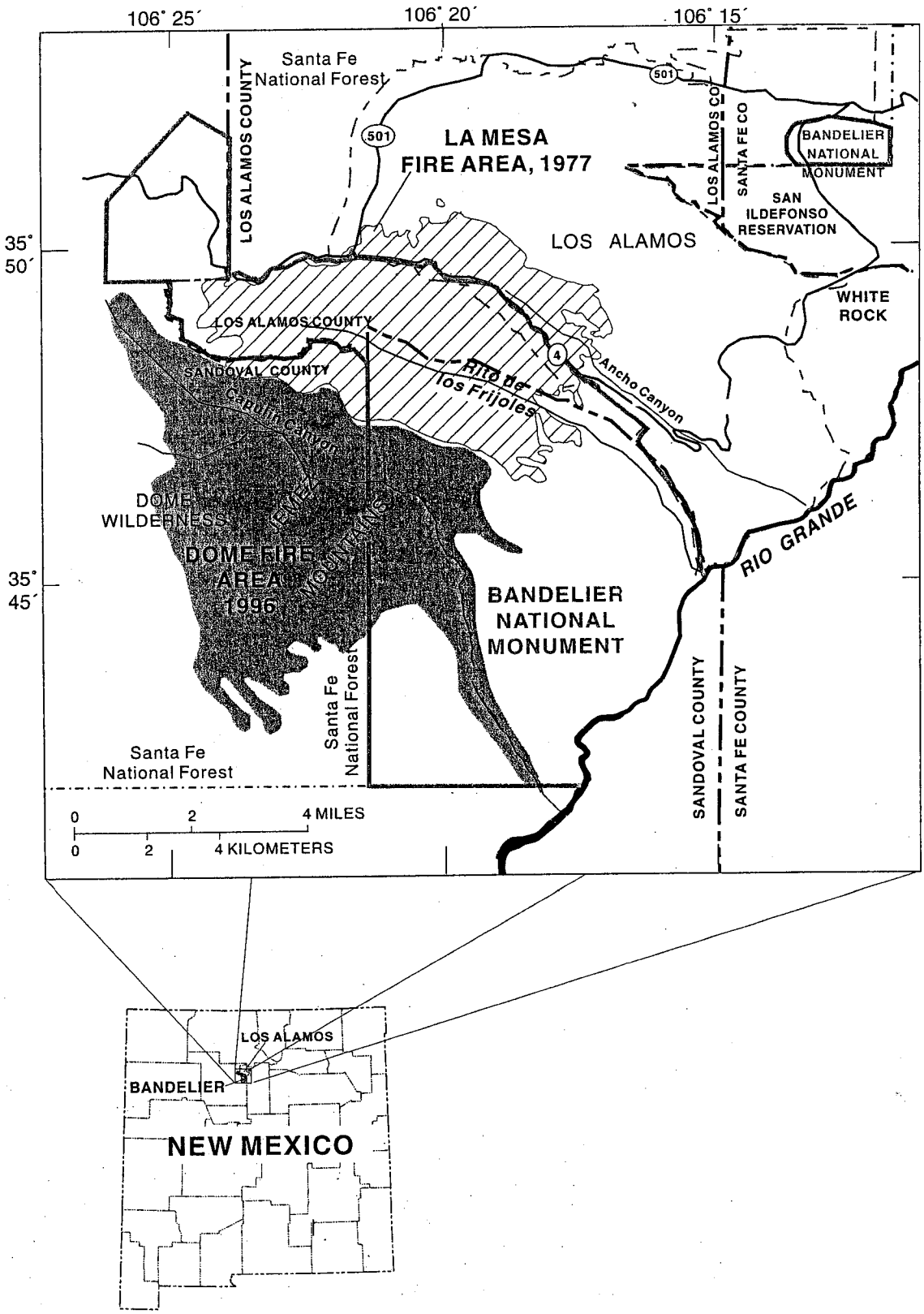
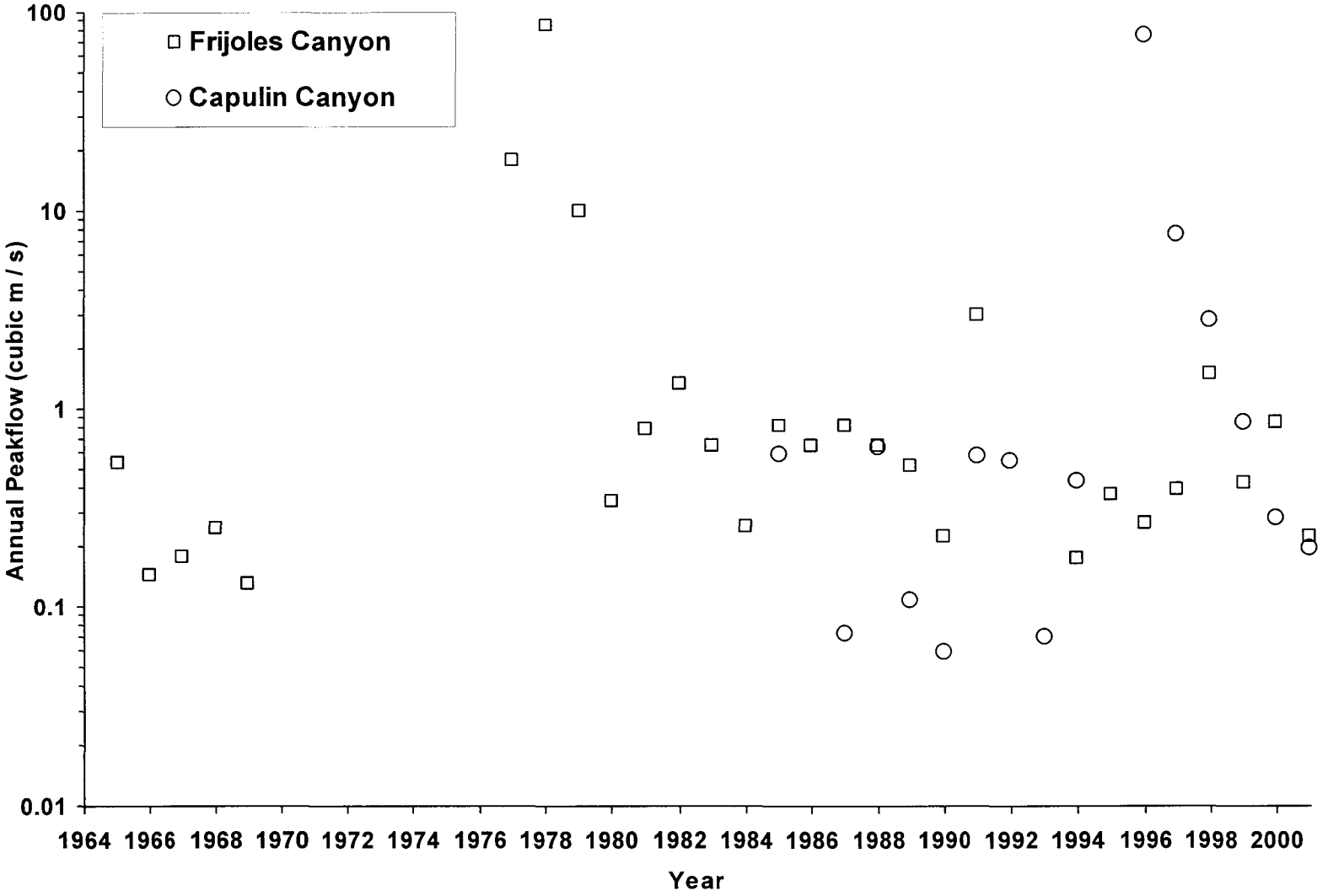
Figure 1.8. Mean canonical discriminant analysis values for insect composition (based on population densities) in an unburned stream (Frijoles), Bandelier National Monument, near Los Alamos, NM for the following years: 1994 (n=18), 1995 (n=27), 1996 (n=9), 1997 (n=18), 1998(n=27), 1999 (n=27), 2000 (n=27), and 2001(n=27). Insect taxa important in discriminating years are listed (see Table 1.5 for correlation values).

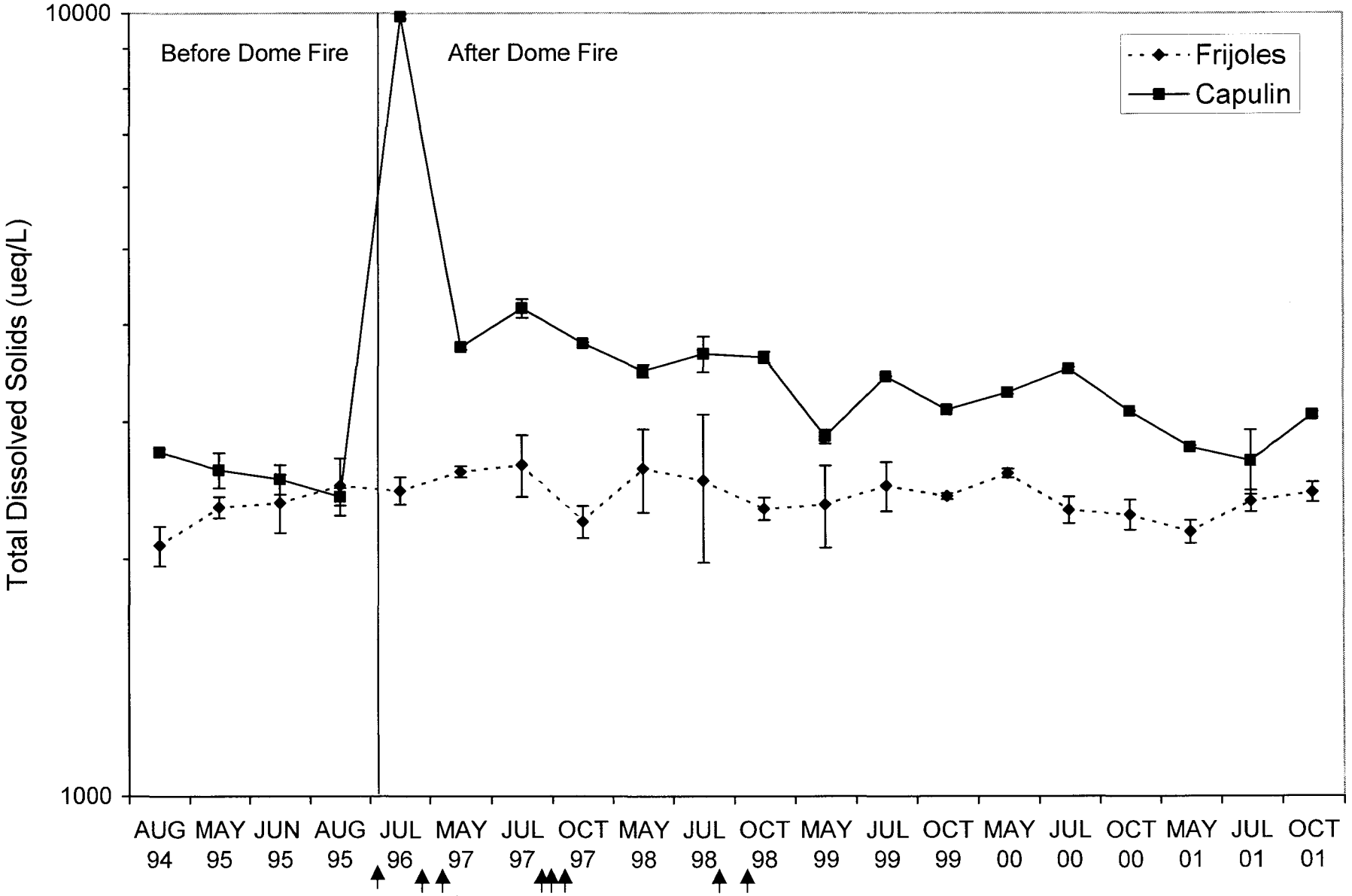
Figure 1.9. Annual trends in mean densities ± 1 SE for insect taxa in a stream burned in the 1996 Dome fire (Capulin; solid line) and an unburned (Frijoles; dotted line) stream in Bandelier National Monument, near Los Alamos, NM. Sample sizes are reported in Figures 1.7 and 1.8. Arrow indicates the 1996 Dome fire.

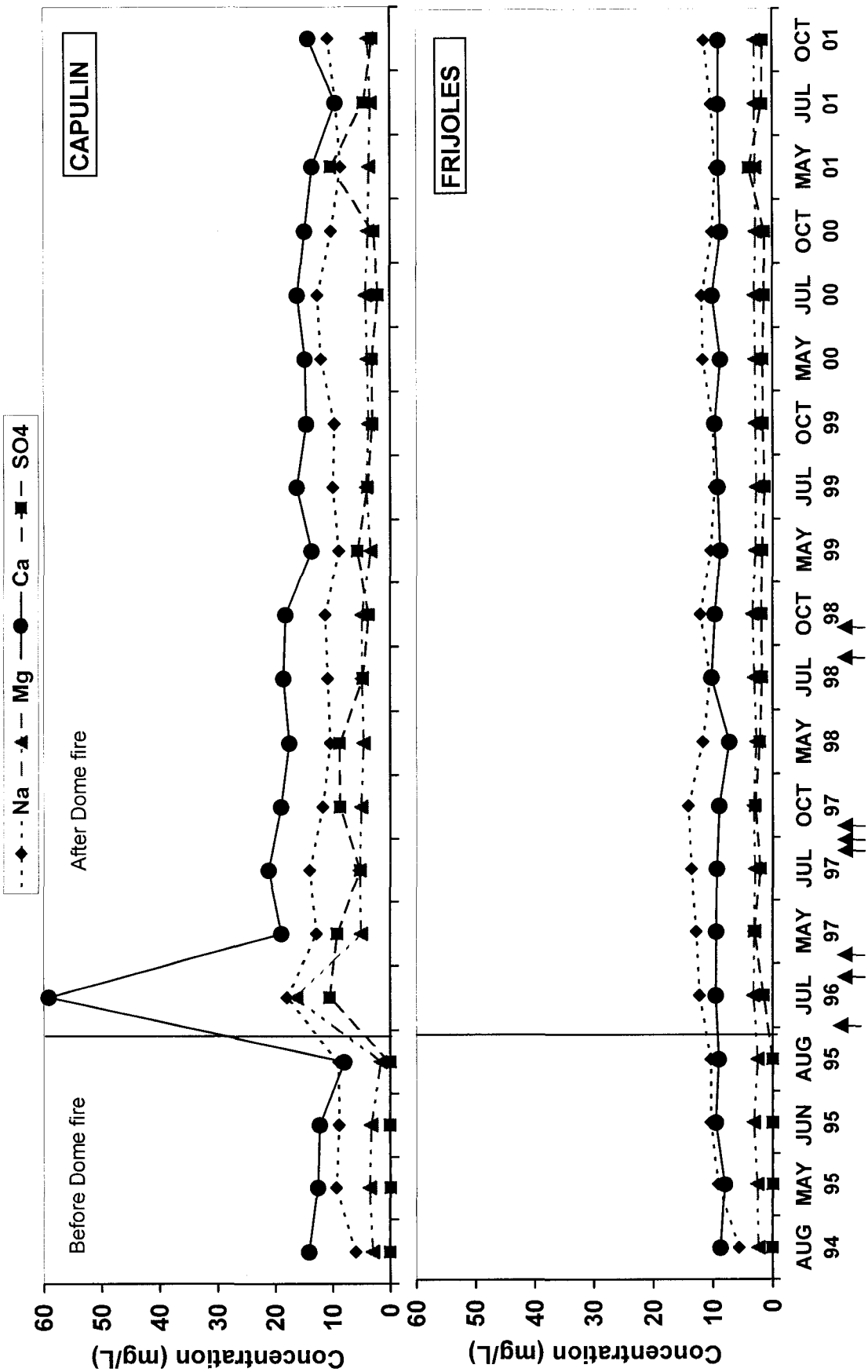
Figure 1.10. Mean canonical discriminant analysis values for insect composition (based on taxa presence) in a stream burned in the 1996 Dome fire (Capulin), Bandelier National Monument, near Los Alamos, NM for the following years: 1994 (n=18), 1995 (n=27), 1996 (n=9), 1997 (n=18), 1998(n=27), 1999 (n=27), 2000 (n=27), and 2001(n=27). Insect taxa important in discriminating years are listed (see Table 1.6 for correlation values).

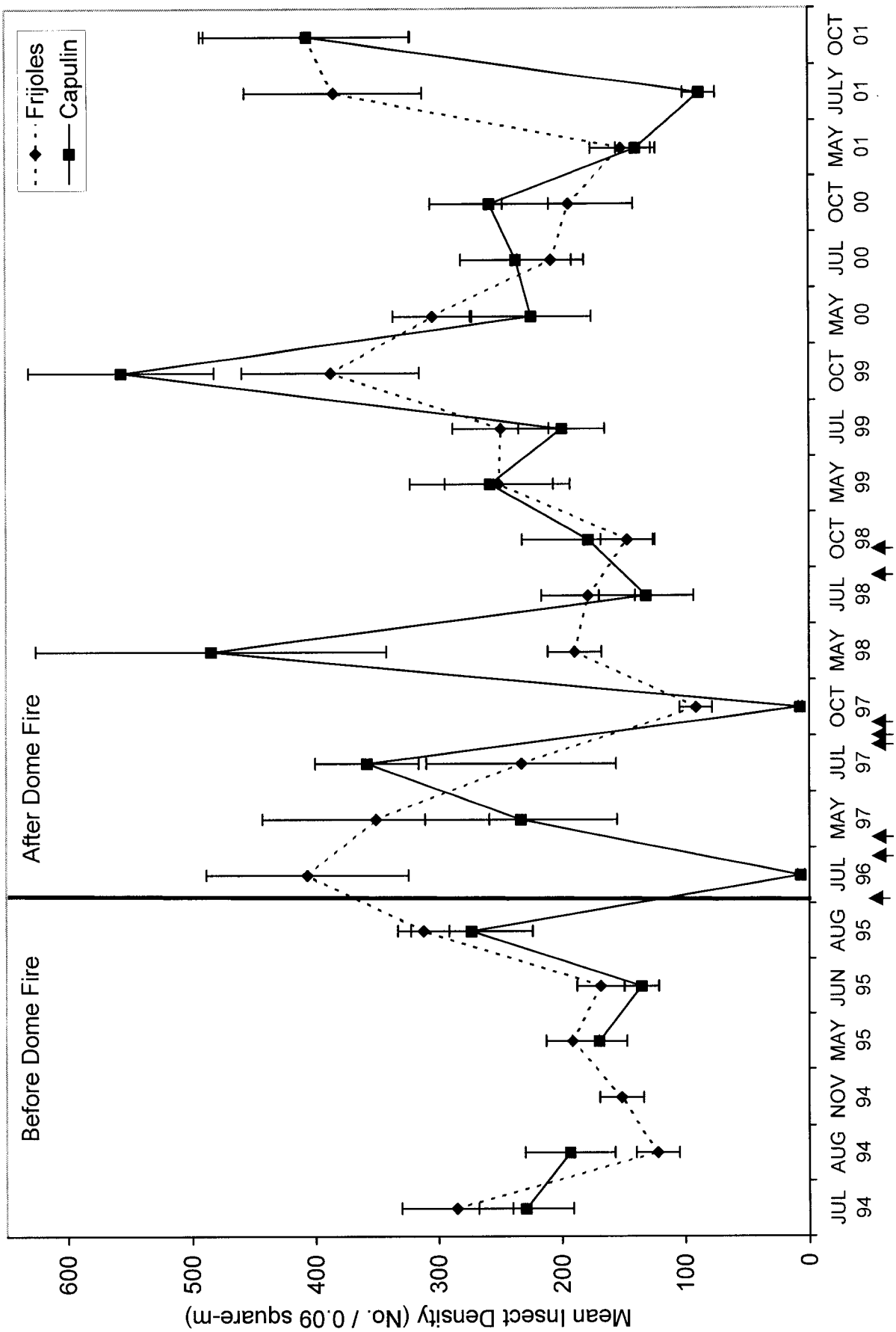
Figure 1.11. Mean canonical discriminant analysis values for insect composition (based on taxa presence) in an unburned stream (Frijoles canyon, Bandelier National Monument, near Los Alamos, NM) for the following years: 1994 (n=18), 1995 (n=27), 1996 (n=9), 1997 (n=18), 1998(n=27), 1999 (n=27), 2000 (n=27), and 2001(n=27). Insect taxa correlated with canonical variables and thus important in discriminating years are listed (see Table 1.7 for correlation values).

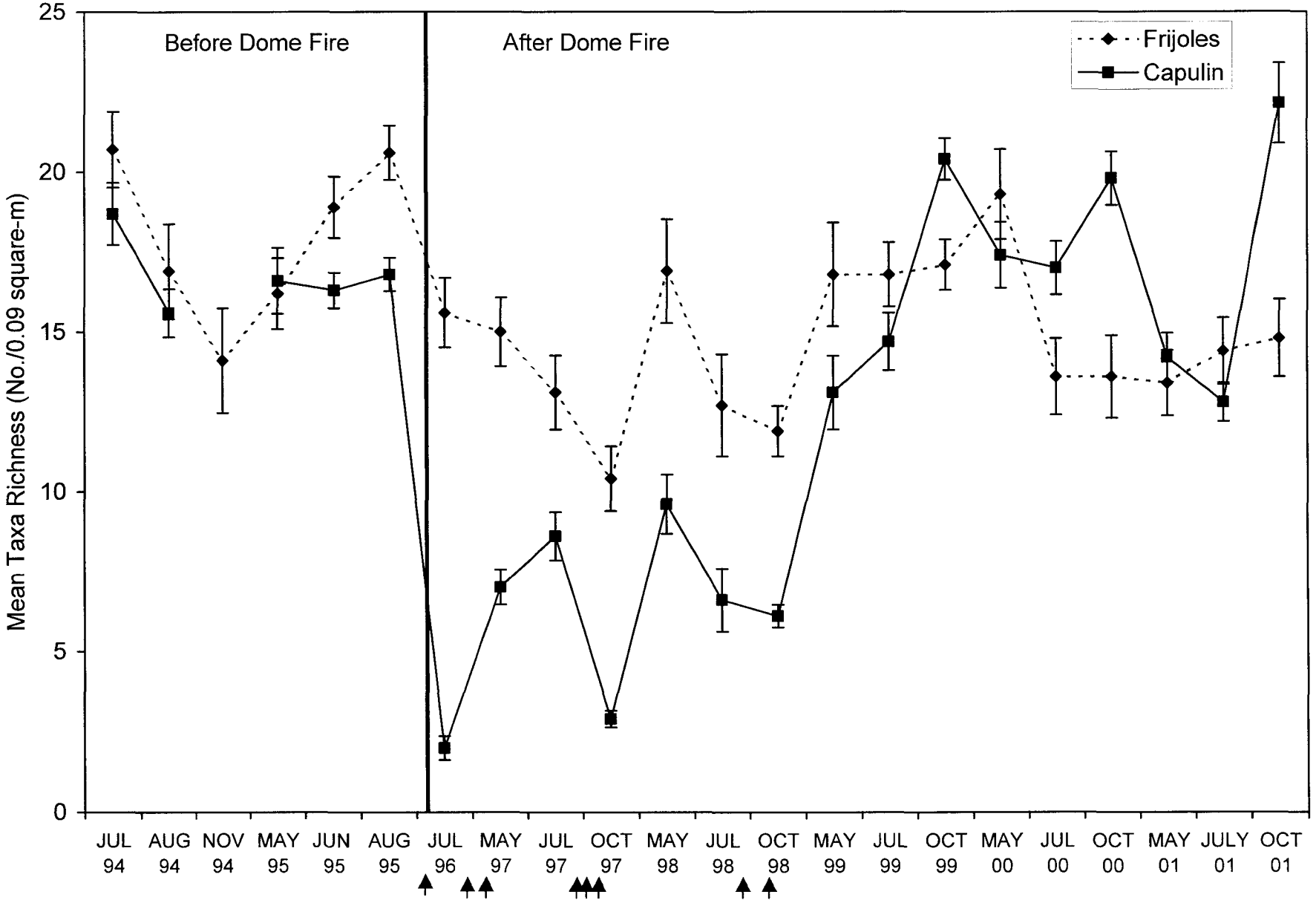


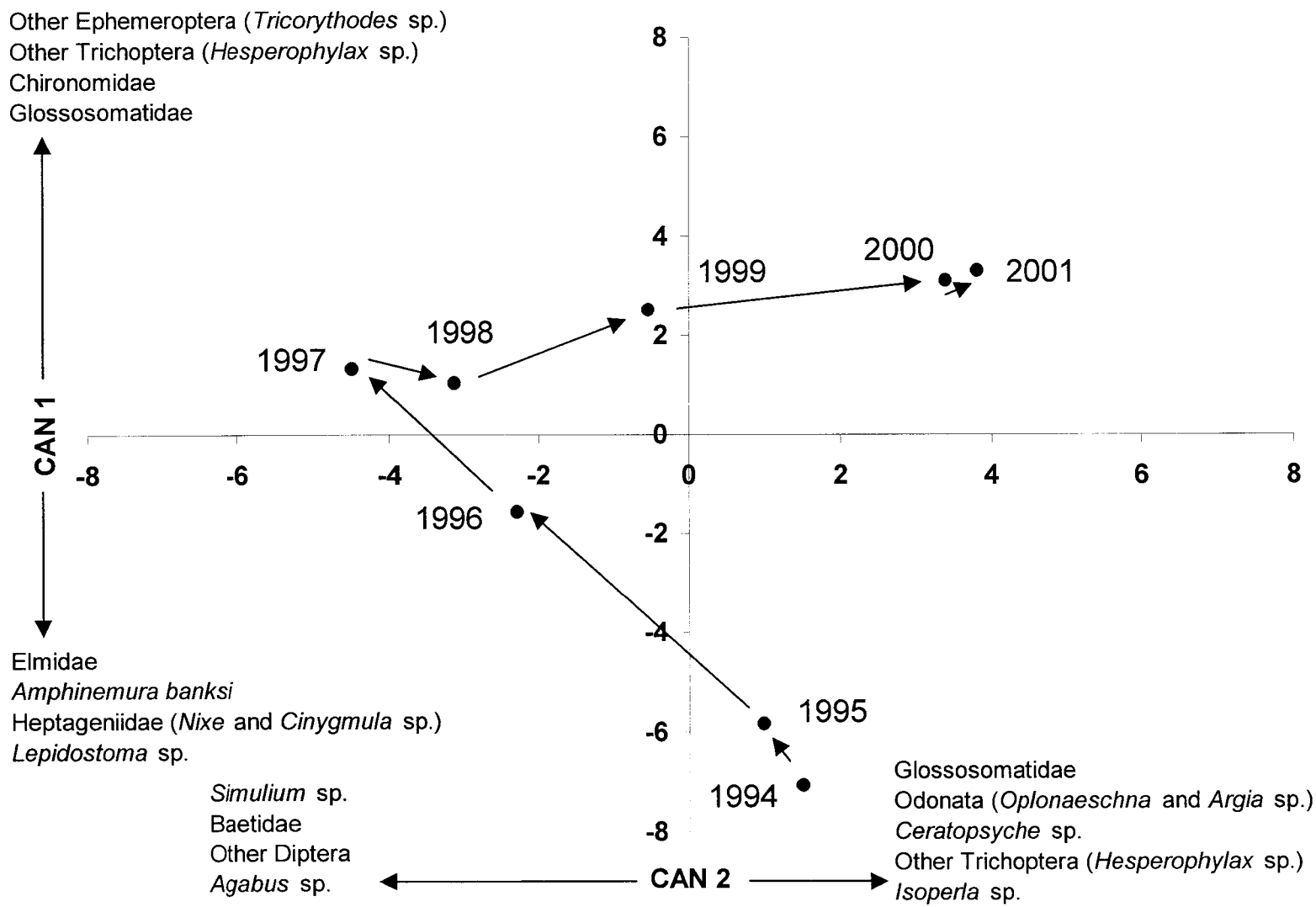


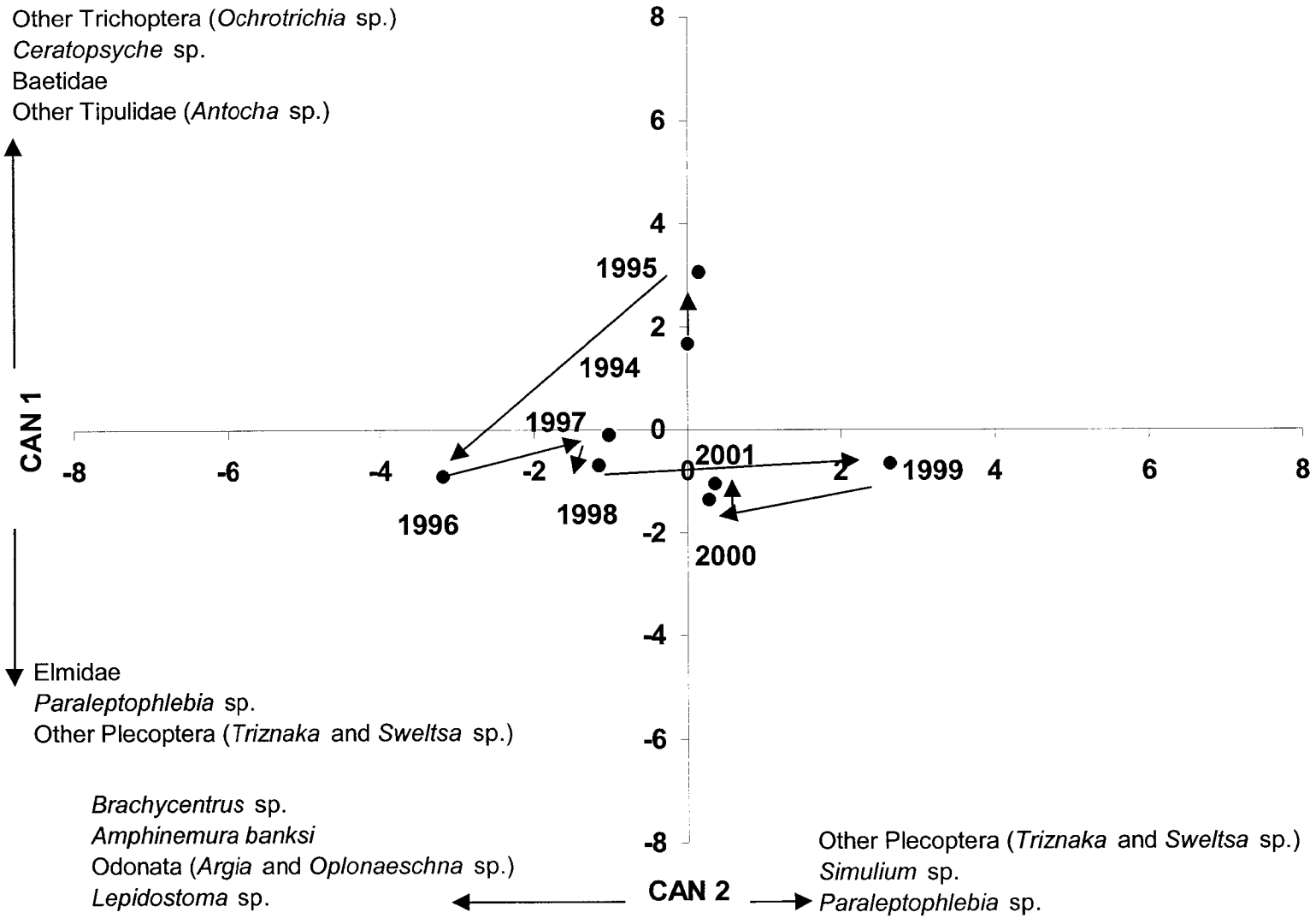


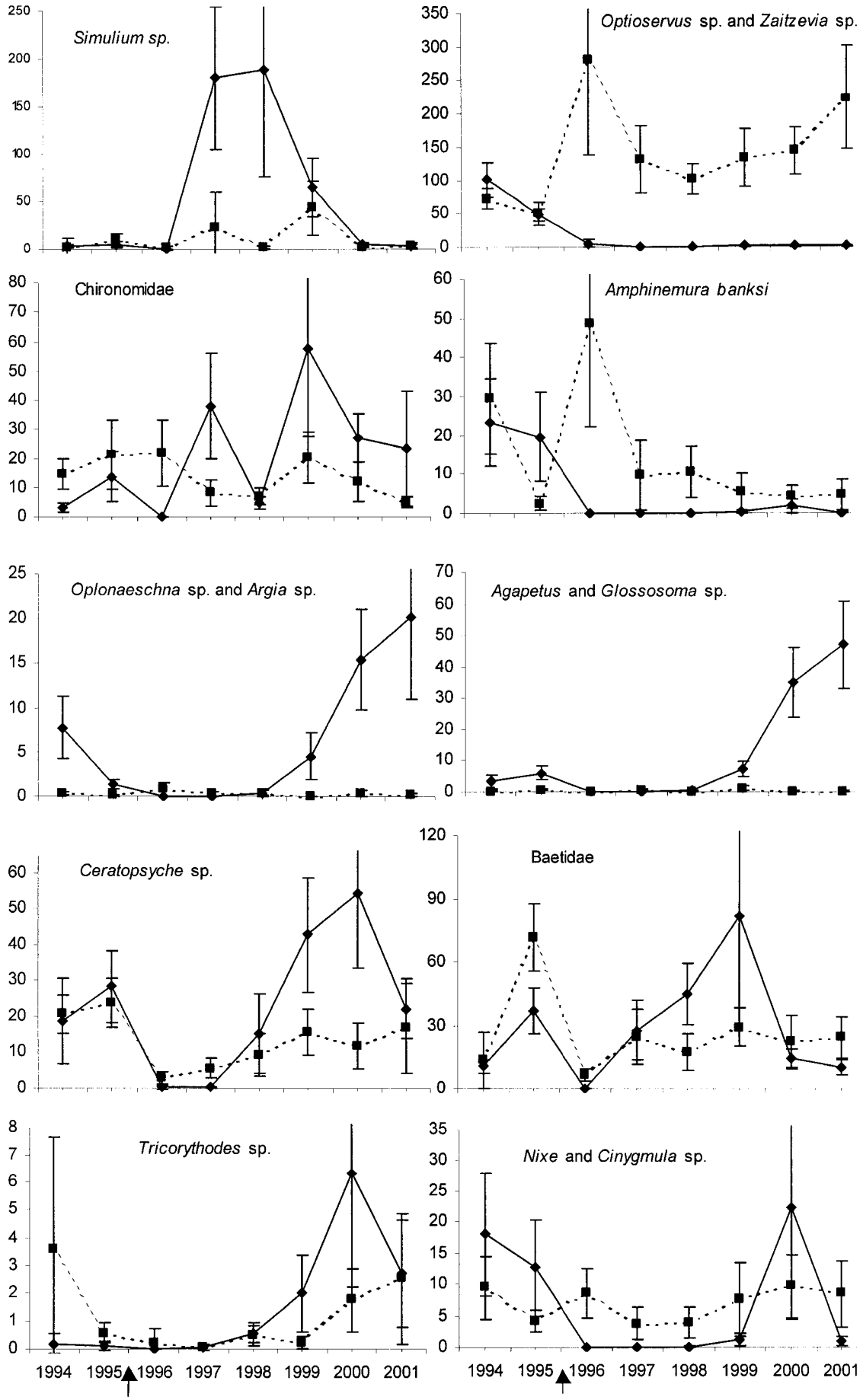


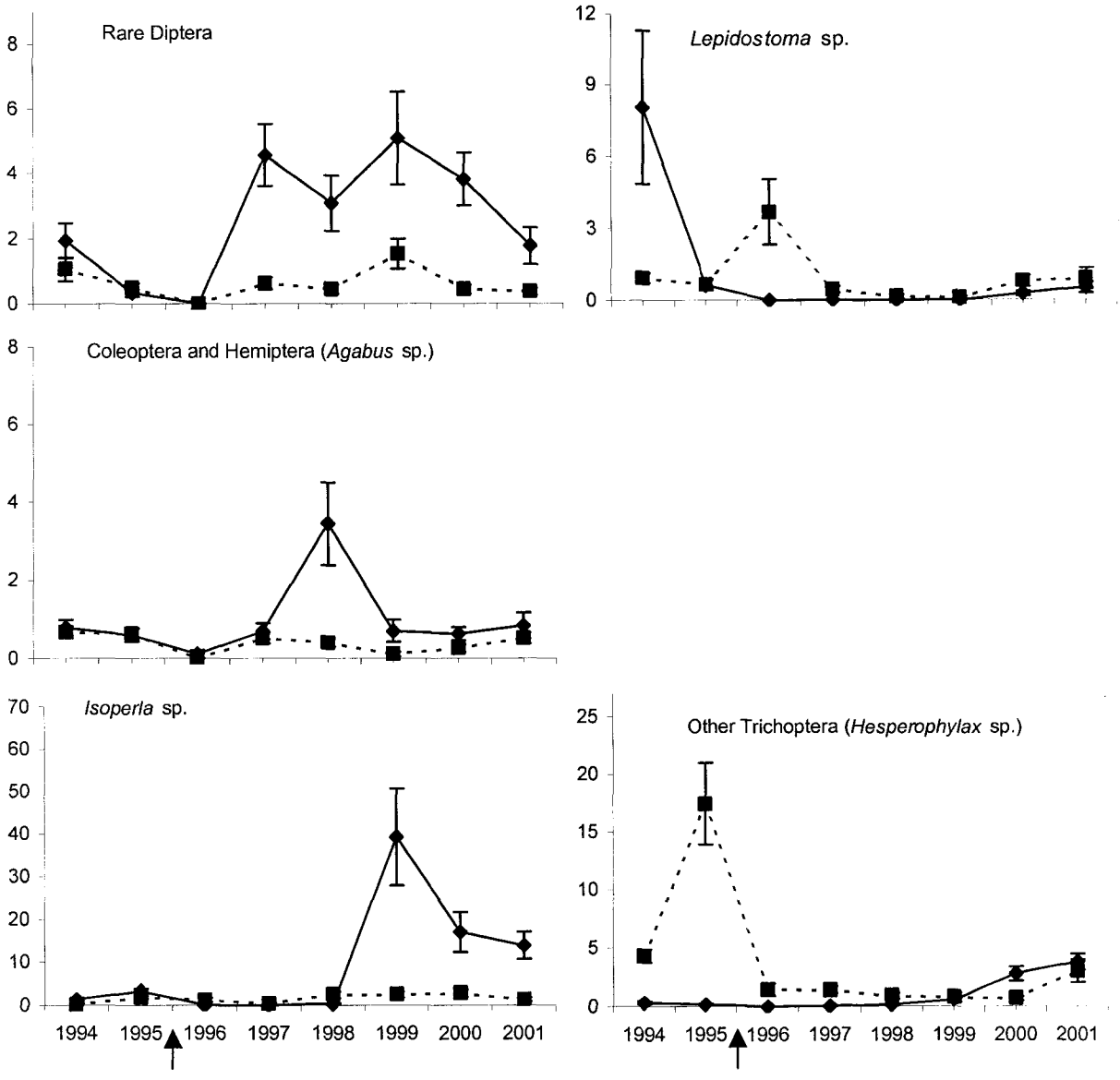


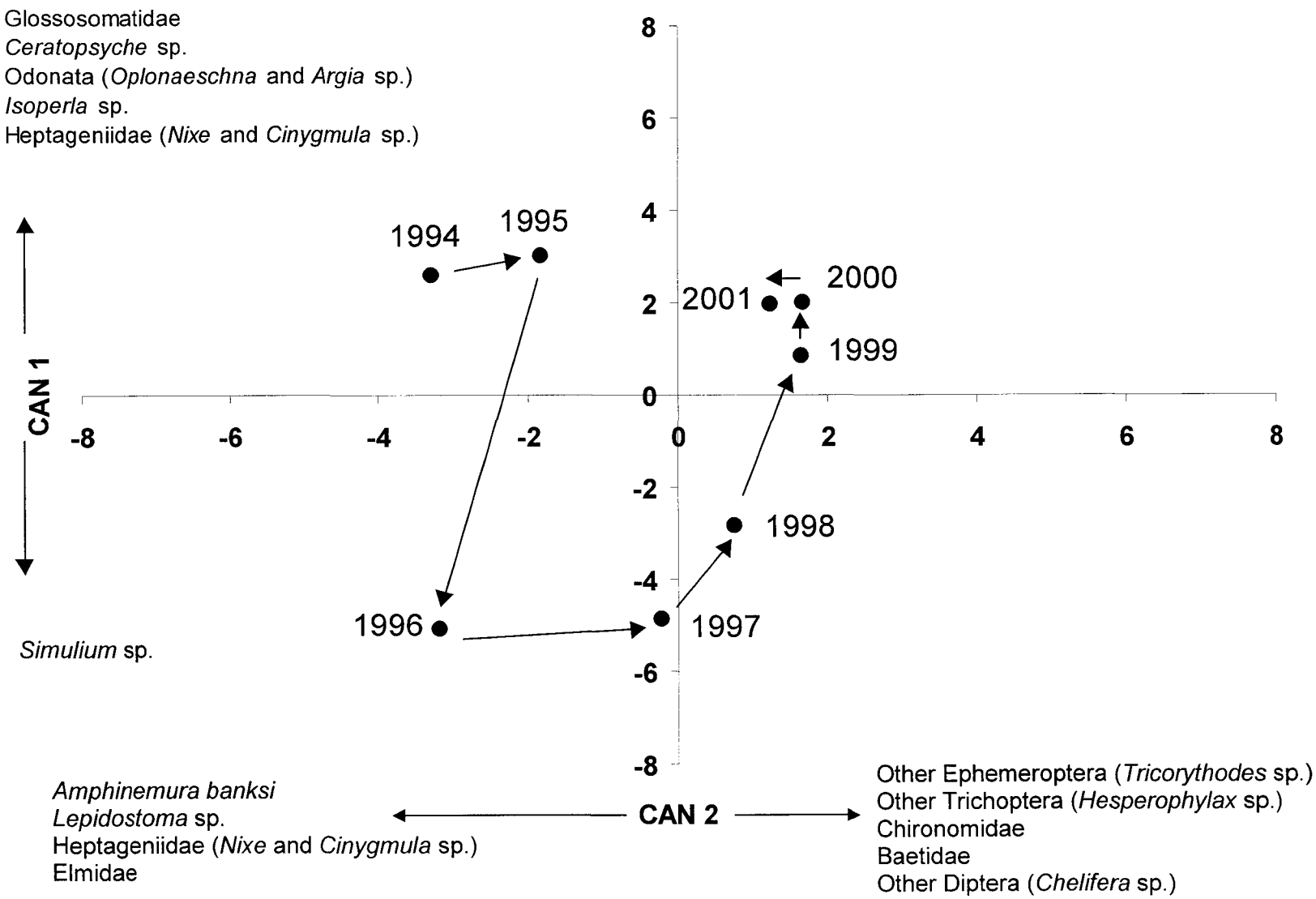


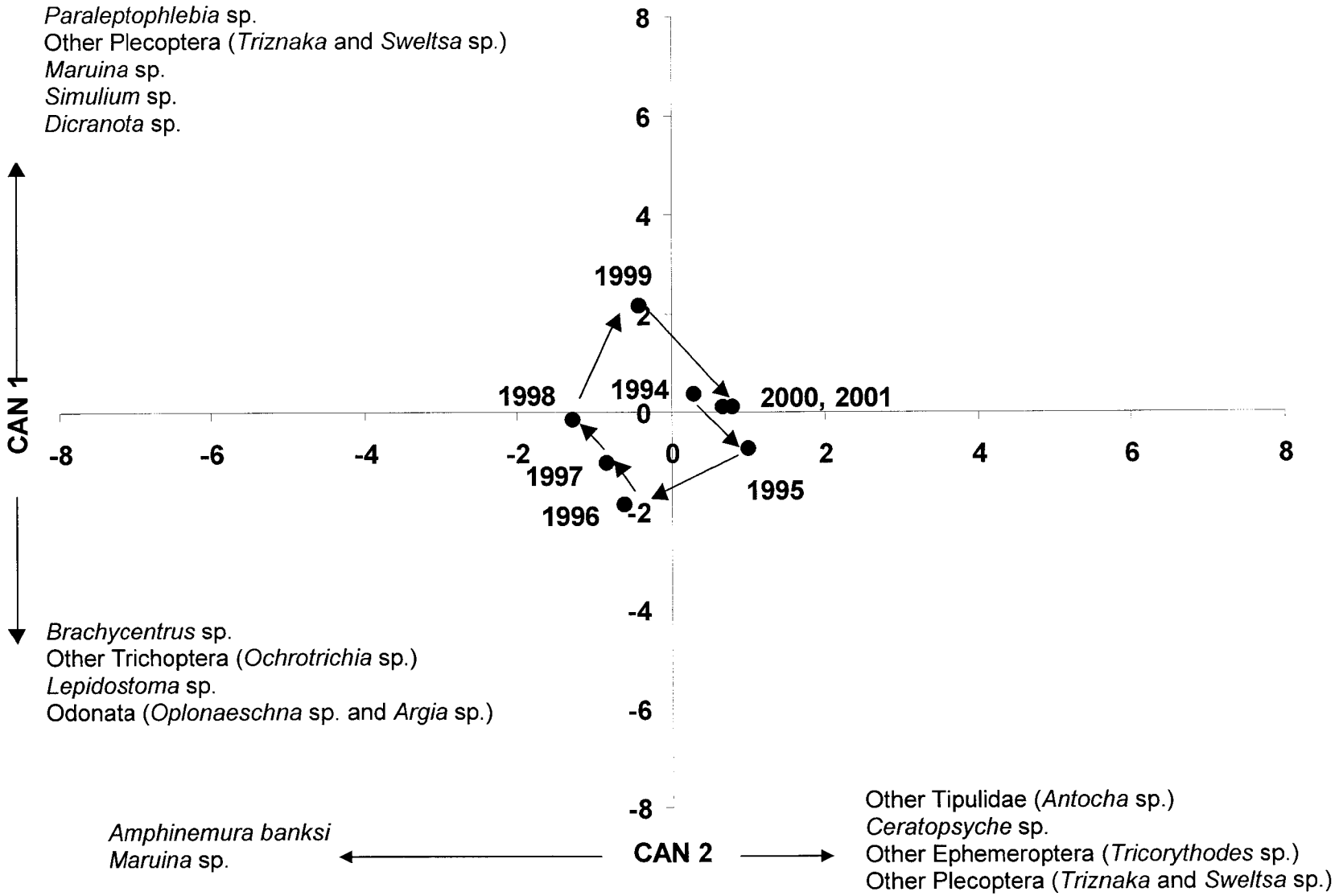












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TAXA CODE LIST

BAETRI = *Baetis tricaudatus* and *Fallceon quilleri*
DRUGRA = *Drunella grandis*
EPHEM = *Ephemerella* sp.
EPEORUS = *Epeorus* sp.
NIXE = *Nixe* sp. and *Cinygmula* sp.
PARALE = *Paraleptophlebia* sp.
AMELET = *Ameletus* sp.
TRICOR = *Tricorythodes minutus*
CAPNIA = *Capnia* sp.
SWELTS = *Sweltsa* sp. and *Triznaka* sp.
AMPHIB = *Amphinemura banksi*
HESPAC = *Hesperoperla pacifica*
ISOPER = *Isoperla* sp.
PTEBAD = *Pteronarcella badia*
AGAPET = *Agapetus* sp.
BRACSP = *Brachycentrus* sp.
GLOSSA = *Glossosoma* sp.
HESPSP = *Hesperophylax* sp.
HYDSP = *Ceratopsyche* sp.
LEPIDO = *Lepidostoma* sp.
NECTO = *Nectopsyche* sp.
OCHRSP = *Ochrotrichia* sp. and other micro caddisflies
OCETSP = *Oecetis* sp.
POLYSP = *Polycentropus* sp.
RHYSPP = *Rhyacophila* sp.
CHIRON = Chironominae
TANYTA = Tanytarsini
ORTHOC = Orthocladiinae
TANYPO = Tanypodinae
ANTOCH = *Antocha* sp.
CALOSP = *Caloparyphus* sp.
CHELIF = *Chelifera* sp.
DICRSP = *Dicranota* sp.
DIXASP = *Dixa* sp.
HEMERO = *Hemerodromia* sp.
HEXAT = *Hexatoma* sp.
MARUIN = *Maruina* sp.
LIMNOP = *Limnophora aequifrons*
OREOG = *Oreogeton* sp.
PALYPO = *Palpomyia* sp.
PEDIC = *Pedicia* sp.
PERIC = *Pericoma* sp.
SIMUSP = *Simulium* sp.
TIPUSP = *Tipula* sp.
AESHSP = *Oplonaeschna armata*
CORDSP = *Cordulegaster* sp.
ARGIA = *Argia* sp.
GERRI = Gerridae
MICROV = *Microvelia* sp.
PETROP = *Petrophila* sp.
AGABSP = *Agabus* sp.
HELICH = *Helichus striatus*
NARPSP = *Narpus concolor*
OPTIOS = *Optioservus* sp.
ZAIPAR = *Zaitzevia parvula*

FIRE	DATE	CANYON	Na	K	Mg	Ca	Cl	NO3	PO4	SO4
BEFORE	Aug-94	FRI	5.67	2.58	2.42	8.72	5.52	0.01	2.16	0.08
		CAP	5.99	2.96	3.04	14.10	2.73	0.04	2.60	0.08
	May-95	FRI	9.12	2.05	2.64	8.03	5.94	0.01	4.83	0.00
		CAP	9.42	2.63	3.64	12.61	2.55	0.01	6.03	0.02
	Jun-95	FRI	10.38	1.98	3.15	9.51	6.18	0.02	4.07	0.00
		CAP	8.88	2.22	3.33	12.24	2.60	0.01	6.06	0.04
	Aug-95	FRI	10.38	3.24	2.51	8.98	4.23	0.19	1.85	0.00
		CAP	8.97	3.74	1.65	7.93	2.65	0.03	3.79	0.03
AFTER	Jul-96	FRI	12.23	1.90	3.27	9.50	2.27	0.00	0.00	1.55
		CAP	17.93	7.47	16.37	59.13	4.31	0.00	0.18	10.59
	May-97	FRI	12.80	2.10	3.07	9.43	5.90	0.00	0.00	3.10
		CAP	12.80	4.03	5.03	18.90	2.23	1.10	0.00	9.30
	Jul-97	FRI	13.67	2.23	3.00	9.37	4.93	0.67	0.00	2.13
		CAP	14.03	4.53	5.37	21.10	2.93	1.20	0.00	5.27
	Oct-97	FRI	14.17	2.27	3.27	8.97	4.73	0.00	0.00	2.93
		CAP	11.73	4.17	5.10	18.93	2.57	0.00	0.00	8.73
	May-98	FRI	11.66	2.19	2.73	7.28	5.21	0.11	0.00	2.17
		CAP	10.40	3.82	4.65	17.50	2.93	0.88	0.17	8.85
	Jul-98	FRI	10.48	4.72	3.07	10.25	6.23	0.14	0.00	1.81
		CAP	10.88	5.80	4.91	18.51	2.44	0.61	0.40	4.75
	Oct-98	FRI	12.09	1.53	3.35	9.63	2.61	0.59	0.00	1.88
		CAP	11.27	2.97	4.91	18.20	3.04	0.66	0.00	3.74
	May-99	FRI	10.45	2.02	2.93	8.80	5.22	0.03	0.00	1.85
		CAP	8.96	3.27	3.48	13.66	2.25	1.12	0.10	5.80
	Jul-99	FRI	9.81	2.17	2.79	9.24	3.36	0.10	0.00	1.39
		CAP	10.00	3.86	4.21	16.22	2.31	0.00	0.00	3.99
	Oct-99	FRI	10.09	2.65	2.98	9.70	4.80	0.00	0.00	1.67
		CAP	9.69	3.11	3.78	14.55	2.46	0.00	0.00	3.09
	Apr-00	FRI	11.69	1.86	2.94	8.73	2.98	0.13	0.03	1.72
		CAP	12.02	3.05	3.95	14.75	2.76	0.19	0.15	3.16
	Jul-00	FRI	11.82	2.38	3.01	10.10	2.36	0.11	0.25	1.39
		CAP	12.58	3.52	4.30	16.09	2.60	0.05	0.24	2.12
	Oct-00	FRI	10.17	2.37	2.89	8.71	2.48	0.00	0.15	1.44
		CAP	10.25	2.68	3.91	14.83	3.24	0.00	0.17	2.90
	May-01	FRI	9.67	2.11	2.97	9.11	7.01	0.00	0.02	4.05
		CAP	8.59	2.92	3.69	13.52	2.74	0.06	0.13	10.33
	Jul-01	FRI	10.30	2.09	3.03	9.11	4.42	4.42	0.00	1.80
		CAP	9.52	3.04	3.37	9.48	2.33	0.00	0.09	4.57
	Oct-01	FRI	11.53	2.27	3.04	8.96	3.57	0.01	0.11	1.73
		CAP	10.76	2.81	3.92	14.17	2.67	0.00	0.16	3.05

CAPULIN	1994		1995		1996		1997		1998		1999		2000		2001	
(APP. 1.2a)	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
BAETRI	11	7	37	27	0	0	28	35	45	35	82	107	14	12	10	9
DRUGRA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPHEM	0	1	9	12	0	0	0	0	0	0	8	15	19	29	13	20
EPEORUS	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
NIXE	18	20	12	19	0	0	0	0	0	0	1	2	22	44	1	2
PARALE	0	0	1	2	0	0	0	0	0	0	1	2	2	4	11	20
AMELET	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
TRICOR	0	1	0	0	0	0	0	0	1	1	2	3	6	10	3	5
CAPNIA	0	0	0	0	0	0	0	0	0	0	6	13	0	0	1	1
SWELTZ	2	2	1	1	0	0	0	0	0	0	0	0	0	1	0	0
AMPHIB	23	23	20	28	0	0	0	0	0	0	0	1	2	4	0	0
HESPAC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ISOPER	1	2	3	3	0	0	0	0	0	1	39	65	17	27	14	17
PTEBAD	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AGAPET	3	5	3	4	0	0	0	0	0	1	2	3	4	8	1	1
BRACSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GLOSSA	0	0	3	6	0	0	0	0	0	0	5	5	31	26	46	33
HESPSP	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	3
HYDSP	19	24	28	25	0	1	0	1	15	27	43	39	54	51	22	20
LEPIDO	8	15	1	1	0	0	0	0	0	0	0	0	0	1	1	1
NECTO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OCHRSP	0	0	0	0	0	0	0	0	0	0	0	1	1	3	0	0
OCETSP	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1
POLYSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RHYSPP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
CHIRON	0	0	0	1	0	0	1	2	1	1	3	7	5	9	1	2
TANYTA	2	2	9	19	0	0	2	3	0	1	0	0	0	0	0	0
ORTHOC	1	1	4	5	0	0	35	43	4	5	52	73	21	16	22	46
TANYPO	0	1	0	0	0	0	0	0	0	0	2	3	0	1	0	0
ANTOCH	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
CALOSP	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
CHELIF	1	1	0	0	0	0	0	1	2	4	1	1	1	2	0	1
DICRSP	1	2	0	1	0	0	0	1	0	1	1	1	1	1	0	0
DIXASP	0	1	0	0	0	0	0	1	0	1	2	2	0	0	0	0
HEMERO	0	0	0	0	0	0	0	0	0	0	0	0	2	4	1	2
HEXAT	0	0	0	0	0	0	0	0	0	0	0	0	1	2	14	34
MARUIN	0	1	0	0	0	0	0	0	0	0	11	26	1	5	0	1
LIMNOP	0	1	0	0	0	0	4	5	0	1	0	0	0	0	0	0
OREOG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PALYPO	1	1	0	0	0	0	0	0	0	0	2	8	0	1	0	1
PEDIC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
PERIC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SIMUSP	3	4	5	7	0	0	180	185	189	282	64	76	4	7	3	4
TIPUSP	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
AESHSP	8	7	1	1	0	0	0	0	0	1	4	6	9	7	11	13
CORDSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ARGIA	0	0	0	0	0	0	0	0	0	0	0	1	6	10	9	11
GERRI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MICROV	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0
PETROP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
AGABSP	0	0	0	0	0	0	1	1	3	6	0	0	0	0	0	2
HELICH	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
NARPSP	2	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0
OPTIOS	59	34	25	13	5	7	0	1	0	0	1	2	1	2	1	2
ZAIPAR	41	22	22	16	1	1	0	0	0	0	0	0	0	1	0	0

FRIJOLES	1994		1995		1996		1997		1998		1999		2000		2001	
(APP. 1.2b)	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
BAETRI	14	14	72	39	7	4	25	32	17	22	29	22	22	30	24	24
DRUGRA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
EPHEM	0	0	1	2	0	0	1	2	3	5	3	4	1	2	0	1
EPEORUS	0	0	1	1	0	0	0	0	0	1	1	3	5	8	1	2
NIXE	9	14	3	4	9	5	4	6	4	6	7	15	5	11	8	13
PARALE	1	1	1	2	0	0	0	0	1	2	5	8	5	7	3	3
AMELET	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	5
TRICOR	4	12	0	1	0	1	0	0	0	1	0	0	1	3	1	3
CAPNIA	0	0	0	0	0	0	0	0	0	0	10	19	0	0	0	1
SWELTZ	0	0	0	0	0	0	0	0	0	1	3	4	1	1	0	1
AMPHIB	30	40	2	4	49	35	10	22	10	16	5	11	4	7	5	10
HESPAC	2	3	1	1	1	1	0	1	1	1	3	3	2	2	2	3
ISOPER	0	1	2	2	1	1	0	1	2	4	3	4	3	5	1	3
PTEBAD	15	17	1	2	5	5	4	9	3	5	1	2	4	7	4	9
AGAPET	0	0	0	1	0	0	0	1	0	0	1	2	0	0	0	0
BRACSP	1	1	4	5	17	15	7	10	3	4	1	2	3	6	6	14
GLOSSA	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
HESPSP	0	0	0	1	0	0	1	1	0	1	0	0	0	1	3	6
HYDSP	21	14	24	17	3	3	6	7	9	14	16	16	12	16	17	31
LEPIDO	1	1	1	1	4	4	0	1	0	0	0	0	1	1	1	2
NECTO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OCHRSP	4	3	17	20	1	1	0	1	0	1	0	1	0	0	0	1
OCETSP	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
POLYSP	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0
RHYSPP	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
CHIRON	0	0	0	1	0	0	0	0	1	3	5	12	2	3	1	1
TANYTA	9	9	15	31	16	12	1	1	3	7	2	6	0	0	0	0
ORTHOC	4	4	6	5	5	4	7	10	3	3	10	8	9	15	4	4
TANYPO	2	3	0	0	1	2	0	0	0	0	3	8	0	0	0	0
ANTOCH	4	7	3	2	0	0	1	1	1	3	1	2	1	2	0	1
CALOSP	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
CHELIF	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
DICRSP	2	2	1	2	1	1	1	1	1	2	3	3	2	3	1	2
DIXASP	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0
HEMERO	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
HEXAT	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1
MARUIN	0	0	0	0	0	0	0	0	0	1	2	5	0	0	0	0
LIMNOP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
OREOG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PALYPO	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
PEDIC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
PERIC	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
SIMUSP	2	1	10	15	1	3	22	90	2	3	43	70	2	4	4	7
TIPUSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AESHSP	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
CORDSP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ARGIA	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
GERRI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MICROV	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PETROP	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1
AGABSP	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
HELICH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NARPSP	0	1	1	2	2	3	0	0	0	1	0	1	0	1	0	1
OPTIOS	65	33	46	39	273	185	128	125	95	53	116	101	126	82	202	173
ZAIPAR	7	6	4	4	6	4	4	4	6	5	17	11	18	13	22	20

CAPULIN	1994		1995		1996		1997		1998		1999		2000		2001	
(APP. 1.2c)	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
BAETRI	1.00	0.00	0.96	0.19	0.00	0.00	0.85	0.36	1.00	0.00	1.00	0.00	1.00	0.00	0.92	0.28
DRUGRA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
EPHEM	0.28	0.46	0.67	0.48	0.11	0.33	0.00	0.00	0.07	0.27	0.56	0.51	0.63	0.49	0.64	0.49
EPEORUS	0.00	0.00	0.44	0.97	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.07	0.27	0.16	0.55
NIXE	1.00	0.00	0.70	0.47	0.00	0.00	0.00	0.00	0.04	0.19	0.44	0.51	0.33	0.48	0.24	0.44
PARALE	0.00	0.00	0.33	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.42	0.48	0.51	0.52	0.51
AMELET	0.00	0.00	0.07	0.27	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.19	0.40	0.00	0.00
TRICOR	0.06	0.24	0.00	0.00	0.00	0.00	0.04	0.19	0.33	0.48	0.59	0.50	0.70	0.47	0.52	0.51
CAPNIA	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.32	0.00	0.00	0.30	0.47	0.00	0.00	0.16	0.37
SWELTZ	0.56	0.51	0.33	0.48	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.40	0.08	0.28
AMPHIB	1.00	0.00	0.78	0.42	0.00	0.00	0.00	0.00	0.07	0.27	0.19	0.40	0.30	0.47	0.08	0.28
HESPAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ISOPER	0.56	0.51	0.85	0.36	0.00	0.00	0.00	0.00	0.22	0.42	0.56	0.51	0.85	0.36	0.76	0.44
PTEBAD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AGAPET	0.56	0.51	0.56	0.51	0.00	0.00	0.00	0.00	0.19	0.40	0.52	0.51	0.48	0.51	0.32	0.48
BRACSP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00
GLOSSA	0.00	0.00	0.41	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.47	0.93	0.27	1.00	0.00
HESPSP	0.06	0.24	0.04	0.19	0.00	0.00	0.00	0.00	0.04	0.19	0.11	0.32	0.37	0.49	0.52	0.51
HYDSP	1.00	0.00	1.00	0.00	0.11	0.33	0.15	0.36	0.74	0.45	0.96	0.19	0.96	0.19	1.00	0.00
LEPIDO	0.83	0.38	0.44	0.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.40	0.20	0.41
NECTO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OCHRSP	0.00	0.00	0.11	0.32	0.00	0.00	0.04	0.19	0.04	0.19	0.19	0.40	0.30	0.47	0.08	0.28
OCETSP	0.22	0.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.41	0.50	0.08	0.28
POLYSP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.15	0.36	0.07	0.27	0.00	0.00
RHYSPP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.44
CHIRON	0.00	0.00	0.15	0.36	0.00	0.00	0.33	0.48	0.30	0.47	0.56	0.51	0.85	0.36	0.52	0.51
TANYTA	0.78	0.43	0.67	0.48	0.00	0.00	0.41	0.50	0.11	0.32	0.15	0.36	0.00	0.00	0.04	0.20
ORTHOC	0.44	0.51	0.85	0.36	0.00	0.00	0.93	0.27	0.70	0.47	0.89	0.32	1.00	0.00	0.84	0.37
TANYPO	0.17	0.38	0.11	0.32	0.00	0.00	0.11	0.32	0.04	0.19	0.52	0.51	0.22	0.42	0.04	0.20
ANTOCH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.27	0.22	0.42	0.04	0.20
CALOSP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.27	0.30	0.47	0.15	0.36	0.04	0.20
CHELIF	0.22	0.43	0.04	0.19	0.00	0.00	0.33	0.48	0.37	0.49	0.48	0.51	0.56	0.51	0.20	0.41
DICRSP	0.50	0.51	0.11	0.32	0.00	0.00	0.15	0.36	0.15	0.36	0.41	0.50	0.59	0.50	0.00	0.00
DIXASP	0.22	0.43	0.04	0.19	0.00	0.00	0.26	0.45	0.15	0.36	0.59	0.50	0.04	0.19	0.12	0.33
HEMERO	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.32	0.00	0.00	0.00	0.00	0.30	0.47	0.32	0.48
HEXAT	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.32	0.26	0.45	0.48	0.51
MARUIN	0.28	0.46	0.04	0.19	0.00	0.00	0.04	0.19	0.00	0.00	0.74	0.45	0.19	0.40	0.08	0.28
LIMNOP	0.28	0.75	0.15	0.36	0.00	0.00	3.63	5.41	0.19	0.68	0.04	0.19	0.00	0.00	0.00	0.00
OREOG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00
PALYPO	0.33	0.49	0.11	0.32	0.00	0.00	0.04	0.19	0.04	0.19	0.44	0.51	0.26	0.45	0.20	0.41
PEDIC	0.06	0.24	0.00	0.00	0.00	0.00	0.07	0.27	0.07	0.27	0.15	0.36	0.15	0.36	0.16	0.37
PERIC	0.11	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.04	0.19	0.00	0.00	0.04	0.20
SIMUSP	0.56	0.51	0.81	0.40	0.00	0.00	0.89	0.32	1.00	0.00	0.93	0.27	0.59	0.50	0.60	0.50
TIPUSP	0.11	0.32	0.26	0.45	0.00	0.00	0.00	0.00	0.04	0.19	0.15	0.36	0.22	0.42	0.24	0.44
AESHSP	1.00	0.00	0.70	0.47	0.00	0.00	0.00	0.00	0.22	0.42	0.59	0.50	0.93	0.27	0.96	0.20
CORDSP	0.06	0.24	0.04	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.44
ARGIA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.47	0.52	0.51	0.92	0.28
GERRI	0.11	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00
MICROV	0.33	0.49	0.37	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.32	0.11	0.32	0.00	0.00
PETROP	0.11	0.32	0.07	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.27	0.26	0.45	0.04	0.20
AGABSP	0.00	0.00	0.00	0.00	0.11	0.33	0.37	0.49	0.44	0.51	0.19	0.40	0.00	0.00	0.20	0.41
HELICH	0.06	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.04	0.19	0.07	0.27	0.24	0.44
NARPSP	0.89	0.32	0.78	0.42	0.11	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.19	0.12	0.33
OPTIOS	1.00	0.00	1.00	0.00	0.78	0.44	0.15	0.36	0.04	0.19	0.48	0.51	0.67	0.48	0.52	0.51
ZAIPAR	1.00	0.00	1.00	0.00	0.33	0.50	0.00	0.00	0.04	0.19	0.04	0.19	0.19	0.40	0.16	0.37

FRIJOLES	1994		1995		1996		1997		1998		1999		2000		2001	
(APP. 1.2d)	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
BAETRI	1.00	0.00	1.00	0.00	1.00	0.00	0.85	0.36	0.93	0.27	1.00	0.00	0.85	0.36	0.93	0.27
DRUGRA	0.06	0.24	0.11	0.32	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.07	0.27	0.00	0.00
EPHEM	0.11	0.32	0.48	0.51	0.00	0.00	0.37	0.49	0.63	0.49	0.63	0.49	0.52	0.51	0.22	0.42
EPEORUS	0.00	0.00	0.93	1.33	0.00	0.00	0.00	0.00	0.41	1.01	1.15	2.55	4.63	8.18	0.78	2.06
NIXE	0.67	0.49	0.63	0.49	1.00	0.00	0.41	0.50	0.56	0.51	0.52	0.51	0.37	0.49	0.37	0.49
PARALE	0.28	0.46	0.48	0.51	0.00	0.00	0.11	0.32	0.48	0.51	0.67	0.48	0.70	0.47	0.59	0.50
AMELET	0.00	0.00	0.07	0.27	0.00	0.00	0.00	0.00	0.07	0.27	0.07	0.27	0.19	0.40	0.15	0.36
TRICOR	0.33	0.49	0.19	0.40	0.11	0.33	0.07	0.27	0.19	0.40	0.07	0.27	0.37	0.49	0.37	0.49
CAPNIA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.48	0.00	0.00	0.07	0.27
SWELTZ	0.22	0.43	0.11	0.32	0.00	0.00	0.07	0.27	0.11	0.32	0.63	0.49	0.19	0.40	0.26	0.45
AMPHIB	0.89	0.32	0.48	0.51	1.00	0.00	0.52	0.51	0.85	0.36	0.67	0.48	0.41	0.50	0.52	0.51
HESPAC	0.72	0.46	0.41	0.50	0.67	0.50	0.33	0.48	0.30	0.47	0.70	0.47	0.81	0.40	0.67	0.48
ISOPER	0.17	0.38	0.63	0.49	0.56	0.53	0.19	0.40	0.41	0.50	0.59	0.50	0.52	0.51	0.33	0.48
PTEBAD	0.89	0.32	0.59	0.50	0.78	0.44	0.63	0.49	0.56	0.51	0.63	0.49	0.63	0.49	0.56	0.51
AGAPET	0.06	0.24	0.22	0.42	0.00	0.00	0.30	0.47	0.15	0.36	0.26	0.45	0.04	0.19	0.00	0.00
BRACSP	0.33	0.49	0.89	0.32	1.00	0.00	0.70	0.47	0.67	0.48	0.19	0.40	0.78	0.42	0.59	0.50
GLOSSA	0.00	0.00	0.19	0.40	0.00	0.00	0.11	0.32	0.00	0.00	0.19	0.40	0.11	0.32	0.07	0.27
HESPSP	0.06	0.24	0.19	0.40	0.22	0.44	0.41	0.50	0.19	0.40	0.04	0.19	0.11	0.32	0.41	0.50
HYDSP	1.00	0.00	1.00	0.00	0.78	0.44	0.81	0.40	0.74	0.45	0.85	0.36	0.93	0.27	0.96	0.19
LEPIDO	0.33	0.49	0.30	0.47	0.78	0.44	0.33	0.48	0.11	0.32	0.11	0.32	0.41	0.50	0.41	0.50
NECTO	0.11	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OCHRSP	0.83	0.38	0.67	0.48	0.33	0.50	0.11	0.32	0.15	0.36	0.22	0.42	0.07	0.27	0.07	0.27
OCETSP	0.33	0.49	0.11	0.32	0.22	0.44	0.04	0.19	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00
POLYSP	0.00	0.00	0.07	0.27	0.11	0.33	0.00	0.00	0.04	0.19	0.04	0.19	0.11	0.32	0.04	0.19
RHYSPP	0.00	0.00	0.00	0.00	0.11	0.33	0.19	0.40	0.11	0.32	0.11	0.32	0.07	0.27	0.07	0.27
CHIRON	0.00	0.00	0.07	0.27	0.00	0.00	0.11	0.32	0.44	0.51	0.59	0.50	0.67	0.48	0.48	0.51
TANYTA	0.94	0.24	0.74	0.45	1.00	0.00	0.44	0.51	0.41	0.50	0.22	0.42	0.00	0.00	0.00	0.00
ORTHOC	0.89	0.32	0.93	0.27	1.00	0.00	0.70	0.47	0.59	0.50	0.93	0.27	0.85	0.36	0.89	0.32
TANYPO	0.50	0.51	0.11	0.32	0.33	0.50	0.07	0.27	0.07	0.27	0.41	0.50	0.07	0.27	0.07	0.27
ANTOCH	0.56	0.51	0.74	0.45	0.00	0.00	0.22	0.42	0.26	0.45	0.37	0.49	0.41	0.50	0.11	0.32
CALOSP	0.00	0.00	0.07	0.27	0.00	0.00	0.00	0.00	0.04	0.19	0.07	0.27	0.04	0.19	0.07	0.27
CHELIF	0.28	0.46	0.19	0.40	0.00	0.00	0.15	0.36	0.00	0.00	0.19	0.40	0.19	0.40	0.11	0.32
DICRSP	0.67	0.49	0.52	0.51	0.44	0.53	0.37	0.49	0.48	0.51	0.78	0.42	0.56	0.51	0.56	0.51
DIXASP	0.17	0.38	0.07	0.27	0.00	0.00	0.11	0.32	0.26	0.45	0.26	0.45	0.00	0.00	0.07	0.27
HEMERO	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HEXAT	0.06	0.24	0.15	0.36	0.00	0.00	0.04	0.19	0.07	0.27	0.15	0.36	0.15	0.36	0.26	0.45
MARUIN	0.17	0.38	0.00	0.00	0.00	0.00	0.04	0.19	0.22	0.42	0.26	0.45	0.07	0.27	0.04	0.19
LIMNOP	0.06	0.24	0.04	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
OREOG	0.11	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PALYPO	0.11	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.42	0.07	0.27	0.04	0.19
PEDIC	0.06	0.24	0.00	0.00	0.00	0.00	0.04	0.19	0.15	0.36	0.07	0.27	0.07	0.27	0.04	0.19
PERIC	0.11	0.32	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.15	0.36	0.04	0.19	0.00	0.00
SIMUSP	0.78	0.43	0.93	0.27	0.22	0.44	0.59	0.50	0.41	0.50	0.93	0.27	0.52	0.51	0.59	0.50
TIPUSP	0.17	0.38	0.00	0.00	0.11	0.33	0.04	0.19	0.00	0.00	0.04	0.19	0.15	0.36	0.15	0.36
AESHSP	0.28	0.46	0.11	0.32	0.11	0.33	0.15	0.36	0.19	0.40	0.00	0.00	0.11	0.32	0.15	0.36
CORDSP	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ARGIA	0.00	0.00	0.00	0.00	0.33	0.50	0.11	0.32	0.15	0.36	0.00	0.00	0.07	0.27	0.00	0.00
GERRI	0.00	0.00	0.07	0.27	0.00	0.00	0.00	0.00	0.04	0.19	0.00	0.00	0.00	0.00	0.04	0.19
MICROV	0.22	0.43	0.11	0.32	0.00	0.00	0.07	0.27	0.15	0.36	0.07	0.27	0.04	0.19	0.22	0.42
PETROP	0.22	0.43	0.15	0.36	0.00	0.00	0.19	0.40	0.11	0.32	0.00	0.00	0.11	0.32	0.11	0.32
AGABSP	0.00	0.00	0.11	0.32	0.00	0.00	0.19	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
HELICH	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.27	0.04	0.19	0.07	0.27	0.04	0.19
NARPSP	0.28	0.46	0.33	0.48	0.78	0.44	0.22	0.42	0.26	0.45	0.15	0.36	0.26	0.45	0.15	0.36
OPTIOS	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00
ZAIPAR	0.94	0.24	0.81	0.40	0.89	0.33	0.89	0.32	0.96	0.19	1.00	0.00	1.00	0.00	1.00	0.00

CHAPTER 2

ASSOCIATING SPECIES TRAITS OF STREAM INSECTS WITH PATTERNS OF COMMUNITY SUCCESSION AFTER A WILDFIRE

ABSTRACT

Species traits such as life-history schedules and morphological or behavioral adaptations convey resistance and resilience to stream insects in highly disturbed lotic systems. Associations between traits and environmental conditions may provide mechanistic explanations behind post-disturbance successional patterns. In this research, I tracked temporal trends in representation of species traits in insect communities following a wildfire, and investigated how traits were associated with severe post-fire floods in a burned stream. I tested *a priori* hypotheses regarding the resistance or resilience strength of species traits in light of post-fire peakflows with both qualitative (taxa presence) and quantitative (taxa densities) measures of trait representation. I also compared temporal trends in traits and trait-peakflow associations between a recently burned stream and an unburned stream. Taxa with traits predicted to convey high resilience (strong larval and adult dispersal, multiple life-cycles, resource generalists) colonized earlier and were positively associated with higher peakflows after the fire. Traits conveying high resistance (ability to avoid or tolerate high flows through swimming, attachment to substrate, or burrowing; low drag forces) were also strongly represented in early post-fire years with floods in the burned stream. In contrast, temporal patterns of trait representation differed in the unburned stream and showed stronger seasonal associations with resistant and resilient traits. Temporal changes in representation of species traits explained mechanisms behind species-based successional patterns in a burned stream.

INTRODUCTION

Physical disturbances such as changes in intensity, frequency, duration and predictability of hydrologic events (Poff and Ward 1989; Poff 1992; Death and Winterbourn 1995; Townsend et al. 1997a) are primary forces structuring stream insect communities (Resh et al. 1988; Reice et al. 1990). Community responses to disturbance depend on how species traits (i.e. life history tactics, morphology, behavior) mediate mortality and displacement (sensu Sousa 1984) and facilitate recovery of insect populations (Wallace 1990). For instance, resistant species traits may allow insects to avoid a disturbance (i.e. through emergence as aerial adults), or to utilize in-stream refugia through physical (i.e. small body size) or behavioral (i.e. use of hyporheic zone) adaptations (Palmer et al. 1992; Lancaster and Hildrew 1993; Lake 2000; Lytle 2002). Species traits such as strong larval or adult dispersal abilities convey resilience by facilitating rapid recolonization after a disturbance (Gray and Fisher 1981; Cushing and Gaines 1989; Boulton et al. 1992). Resistant and resilient traits interact with environmental "filters" associated with disturbance to influence assemblage structure and community recovery trajectories (Poff 1997; Townsend et al. 1997b).

Habitat template theories have been proposed to predict community organization based on how species traits are evolutionarily "forged" and environmentally "filtered" along gradients of stress and disturbance (Southwood 1977, 1988), habitat predictability and adversity (Greenslade 1983), productivity (Townsend and Hildrew 1994), and spatial heterogeneity (Poff 1997). In lotic systems, strong resistant and resilient species traits are predicted to increase in representation along a gradient of increasingly harsh historical disturbance regime (Townsend 1989; Poff and Ward 1990; Poff 1992; Townsend et al. 1997b). Trait-based investigations of stream insect communities (Richards et al. 1997; Townsend et al. 1997b), fish assemblages (Poff and Allan 1995; Lamouroux et al. 2002), and riparian foodwebs (Statzner et al. 1994) along hydrologic gradients have generally supported this hypothesis. Employing trait-based approaches to investigate temporal trends in community organization, or successional patterns, after a disturbance has been proposed (i.e. Townsend 1989; Poff and Ward 1990) but not adequately explored.

Species-based studies attempting to characterize succession in stream insect communities, and to relate succession to environmental conditions associated with disturbance, have been met with limited success (Fisher 1990). Natural diel, seasonal, or longer-term (i.e. climate cycles) effects on abiotic conditions are often superimposed on disturbance effects to influence community structure (Fisher 1990). Thus, identifying successional patterns can be confounded by seasonal turnover of species, since it is unclear whether species are responding to natural environmental variation or to a disturbance (Fisher et al. 1982; Boulton et al. 1992). Further, species recovery mechanisms (i.e. through traits) and disturbances may operate under different spatio-

temporal scales. For instance, species with strong larval dispersal through drift or swimming are often responsible for rapid redistribution after small-scale spates (Townsend 1989; Lake 2000). In contrast, recovery after larger-scale disturbances that alter physical habitat and reduce in-stream refugia (e.g. Scrimgeour et al. 1988; see reviews in Yount and Niemi 1990; Niemi et al. 1990; Mackay 1992) likely requires a more suite of different species traits. A mechanistic trait-based approach to succession may better account for scale-dependency and influences of natural variation, since traits, rather than species, interact with spatio-temporal gradients of environmental conditions.

Wildfire disturbance has been shown to create strong spatio-temporal environmental gradients, where post-fire disturbances in burned streams vary in severity, spatial extent, and persistence (see review in Gresswell 1999). Changes in water chemistry (Spencer and Hauer 1991), sediment transport (Troendle and Bevenger 1996; White 1996), flooding (Novak and White 1989; Scott and Van Wyk 1990; Lavabre et al. 1993), and organic material inputs (McIntyre and Minshall 1996) have been documented for days up to decades after wildfires. Minshall et al. (1989) predicted that these disturbances would increase insect drift and reduce species that prefer gravel and cobble due to increased siltation in burned streams. They also predicted that loss of riparian canopy and increased algae biomass would favor grazers and reduce detritivore specialists such as shredders. Species-based studies have provided anecdotal evidence for these hypotheses, where shifts from specialist to generalist feeding modes have been observed following a wildfire (Mihuc et al. 1996; Minshall et al. 1997; Chapter 1). Also,

I found that longer-lived species with weak dispersal abilities were replaced with multi-voltine, strong dispersing species in recently burned streams (Chapter 1; Chapter 3).

In this research, I applied a trait-based approach to investigate recolonization patterns of stream insect communities following a severe wildfire. The 1996 Dome fire burned the western half of the Pajarito Plateau and several of its canyons (including Capulin canyon) in the Jemez Mountains, NM. This fire resulted in multiple 100-year flash floods in the year of the fire, followed by elevated but dampened floods for up to three post-fire years in Capulin (Veenhuis 2002). Strong temporal changes in insect community composition were observed in Capulin, and these trajectories corresponded to post-fire hydrologic changes (Chapter 1). In contrast, insect communities in a nearby, unburned canyon (Frijoles) only experienced typical monsoon flood events (Veenhuis 2002) and showed little change in composition (Chapter 1). In this study, I investigated changes in representation of species traits in Capulin communities for two years before and six years after the Dome fire. I compared temporal patterns in trait representation in Capulin to patterns observed in Frijoles communities. I also investigated how patterns of representation were associated with changes in peakflow magnitudes and season in both canyons.

I chose traits previously shown to be related to resistance (body shape, size, drag, and habit/attachment) and resilience (dispersal, voltinism, and food and substrate preferences) to hydrologic variability (Townsend et al. 1997b). I investigated how different states of these traits were associated with recovery time (number of years since a

wildfire) and peakflow magnitude. I also tested *a priori* hypotheses regarding the resistance and resilience strengths of different trait states (Table 2.1). Hypotheses were based on predictions for stream insect community recovery after wildfire (Minshall et al. 1989) and spates (Townsend 1989). Hypotheses were also developed from previous trait-based studies investigating relationships between hydrologic gradients and species traits of insects (Richards et al. 1997; Townsend et al. 1997b) or fish (when appropriate; Poff and Allan 1995; Lamouroux et al. 2002). Based on the severity of post-fire flood disturbances (Veenhuis 2002), and strong colonization barriers presented to insects in Pajarito Plateau canyons (Chapter 1), species traits predicted to be highly resistant or resilient to hydrologic disturbances were expected to contribute strongly to post-fire succession in Capulin.

A priori hypotheses of trait-environment associations were tested using both quantitative (number of individuals with a trait state) and qualitative (presence/absence of taxa with a trait state) measures of trait representation. Quantitative measures best reflect responses to a disturbance event at small spatial scales (i.e. riffle), since taxa that optimize population growth under local post-disturbance conditions can numerically dominate a community (Poff and Ward 1990). In contrast, coarser-grained qualitative measures based on species presence in segments or whole streams are less influenced by temporal fluctuations in local environmental conditions. Qualitative measures also account for which species "selected" under the historical disturbance regime can persist after a disturbance (Poff and Allan 1995). Trait-environment associations generated from both quantitative and qualitative data were compared to temporal changes in species-

specific density and persistence in Capulin (Chapter 1) to investigate mechanisms underlying successional patterns.

STUDY SITE DESCRIPTION

Bandelier National Monument is located on the eastern slopes of the Sierra de Los Valles range and Pajarito Plateau, west of the Rio Grande River, in north-central New Mexico (Figure 2.1). Streams flow in a series of canyons from spring seeps at approximately 3100 m elevation to the Rio Grande River at 1590 m elevation. Capulin and Frijoles canyons are similar in drainage area (50 km^2), stream order (spring-fed 1st order streams with no perennial tributaries), permanency (perennial reaches from 1500-3000 m), gradient (3-4% at lower elevation and 6-7% at higher elevations), and baseflow (0.04 - 0.06 m^3/s; lower in La Niña years). Riparian vegetation in both canyons consists primarily of Western box elder (*Acer negundo*), narrowleaf cottonwood (*Populus angustifolia*), alder (*Alnus oblongifolia*), and ponderosa pine (*Pinus ponderosa*). Annual hydrographs are snowmelt driven in mid-spring and show flashy responses to localized monsoon precipitation in summer. Cyclic La Niña climate events bring decreased spring and summer precipitation approximately every four years (Andrade and Sellers 1988) and can result in extensive drying of perennial reaches in Pajarito canyons.

Wildfire has played a central role in this arid ecosystem. Historical (before the year 1900) high-frequency, low-intensity ground fires have been replaced by low-frequency, high-intensity canopy fires due to fire suppression (Touchan et al. 1996). In

June 1977, the La Mesa fire consumed 61.9 km^2 of the Plateau, including 58% of Frijoles canyon watershed in the eastern half of Bandelier National Monument (Figure 2.1). In April 1996, the Dome fire burned 66.8 km^2 of the Monument, including over 90% of Capulin canyon watershed (Figure 2.1). Annual peakflows and suspended sediment loads increased dramatically after both the La Mesa and Dome fires, where 100-year floods were followed by dampened but elevated floods for up to three post-fire years (Veenhuis 2002). Capulin was also slightly burned in the La Mesa fire (6%), but this burn did not generate post-fire floods (Veenhuis 2002). Invertebrate communities in the two canyons were similar in the two years before the 1996 Dome fire (Stevens 1996), but differed markedly for up to six years after the fire (Chapter 1).

METHODS

Stream insects and streamflow data in Frijoles and Capulin streams were collected in spring, summer, and fall for two years prior to the 1996 Dome fire (1994 – 1995; Stevens 1996) and six years after the fire (1996-2001; Chapter 1). To determine densities of stream insect taxa, I sampled insect communities with a Surber sampler (750-μm) mesh in three riffles (i.e. local scale) in each of three study reaches per stream. Further detail on collection methods are described elsewhere (Stevens 1996; Chapter 1). Insect samples collected in all three reaches were pooled (i.e. segment scale) to determine presence or absence of taxa (genera or Tribe) for each sample period. To determine trait densities and persistence, each individual insect or each taxon was recoded with the trait states that define that particular individual or taxon. Annual and monthly peakflow data

were obtained from publications (Veenhuis 2002), a USGS stream gauge in Frijoles (gauge: 08313350), and measurements of painted cobble movement, flood stages, and post-flood debris lines (see Chapter 1 for further detail).

States of the following resistant and resilient traits were identified for each taxon: functional feeding groups, body shape, body size, drag (i.e. potential for mediating drag forces), voltinism, larval and adult dispersal, substrate preference, and habit (i.e. mode of locomotion, attachment, or concealment) (Table 2.1). Trait information (Table 2.2) was derived from invertebrate keys and texts (Ward and Kondratieff 1992; Merritt and Cummins 1996); publications with lists of species traits (Rader 1997); expert opinion (B. Kondratieff and N. L Poff, Colorado State University); and my personal observations of insect populations in Pajarito Plateau streams. Adult dispersal strength was rated as weak, moderate, or strong based on equal consideration of adult flying ability, typical flight distance, and life span during the adult phase. Juvenile dispersal strength was also rated as weak, moderate, or strong based primarily on propensity to drift, and to a lesser degree on swimming ability and crawling rates. Body size (small: 0-8 mm, medium: 9-16 mm, and large: >16 mm length) and drag (low, moderate, and high) categories were modified from categories developed in Rader (1997). Body shapes ranged from highly streamlined (fusiform and flattened) to non-streamlined ("bluff" bodies). For taxa with ontogenetic shifts in trait states, both states were modeled based on densities or presence of aquatic larvae and aquatic adults.

I investigated how trait states in Frijoles and Capulin were associated with the length of time passed since a wildfire (Table 2.3). "Time since fire" (hereafter referred to as "time") represented recovery time and encompassed effects of post-fire flooding as well as distance to colonist sources in Capulin. Time was considered to be primarily an indicator of changes in baseflow due to climate oscillations in Frijoles (see Chapter 1). Post-fire sample periods for Capulin were established as the length of time since the April 1996 Dome fire. Capulin sample periods before 1996 and all Frijoles sample periods were established as the amount of time passed since the 1977 La Mesa fire. For qualitative trait representation data, I also explored how trait states were statistically associated with season (spring, summer, fall) and changes in monthly peakflow (Table 2.3). Peakflows were expressed as a semi-quantitative index to account for qualitative data collected from 1999-2001 (see Chapter 1). Peakflow values were natural-log transformed and then rounded up to the nearest whole number to create a discrete index number (e.g. a 100-year peakflow event of 2700 ft^3/s in Capulin was log-converted to 7.90 and then rounded up to an index value of 8). Index values represented the highest magnitude flood event that occurred between sampling periods.

Analysis for qualitative measures of trait representation

I employed the fourth corner problem (FCP) method (Legendre et al. 1997) to investigate trait-environmental associations with qualitative trait state data. FCP analysis manipulates matrices **A**, **B**, and **C** (below) to obtain the desired "fourth-corner" matrix **D**:

$$\begin{bmatrix} \mathbf{A}(k \times m) & \mathbf{B}(k \times n) \\ \mathbf{C}(p \times m) & \mathbf{D}(p \times n) \end{bmatrix}$$

A is the presence/absence of k species at m locations, **B** is the n trait "states" of the k species, and **C** is the p environmental variables for each of m locations. While matrix **A** requires presence/absence or frequency data, **B** and **C** can be qualitative variables, in nominal or disjunctive coding form, or ordinal/quantitative variables. Matrices **A**, **B** and **C** are multiplied, and matrix **A** is permuted under one of three null hypotheses (see below), to produce matrix **D**. Matrix **D** contains associations between states of species traits and environmental variables, calculated with chi-squared contingency tests, Pearson product-moment correlation coefficients on normalized data, or analysis of variance tests on normalized data. Global model statistics and statistics for each cell in **D** are generated by constrained permutations of matrix **A**, rather than completely random permutations, to account for lack of independence in rows (species can occur at more than one site; see Legendre et al. 1997). The FCP analysis employs Holm's correction for multiple testing (Holm 1979) to adjust significance levels for cells in matrix **D**. This method adjusts individual probabilities for each trait state-environment association within (but not between) each matrix manipulation (see Legendre et al. 1997).

In this study, matrix **A** consisted of presence/absence of 50 (Capulin) or 51 (Frijoles) taxa at 21 "locations" for each canyon, where sample periods were substituted for locations (Appendix 2.1 a-b). Nine **B**- matrices and three **C**-matrices were constructed, each with one of the nine species trait types (and its n states) and one of the

three environmental variables, respectively. Thus, separate model analyses were conducted for each possible trait-environment combination, producing 27 total **D**-matrices for each canyon. Within each trait category, trait states were coded in nominal disjunctive form (dummy variables where each trait state is expanded to a series of binary variables 0/1). Environmental seasonal variables (spring, summer, and fall) were also coded in nominal disjunctive form. Monthly peakflow index and time since fire were coded as ordinal environmental variables. Given strong seasonal and inter-annual variability in insect community measures (Chapter 1), adjusting FCP model permutations for autocorrelation was deemed unnecessary.

Matrix **A** in each analysis was permuted under the null hypothesis of "environmental control of individual species " (Permutation Model 1, Legendre et al. 1997) to investigate influences of temporal and environmental variables on trait representation. This model states that species persist in locations where environmental conditions are appropriate, and they do so independently of one another. Thus if all environments across pre- and post-fire sample periods were similar, the same species could be present in any sample period. Other models were deemed inappropriate for the question of interest. The "environmental control over species assemblages" model (Model 2) is similar to Model 1 but implies influences of strong biotic ties among community members. The importance of biotic interactions is debatable in highly disturbed lotic systems (Reice 1994) and was considered to be minimal immediately after a wildfire disturbance. The "lottery hypothesis" model (Model 3) implies that a fixed number of niches are available for colonization, and that chance plays an important role

in determining which species occupies these niches. In my study, the number of niches was expected to change with post-fire recovery of stream habitat. Model 4, random species attributes, does not make sense in regards to stream insects, as taxa are defined by a set of fixed (not randomly assigned) traits.

Each canyon was modeled separately and 9999 permutations were conducted for each "species trait versus environmental variable" model combination. All statistics for global models and specific cells in matrix **D** were compared against an *a priori* alpha level of 0.1. I selected this less stringent significance level because my observational study lacked control of extraneous variation influencing taxa presence in samples. If the global model was not significant for a particular combination of trait category and environmental variable, cells in matrix **D** were not interpreted for statistical significance. Further description of FCP statistical procedures and analysis output can be found in Legendre et al. (1997).

Analysis for quantitative measures of trait representation

To describe temporal patterns in densities of species traits after the Dome fire, I conducted a canonical discriminant analysis (CDA) using taxa density data presented in Chapter 1. This descriptive, dimension-reducing multivariate technique constructs linear combinations of independent variables (densities of trait states) to maximize separation between pre-assigned groups (years 1994-2001) using a set of observations (individual Surber samples). Samples sizes for groups were 1994 (n = 18), 1995 (n = 27), 1996 (n =

9), and 1997 - 2001 (n = 27 each) for each canyon. Trait density data were log-transformed to reduce variability in statistical analyses and to better meet parametric requirements (Ott 1993). Traits that were low in density (rare) and did not meet normal-distribution requirements were not included in CDA analysis. Trait states that lacked strong explanatory power (i.e. $P > 0.1$) in defining differences between years (univariate one-way ANOVA's testing for differences in density of each trait state between years) were removed from final CDA models. All univariate and multivariate analyses were conducted with SAS Statistical software (PROC CANDISC; SAS Institute 1996).

RESULTS

Fourth corner problem analysis

FCP analysis with qualitative trait data revealed that most trait states (80%) were significantly associated with time and peakflow in Capulin, while more trait states were associated with season (61%) in Frijoles (Figure 2.2). In both canyons, Pearson product-moment correlation coefficients were low for all associations between trait states and time or peakflow ($r < 0.15$). Low correlation between quantitative and nominal variables can be partially explained by the fact that nominal disjunctive data, while numerically coded as binary (0/1), are actually categorical variables. Therefore, I adopted the approach of Legendre et al. (1997) and focused on differences in direction of associations and relative statistical significance of these coefficients. Since both trait states and seasons were coded as nominal disjunctive variables, I determined direction and strength of trait-state versus season associations by comparing expected versus observed frequency of number of taxa with a particular trait state (chi-squared statistics).

Resistance Traits

Capulin showed a higher number of associations between habit and environmental variables, and these associations differed compared to those in Frijoles (Table 2.4; Appendix 2.2). In Capulin, swimmers, sprawlers, and burrowers were negatively associated with time, where these traits were more strongly represented in early post-fire years. Swimmers and attached taxa were positively associated with higher peakflows in Capulin. In contrast, clingers were negatively associated with peakflow and positively associated with time. Clingers were also negatively associated with peakflow in Frijoles. In contrast to relationships found in Capulin, burrowers were positively associated with "time since fire" in Frijoles. Seasonal relationships in Frijoles included over representation of clingers and under representation of sprawlers in the spring. Clingers were under represented in summer and fall, while sprawlers were over represented in summer. In Capulin, swimmers and clingers were represented more strongly in spring than expected (Table 2.4). Attached taxa were under represented in spring but over represented in fall, while burrowers were under represented in summer.

No relationships between body shape and environmental variables existed in Capulin and only a few seasonal relationships were found in Frijoles (Table 2.4; Appendix 2.3). Fusiform and flattened taxa were over represented in spring and under represented in summer or fall in Frijoles. Drag was related to peakflow in Capulin, where taxa with low drag were positively associated with higher peakflows (Table 2.4; Appendix 2.4). Taxa experiencing moderate drag forces were negatively associated with

peakflow. In contrast, drag was only associated with seasonal in Frijoles, where taxa with intermediate drag were over represented in spring and under represented in summer. More relationships between body size and environmental variables existed in Frijoles (Table 2.4; Appendix 2.5). Taxa with medium -sized bodies were associated with lower peakflows, while taxa with larger bodies were found at higher peakflows. Also, taxa with intermediate sizes were over represented in spring and under represented in summer and fall. In Capulin, large-bodied taxa occurred earlier after the fire while taxa with small bodies appeared in collections as time since fire increased (Table 2.4).

Resilience Traits

Relationships between larval dispersal and environmental variables were similar for Capulin and Frijoles (Table 2.5; Appendix 2.6). In both canyons, weak larval dispersers were negatively associated with peakflow, while moderate and strong larval dispersers were found at higher peakflows. Larval dispersal did not show significant associations with time or season in either canyon. A higher number of significant associations between adult dispersal and environmental variables occurred in Capulin compared to Frijoles (Table 2.5; Appendix 2.7). Taxa with strong adult dispersal were positively associated with increased peakflow in both canyons. In Capulin, moderate adult dispersers were negatively associated with increasing peakflow. Strong larval dispersers also occurred at earlier time periods after the fire in Capulin, while weak larval dispersers showed the opposite trend (more taxa with increased time since fire) (Table 2.5). No significant associations between adult dispersal and time were found in Frijoles and season was not important in either canyon.

Trait states for voltinism were similarly associated with peakflow in Capulin and Frijoles (Table 2.5; Appendix 2.8). Uni-voltinism was negatively associated with peakflow, while both multi-voltine and semi-voltinism were positively associated with higher peakflows. In Capulin, multi-voltine taxa were collected more often at earlier sample periods after the Dome fire. In contrast, semi-voltine taxa were associated with later sample periods after the fire. No significant relationships existed between voltinism and time in Frijoles, or between voltinism and season in either canyon (Table 2.5). For substrate preference in Capulin, erosional sediment and sand/silt dwellers were negatively associated with time, where more taxa with these substrate preferences were collected sooner after the fire (Table 2.5; Appendix 2.9). In contrast, cobble dwellers were positively associated with time, where more taxa dwelling on erosional cobbles were collected in later post-fire years. Substrate preference was only significantly associated with season in Frijoles. Seasonally, erosional cobble dwellers were over represented in spring and under-represented in summer and fall.

Significant associations between functional feeding groups and environmental variables differed between canyons (Table 2.5; Appendix 2.10). In Capulin, collectors (filterers and gatherers) were positively associated with peakflow while specialist feeders (grazers and shredders) were negatively associated with peakflow (Table 2.5). In contrast, no associations between function feeding groups and peakflow existed in Frijoles. Grazers and shredders in Capulin were negatively associated with time since fire, while predators were collected earlier after the fire (Table 2.5). In Frijoles, collector

gatherers increased over time while collector-filterers and grazers decreased with time since a wildfire. Seasonal associations occurred in Frijoles, where grazers were over represented and shredders were under represented in spring (Table 2.5). Collector-gatherers were under represented and shredders were over represented in summer, while grazers were under represented in fall.

Multivariate analysis

CDA conducted on quantitative trait representation data revealed significant changes in densities of trait states across sample years in Capulin (Wilks' Lambda: $F_{df=189} = 21.16$; $p < 0.0001$). The first two canonical variables explained 71.9 % of the variation in trait representation among years. The first canonical variable (CAN1) explained 38.4 % of the total variation among years ($F_{df=189} = 21.16$; $p < 0.0001$) and generally distinguished all post-fire years (1996-2001) from pre-fire years (1994-1995)(Figure 2.3). Taxa that were semi-voltine, grazers or shredders, clingers or sprawlers, or weak adult dispersers were more abundant in pre-fire years compared to post-fire years and thus were positively correlated with CAN1 (Table 2.6). Trait states that were negatively correlated with CAN1 were more strongly represented in post-fire samples, and included moderate adult dispersal ability, sediment/silt preference, multi-voltinism, burrower or attachment habits, and strong larval dispersal ability (Table 2.6).

Canonical variable-2 (CAN2) explained 33.5% of the total variation among years ($F_{df=156} = 16.67$; $p < 0.0001$) and separated post-fire years with moderate to severe flash floods (1996-1998) from those with more typical peakflows (1999-2001) (Figure 2.3).

CAN2 also separated late post-fire flood years (1999-2001) from pre-fire years (1994-1995). Taxa with strong larval dispersal were abundant in early post-fire years and were negatively correlated with CAN2 (Table 2.6). To a lesser degree, multi-voltine taxa (common in early post-fire years) and leafpacks dwellers (abundant in pre-fire years) were also negatively correlated with CAN2. Taxa with preferences (or tolerance) for sand or silt, large body size, uni-voltinism, weak larval dispersal, strong adult dispersal, and predatory feeding modes were more abundant in later post-fire years (1999-2001) compared to pre-fire and early post-fire years and were positively correlated with CAN2 (Table 2.6).

CDA conducted for Frijoles revealed different and less distinct temporal patterns in trait representation compared to patterns in Capulin (Wilks' Lambda: $F_{df=189} = 5.49$; $p < 0.0001$). The first two canonical variables explained 67.2% of the variation in trait representation among years. CAN1 explained 43.9 % of the total variation among years ($F_{df=189} = 21.16$; $p < 0.0001$) and generally distinguished differences in trait representation between the years 1995 and 1996 (Figure 2.4). Taxa that were swimmers, strong larval and adult dispersers , multi-voltine, collector-gatherers and attached to substrate were more abundant in 1995 and were positively associated with CAN1 (Table 2.6). Taxa that were semi-voltine, clingers, grazers or shredders, and moderate adult dispersers were more abundant in 1996 and were negatively correlated with CAN1 (Table 2.6). CAN2 explained 23.3% of the total variation among years ($F_{df=156} = 4.12$; $p < 0.0001$) and separated years the 1999-2001 from other years (Figure 2.4). Taxa with weak larval dispersal, shredder or collector-filterer feeding modes, and leafpack substrate preferences

were positively correlated, while predators and collector-gatherers, burrowers, sand or silt dwellers, and moderate larval dispersers were negatively correlated with CAN2 (Table 2.6).

DISCUSSION

Species traits predicted to convey strong resilience and resistance to hydrologic disturbance were positively associated with post-fire flashfloods and characterized insect communities in early recovery stages in a burned stream. Resilient traits such as strong dispersal, multiple life-cycles within a year, general resource use, and silt/sand tolerance were important mechanisms behind post-fire changes in community structure. Resistant traits, such as the ability to seek refugia during floods (i.e. by swimming or burrowing) or to tolerate high flows (i.e. by attaching to substrate or mediating drag forces) were also important in years with moderate to severe flashfloods. These temporal trends in resistant and resilient traits were supported with both coarser-grain qualitative (i.e. persistence in segments) and finer-grained quantitative (i.e. density in riffles) measures of trait representation. In a geomorphically similar stream not burned in the Dome fire, changes in representation of resistant and resilient traits were more often associated with season than with wildfire variables. In contrast, few traits-season relationships existed in the burned stream, indicating that "filters" associated with wildfire disrupted natural seasonal patterns to shape temporal patterns in community structure.

My findings in the burned stream supported independently derived *a priori* predictions regarding the resistance and resilience strength of trait states. Resistant traits such as swimming and burrowing habits, and low drag, characterized communities in earlier post-fire years when moderate to severe post-fire floods occurred. In contrast, taxa that cling to substrate with claws (most clinger taxa lacked specially adapted hooks) and experience higher drag forces were more common in pre-fire or later post-fire communities when "normal" magnitude floods occurred. Similarly, Richards et al. (1997) found that insect taxa resisted disturbance through small body size, or by swimming/burrowing to refugia, in streams with greater hydrologic disturbances (i.e. flashy and ephemeral Midwestern streams). Taxa with less resistant traits, including sprawling or clinging to substrate with claws and larger body sizes, were found more often in hydrologically stable streams (Richards et al. 1997). Townsend et al. (1997b) also found stronger representation of resistant insect traits in streams where flooding was more recent and severe. These traits included body forms with low drag (streamlined or flattened) and the ability to attach to substrate with special morphological adaptations such as hooks or silk production.

More of my *a priori* predictions regarding strength of resilience traits states were supported compared to predictions for resistant trait states. Strong larval and adult dispersal, multi-voltinism, general substrate preferences (i.e. erosional sediments), tolerance of depositional silt/sand habitats, and generalist feeding strategies (collector-gatherers and collector-filterers) were common in early post-fire years or were associated with higher peakflows in the burned stream. In contrast, taxa with weak adult dispersal

and specialist resource uses (grazers on erosional cobbles, shredders in depositional leafpacks) were less resilient to wildfire and post-fire floods. These findings are consistent with predictions of Minshall et al. (1989) that sediment and sand/silt dwelling insect taxa would colonize earlier than cobble dwelling taxa in burned streams, and that shredders would show low resilience due to reduced riparian food sources. Similar to my study, other trait-based studies on stream insects (Richards et al. 1997; Townsend et al. 1997b) and fish (Poff and Allan 1995) have found higher representation of taxa with strong larval and adult mobility, short generation times or multi-voltinism, generalist resource use, and silt-tolerance in streams with less hydrologic stability.

While most of my *a priori* predictions about resistance and resilience strength were supported, there were several notable exceptions. While low drag was associated with higher peakflow, hydrologic disturbance was not related to streamlined body shapes or small body size as others have found for insects (Richards et al. 1996; Townsend et al. 1997b) and fish (Lamouroux et al. 2002). The severity of 100-year flood events in the burned stream may have overwhelmed the resistance typically associated with streamlining or small size. The counterintuitive finding of larger body sizes in earlier post-fire years was probably a spurious result due to the fact that large-bodied juveniles were also strong dispersers as adults (Pearson product-moment correlation coefficient $r = 0.88$, $P < 0.0001$). Correlation with adult dispersal also partially explains the unexpected finding that semi-voltine taxa were associated with high peakflows ($r = 0.65$, $P < 0.0001$). Finally, I did not find that grazers were highly resilient to wildfire as predicted by Minshall et al. (1989). Discrepancies may be due to the fact that Minshall et al.'s (1989)

examined effects of fire on snowmelt-driven, hydrologically stable streams with tributaries. Pajarito Plateau canyons of this study are highly erodible and streams that drain these canyons are hydrologically flashy. Thus, scouring sediment-laden flood events may have mediated the expected increased algal growth due to a more open canopy. Also, lack of tributaries and the extensive damage to the entire perennial segment of the burned stream (Veenhuis 2002) may have precluded recolonization of grazers, since most of these taxa have weak-moderate dispersal abilities.

The importance of resilient traits in this study made sense in light of severe post-fire hydrologic disturbance and strong colonization barriers presented to stream insects in Pajarito Plateau canyons. Multiple 100-year flood events moved large substrate (i.e. boulders, woody debris) and scoured the burned stream to bedrock in the entire perennial segment (Cannon and Reneau 2000; Veenhuis 2002), greatly reducing in-stream flow and hyporheic refugia (Palmer et al. 1992; Lancaster and Hildrew 1993). Not surprisingly, insect densities were reduced to near zero (1 -2 individuals per Surber sample) after the first post-fire flashflood (Chapter 1), indicating that even taxa with highly resistant traits were eliminated. With few survivors, resilient traits contributed more strongly to temporal changes in community structure after the fire. Although in-stream colonist sources were limited, insects with strong larval dispersal probably recolonized via drift (approx. 6-8 km) from ephemeral headwater reaches experiencing only moderate flooding (N. K. M. Vieira, Colorado State University, unpublished data). Since many of these early colonists were multi-voltine, some individuals may have avoided floods through emergence and thus persisted in burned reaches.

Given the limited species diversity in ephemeral headwater reaches of the burned stream (N. K. M. Vieira, unpublished data), adult dispersal from adjacent Pajarito Plateau canyons was an important resilient trait. The deep canyons and wide mesas (4-6 km) of the Plateau, unidirectional winds within canyons, lack of tributaries, and long intermittent reaches between perennial stream segments and the Rio Grande River pose severe colonization barriers to aerial adults. In fact, major differences in community composition can occur in adjacent canyons, even though canyons share similar disturbance histories (Chapter 3). Not surprisingly, I found that taxa with strong adult dispersal abilities colonized earlier than weak fliers in the burned stream. Others have shown that adult emergence timing and dispersal ability contribute to post-flood recolonization in desert streams (i.e. Gray and Fisher 1981; Lytle 2002). Once strong adult or larval dispersers arrived in burned reaches, taxa tolerant of silt (deposited during post-fire floods and repeatedly mobilized during high flow events) were likely more resilient than colonists requiring other substrates which were embedded (cobbles) or absent (leafpacks) during early post-fire years.

Flashy hydroclimatology (sensu Poff and Ward 1989) in Pajarito Plateau streams and climatic oscillations between wet and drought years were likely responsible for trait-environment associations in the unburned stream. Associations between peakflow and both high larval dispersal and multi-voltinism were similar to those found in the burned stream. These traits would be expected in communities that are subjected to a harsh disturbance regime, including periods of drought (drying of perennial reaches) and

repeated flashfloods during the monsoon season (Lake 2000). Thus, even without the effects of wildfire, all Pajarito streams can be considered highly disturbed systems. The fact that taxa with resistant and resilient traits (swimmers, strong dispersers, multivoltine, collectors) dominated communities in the unburned stream in 1995 supports this idea. This year was a severe drought year, where precipitation in New Mexico was the fourth lowest on record from 1974 - 2002 and the 27th lowest from 1895 - 2002 (NCDC; data published on www.ncdc.noaa.gov). As a result, baseflow in Frijoles was greatly reduced and taxa such as Baetidae, Chironomidae, and *Ceratopsyche* sp. increased in density (Chapter 1).

Linking traits with succession patterns of species

Associations between traits and environmental variables in the burned stream were linked back to taxa characterizing communities in the burned stream (Figure 2.5). Resistance or resilience "strength" of traits was determined by considering the number and direction of associations with disturbance-related environmental variables. For example, swimmers were both early colonizers and flood-tolerant, and were thus considered highly resistant. Clingers colonized later and were not flood-tolerant, and were thus highly sensitive. Sprawlers were identified as early colonists with qualitative trait data but were identified as poorly resilient with quantitative data. Similarly, body shapes were not significantly associated with time or peakflows. Therefore, these traits were considered neutral. Patterns in trait strengths were expressed along a gradient of

decreasing resistance and resilience (high, neutral, and poor) and were linked to patterns of taxa densities reported in Chapter 1 (see Figure 1.9 and Appendix 1.2 in Chapter 1).

Resistance and resilience strength of species traits explained patterns of species succession in the burned stream following the wildfire. Taxa (e.g. Baetidae, *Simulium* sp., Orthocladiinae) with traits that were identified to be highly resistant (swimming or attachment habits, low drag) and resilient (strong larval dispersal, multi-voltine, generalist feeders) recolonized by the first post-fire year (Figure 2.5). Other early colonists in the first post-fire year (*Agabus* sp. and *Ceratopsyche* sp.) were strong adult dispersers that were either strong swimmers or attached to substrate (Figure 2.5). Taxa that colonized in post-fire years with reduced or nearly normal peakflows (1998-1999) showed stronger resilience traits compared to resistance traits. For instance, *Tricorythodes minutus* Traver and Tanypodinae were multi-voltine, strong larval dispersers, and silt or sediment dwelling taxa, but were also sprawlers (Figure 2.5). *Oplonaeschna armata* Hagen, *Dicranota* sp., and Glossosomatidae had moderate to strong adult dispersal ability, but also had habits (i.e. clinging, sprawling) with lower resistance. Finally, taxa that did not recolonize until after several years after post-fire flashfloods abated (elmids, *Epeorus* sp., *Helichus striatus* LeConte, *Amphinemura banksi* Baumann and Gaufin, and *Lepidostoma* sp.) lacked strong resilience traits. For instance, these taxa were weak adult dispersers with specialized substrate and feeding preferences (Figure 2.5). In general, trait-based mechanisms explained species-based patterns of succession.

Although I demonstrated strong links between resistant or resilient traits and recolonization patterns for many taxa, notable exceptions existed. For instance, *Ephemerella* sp. recolonized during post-fire flashfloods despite clinging habits, weak dispersal, and specialized resource needs. *Chelifera* sp. also colonized early with only moderate resistance and weak resilience traits. Discrepancies may be due to chance survival of these taxa in upstream reaches. Also, I chose species traits that were previously linked with hydrologic disturbance in the literature, and for which I had species-specific information. Other species traits not investigated in this study, including timing of emergence, developmental rates, egg resistance, or diapause, may have been equally important. Finally, stream insect taxa likely have adaptive "suites" of traits (Resh et al. 1988; Townsend et al. 1997b; Poff 1997) that interact to convey non-additive resistance or resilience to disturbance. Conversely, a trait or subset of traits may be disproportionately important for certain environmental filters. For example, strong adult flight allowed odonates to recolonization during moderate flood years, despite the fact that these species had other traits conveying weak resilience and resistance. As a result, some unexpected trait-environment associations (i.e. semi-voltinism; large body size) were generated.

Linking species traits with community organization along environmental gradients is currently limited to "one-trait-at-a-time" analyses (i.e. Doledec et al. 1996; Legendre et al. 1997; Billheimer et al. 2001). Despite this simplistic approach, I uncovered meaningful and predictable relationships between species traits and environmental factors associated with wildfire disturbance. Further, temporal trends in

community representation of resistant and resilient traits explained species-based successional patterns observed after a wildfire and post-fire flashfloods. Interpreting spatiotemporal dynamics of streams insect communities in terms of species traits should be the focus of future studies on disturbance for several reasons. First, trait-based approaches are both ecologically and evolutionarily relevant since real-time trait-environment interactions determine species persistence, and traits are a result of natural selection (Poff 1997). Second, traits also reflect functional significance (i.e. foodweb position and productivity) of insect species in stream communities. Finally, traits conveying tolerance to environmental filters can occur across taxonomic boundaries (Poff and Olden, unpublished data). Thus, trait representation in communities can be compared across regions with different species pools, allowing for broader tests of ecological theory.

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Table 2.1. States of resistant and resilient species trait categories for stream insects, the number of insect taxa with these trait states, and *a priori* hypotheses regarding resistance or resilience strength of trait states to hydrologic disturbance developed from previous literature.

TRAITS TYPES	TRAIT STATES	# Taxa	*a priori* Hypotheses*
RESISTANT TRAITS			
Behavioral habit	Swimmer	6	H
	Clinger	19	L
	Sprawler	12	L
	Attached	6	H
	Burrower	10	H
Body shape	Fusiform	5	H
	Flattened	10	H
	Bluff	15	L
	Tubular	24	M
Drag	Low	22	H
	Moderate	18	M
	High	13	L
Size	Small	21	H
	Medium	21	M
	Large	11	L
RESILIENT TRAITS			
Larval dispersal ability	Weak	29	L
	Moderate	21	M
	Strong	3	H
Adult dispersal ability	Weak	22	L
	Moderate	27	M
	Strong	4	H
Voltinism	Bi- or multi-voltine	7	H
	Uni-voltine	37	M
	Semi-voltine	9	L
Substrate preference	Erosional sediments	9	H
	Erosional cobble	25	L
	Depositional sand/silt	5	H
	Depositional leafpack	14	L
Functional feeding group	Collector-gatherer	13	H
	Collector-filterer	4	H
	Grazer	10	L
	Predator	20	M
	Shredder	6	L

* Prediction of resistance/resilience strength: H = high, M = medium, L =low
based on the following sources: Townsend 1989; Townsend et al. 1997b; Minshall et al. 1989; Richards et al. 1997; Poff and Allan 1995; and Lamouroux et al. 2002

Table 2.2. Traits states for stream insect taxa for the following species traits: functional feeding group (FFG; CG = collector-gatherer, GR = grazer, P= predator, S= shredder, and CF = collector-filterer), voltinism (VOLT), drag force (low, moderate, high), body shape, habit, larval dispersal ability (LDISP), adult dispersal ability (ADISP), body length (SIZE; small, medium, large), and substrate preference (SUBST). See text for further details on how trait states were assigned.

SPECIES (TAXA)	FFG	VOLT	DRAG	Body	HABIT	LDISP	ADISP	SIZE	Substrate
Ameletus sp.	GR	uni	M	fusiform	swimmer	moderate	moderate	M	sediments
Baetidae	CG	multi	L	fusiform	swimmer	strong	weak	S	cobble
Ephemerella sp.	CG	uni	M	bluff	clingers	weak	weak	M	leafpack
Epeorus sp.	CG	uni	L	flattened	clingers	moderate	weak	M	cobble
Cinygmula and *Nixe* sp.	GR	uni	L	flattened	clingers	moderate	weak	M	cobble
Paraleptophlebia sp.	CG	uni	L	fusiform	swimmer	moderate	weak	M	cobble
Tricorythodes minutus	CG	multi	M	bluff	sprawler	moderate	weak	S	sand/silt
Siphlonurus sp.	CG	uni	M	fusiform	swimmer	strong	weak	M	sand/silt
Amphinemura banksi	S	uni	L	bluff	sprawler	weak	weak	S	leafpack
Capnia sp.	S	uni	L	flattened	sprawler	weak	weak	S	leafpack
Sweltsa and *Triznaka* sp.	P	uni	M	bluff	clingers	weak	moderate	S	cobble
Hesperoperla pacifica	P	semi	H	bluff	clingers	moderate	moderate	L	cobble
Isoperla sp.	P	uni	M	bluff	clingers	moderate	weak	M	cobble
Pteronarcella badia	S	semi	H	bluff	clingers	weak	moderate	L	leafpack
Agapetus sp.	GR	uni	L	bluff	clingers	weak	moderate	S	cobble
Glossosoma sp.	GR	uni	L	bluff	clingers	weak	moderate	S	cobble
Brachycentrus sp.	CF	uni	M	tubular	attached	weak	moderate	M	cobble
Hesperophylax sp.	S	uni	H	bluff	sprawler	weak	moderate	L	leafpack
Ceratopsyche sp.	CF	uni	H	bluff	attached	moderate	strong	L	cobble
Lepidostoma sp.	S	uni	M	tubular	sprawler	weak	moderate	M	leafpack
Ochrotrichia sp.	GR	uni	L	flattened	attached	weak	moderate	S	cobble
Oecetis sp.	P	uni	L	tubular	clingers	weak	moderate	S	cobble
Polycentropus sp.	P	uni	H	bluff	attached	weak	moderate	L	cobble
Rhyacophila sp.	P	uni	M	tubular	clingers	moderate	moderate	M	cobble
Tribe Chironomini	CG	multi	L	tubular	burrower	moderate	moderate	S	sediments
Tribe Tanytarsini	CF	multi	L	tubular	burrower	moderate	moderate	S	cobble
Tribe Orthocladiinae	CG	multi	L	tubular	burrower	moderate	moderate	S	sediments
Tribe Tanypodinae	P	multi	L	tubular	sprawler	moderate	moderate	S	sediments
Antocha sp.	CG	uni	M	tubular	clinger	weak	moderate	M	cobble
Caloparyphus sp.	CG	uni	L	flattened	sprawler	weak	weak	M	cobble
Chelifera sp.	P	uni	M	tubular	sprawler	weak	weak	M	leafpack
Dicranota sp.	P	uni	M	tubular	sprawler	weak	moderate	M	sediments
Dixa sp.	CG	uni	L	tubular	swimmer	moderate	weak	S	leafpack
Hexatoma sp.	P	uni	H	tubular	burrower	weak	moderate	L	leafpack
Maruina sp.	GR	uni	L	flattened	clinger	weak	weak	S	cobble
Limnophora aequifrons	P	uni	H	tubular	burrower	weak	weak	M	sediments
Hemerodromia sp.	P	uni	H	tubular	sprawler	weak	weak	M	sediments
Palpomyia sp.	P	uni	L	tubular	burrower	weak	weak	S	leafpack
Pedicia sp.	P	uni	M	tubular	burrower	weak	moderate	M	leafpack
Pericoma sp.	CG	uni	M	tubular	burrower	weak	weak	S	sand/silt
Simulium sp.	CF	multi	L	tubular	attached	strong	moderate	S	cobble
Tipula sp.	S	uni	H	tubular	burrower	weak	moderate	L	leafpack
Tabanus sp.	P	uni	H	tubular	sprawler	weak	moderate	L	leafpack
Rhabdomastix sp.	P	uni	M	tubular	burrower	weak	moderate	M	sand/silt
Oplonaeschna armata	P	semi	H	bluff	sprawler	moderate	strong	L	leafpack
Argia sp.	P	uni	M	flattened	clinger	moderate	strong	L	sediments
Cordulegaster sp.	P	semi	H	bluff	burrower	moderate	strong	L	sand/silt
Petrophila sp.	GR	uni	H	tubular	attached	weak	weak	M	cobble
Agabus sp.	P	semi	L	fusiform	swimmer	moderate	strong	M	sediments
Helichus striatus	GR	semi	M	bluff	clingers	weak	weak	M	cobble
Narpus concolor	CG	semi	L	bluff	clingers	moderate	weak	S	cobble
Optioservus sp.	GR	semi	L	bluff	clingers	moderate	weak	S	cobble
Zaitzevia parvula	CG	semi	L	bluff	clingers	moderate	weak	S	cobble

Table 2.3. Environmental variables associated with wildfire measured from 1994-2001 for recently burned (Capulin) and historically burned (Frijoles) streams, near Los Alamos, NM. See text for further details on derivation of peakflow index.

Canyon	"Sites"	Season	Years since fire	Peakflow index
CAPULIN	1994-1	SP	16.8	1
	1994-2	SU	17.0	2
	1995-1	SP	17.8	1
	1995-2	SU	18.0	2
	1995-3	FA	18.2	1
	1996-1	SU	0.0	8
	1997-1	SP	1.0	2
	1997-2	SU	1.3	3
	1997-3	FA	1.5	5
	1998-1	SP	2.0	2
	1998-2	SU	2.3	3
	1998-3	FA	2.5	4
	1999-1	SP	3.0	2
	1999-2	SU	3.3	3
	1999-3	FA	3.5	2
	2000-1	SP	4.0	1
	2000-2	SU	4.3	1
	2000-3	FA	4.5	1
	2001-1	SP	5.0	1
	2001-2	SU	5.3	1
	2001-3	FA	5.5	1
FRIJOLES	1994-1	SP	16.8	1
	1994-2	SU	17.0	1
	1995-1	SP	17.8	1
	1995-2	SU	18.0	2
	1995-3	FA	18.2	1
	1996-1	SU	19.0	2
	1997-1	SP	19.8	1
	1997-2	SU	20.0	2
	1997-3	FA	20.5	2
	1998-1	SP	20.8	1
	1998-2	SU	21.0	2
	1998-3	FA	21.5	3
	1999-1	SP	21.8	1
	1999-2	SU	22.0	2
	1999-3	FA	22.5	1
	2000-1	SP	22.8	1
	2000-2	SU	23.0	1
	2000-3	FA	23.5	2
	2001-1	SP	23.8	1
	2001-2	SU	24.0	1
	2001-3	FA	24.5	1

Table 2.4. Relationships between species traits conveying resistance and time passed since a wildfire (in years), peakflow index (see text for detail), and season in recently burned (CAP) and historically burned (FRI) streams near Los Alamos, NM. Significance (P-value) and sign or direction of associations (s) are presented when P values of global models and trait-environment associations are < 0.1. ns = not significant. See Appendices 2.2 – 2.5 for more detailed statistical output.

Trait States		Peakflow		Time		Spring		Summer		Fall	
		CAP	FRI	CAP	FRI	CAP	FRI	CAP	FRI	CAP	FRI
Habit											
Swimmer	s	+	0	-	0	+	0	-	0	0	0
	P	0.030	ns	0.041	ns	0.043	ns	0.054	ns	ns	ns
Clinger	s	-	0	+	-	+	+	0	-	0	-
	P	0.023	ns	0.001	0.043	0.093	0.001	ns	0.017	ns	0.008
Sprawler	s	0	0	-	0	0	-	0	+	0	0
	P	ns	ns	0.037	ns	ns	0.016	ns	0.034	ns	ns
Attached	s	+	0	0	0	-	0	0	0	+	0
	P	0.001	ns	ns	ns	0.002	ns	ns	ns	0.010	ns
Burrower	s	0	0	-	+	0	0	-	0	0	0
	P	ns	ns	0.066	0.009	ns	ns	0.023	ns	ns	ns
Body shape											
Fusiform	s	0	0	0	0	0	+	0	-	0	0
	P	ns	ns	ns	ns	ns	0.000	ns	0.020	ns	ns
Flattened	s	0	0	0	0	0	+	0	0	0	-
	P	ns	ns	ns	ns	ns	0.033	ns	ns	ns	0.007
Blocky	s	0	0	0	0	0	0	0	0	0	0
	P	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tubular	s	0	0	0	0	0	0	0	0	0	0
	P	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Drag											
Low	s	+	0	0	0	0	0	0	0	0	0
	P	0.004	ns	ns	ns	ns	ns	ns	ns	ns	ns
Medium	s	-	0	0	0	0	+	0	-	0	0
	P	0.005	ns	ns	ns	ns	0.001	ns	0.004	ns	ns
High	s	0	0	0	0	0	0	0	0	0	0
	P	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Size											
Small	s	0	0	+	0	0	0	0	0	0	0
	P	ns	ns	0.076	ns	ns	ns	ns	ns	ns	ns
Medium	s	0	-	0	0	0	+	0	-	0	-
	P	ns	0.028	ns	ns	ns	0.001	ns	0.003	ns	0.087
Large	s	0	+	-	0	0	0	0	0	0	0
	P	ns	0.031	0.011	ns	ns	ns	ns	ns	ns	ns

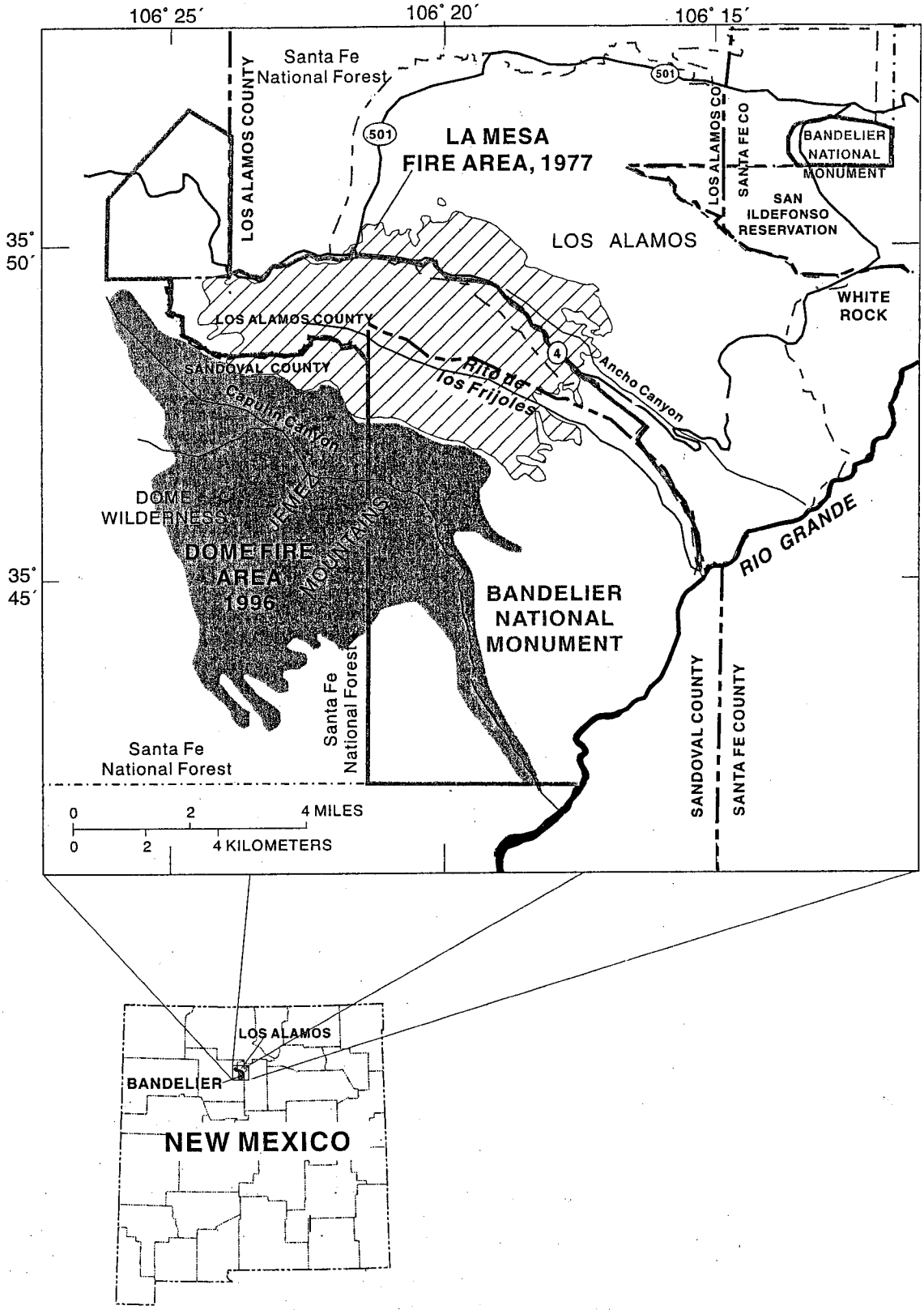
Table 2.5. Relationships between species traits conveying resilience and environmental variables related to wildfire in recently burned (CAP) and historically burned (FRI) streams near Los Alamos, NM. See Table 2.4 and Appendices 2.6 – 2.10 for further statistical details.

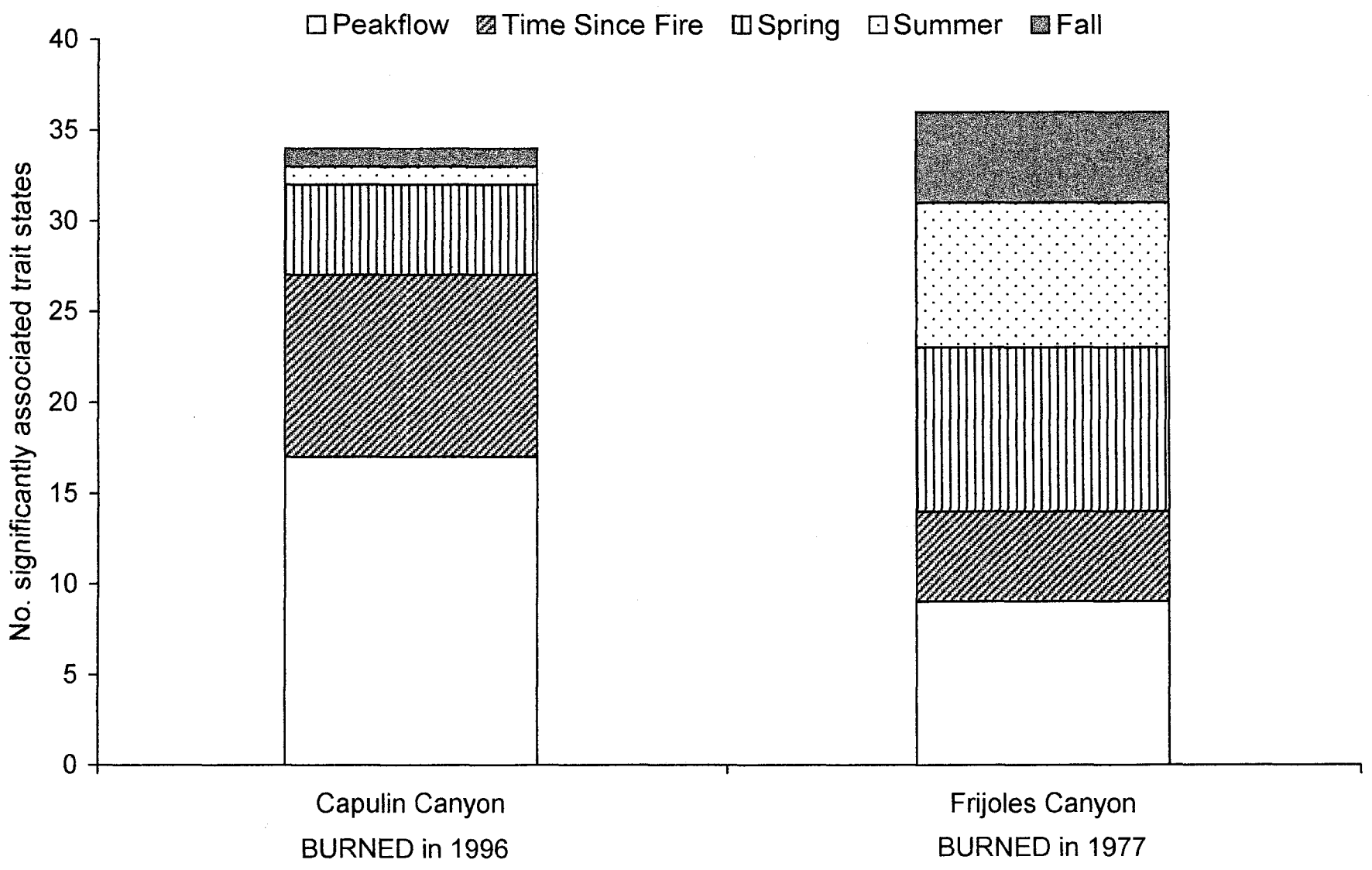
Trait states		Peakflow		Time		Spring		Summer		Fall	
		CAP	FRI	CAP	FRI	CAP	FRI	CAP	FRI	CAP	FRI
Larval dispersal											
Weak	s	-	-	0	0	0	0	0	0	0	0
	P	0.001	0.020	ns	ns	ns	ns	ns	ns	ns	ns
Moderate	s	+	+	0	0	0	0	0	0	0	0
	P	0.005	0.038	ns	ns	ns	ns	ns	ns	ns	ns
Strong	s	+	+	0	0	0	0	0	0	0	0
	P	0.004	0.007	ns	ns	ns	ns	ns	ns	ns	ns
Adult dispersal											
Weak	s	0	0	+	0	+	0	0	0	0	0
	P	ns	ns	0.034	ns	0.034	ns	ns	ns	ns	ns
Moderate	s	-	0	0	0	0	0	0	0	0	0
	P	0.028	ns	ns	ns	ns	ns	ns	ns	ns	ns
Strong	s	+	+	-	0	-	0	0	0	0	0
	P	0.002	0.009	0.012	ns	0.012	ns	ns	ns	ns	ns
Voltinism											
Multi-voltine	s	+	+	-	0	0	0	0	0	0	0
	P	0.002	0.090	0.016	ns	ns	ns	ns	ns	ns	ns
Uni-voltine	s	-	-	0	0	0	0	0	0	0	0
	P	0.001	0.016	ns	ns	ns	ns	ns	ns	ns	ns
Semi-voltine	s	+	+	+	0	0	0	0	0	0	0
	P	0.026	0.047	0.043	ns	ns	ns	ns	ns	ns	ns
Substrate											
Erosional sediment	s	0	0	-	0	0	0	0	0	0	0
	P	ns	ns	0.001	ns	ns	ns	ns	ns	ns	ns
Erosional cobble	s	0	0	+	0	0	+	0	-	0	-
	P	ns	ns	0.001	ns	ns	0.001	ns	0.070	ns	0.005
Sand/silt	s	0	0	-	0	0	0	0	0	0	0
	P	ns	ns	0.005	ns	ns	ns	ns	ns	ns	ns
Leafpack	s	0	0	0	0	0	0	0	0	0	0
	P	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Feeding Group											
Collector gatherer	s	+	0	0	+	0	0	0	-	0	0
	P	0.014	ns	ns	0.007	ns	ns	ns	0.028	ns	ns
Collector filterer	s	+	0	0	-	0	0	0	0	0	0
	P	0.001	ns	ns	0.003	ns	ns	ns	ns	ns	ns
Grazer	s	-	0	+	-	0	+	0	0	0	-
	P	0.059	ns	0.047	0.020	ns	0.001	ns	ns	ns	0.001
Predator	s	0	0	-	0	0	0	0	0	0	0
	P	ns	ns	0.011	ns	ns	ns	ns	ns	ns	ns
Shredder	s	-	0	+	0	0	-	0	+	0	0
	P	0.019	ns	0.026	ns	ns	0.065	ns	0.053	ns	ns

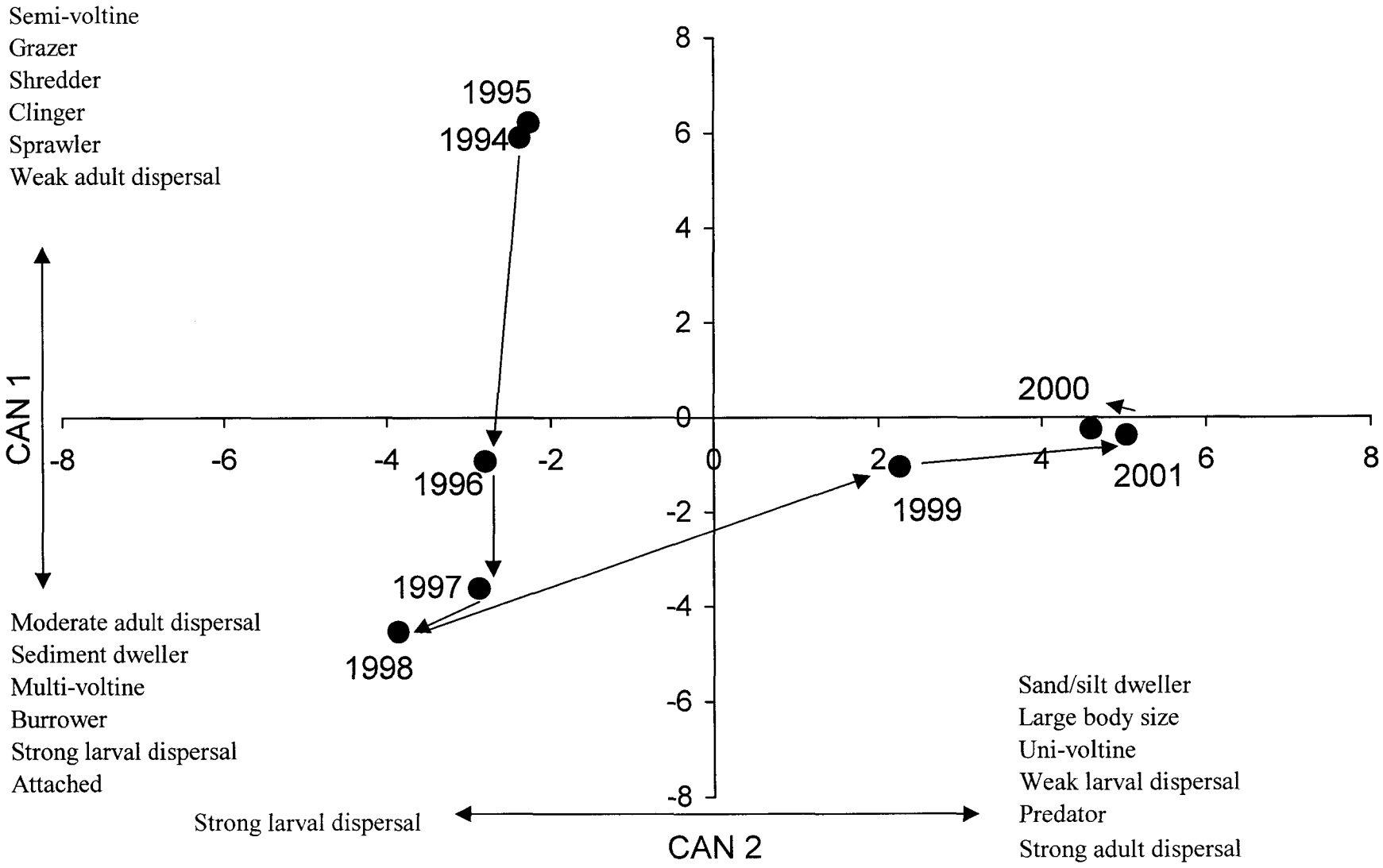
Table 2.6. Summary of canonical discriminant analysis for eight sample years in recently burned (Capulin) and historically burned (Frijoles) streams near Los Alamos, NM, defined in terms of densities of species traits. Taxa correlations with the first two canonical variables (CAN1 and CAN2) are presented for all traits with significant univariate statistics (all $F > 11.5$ and all $P < 0.0001$).

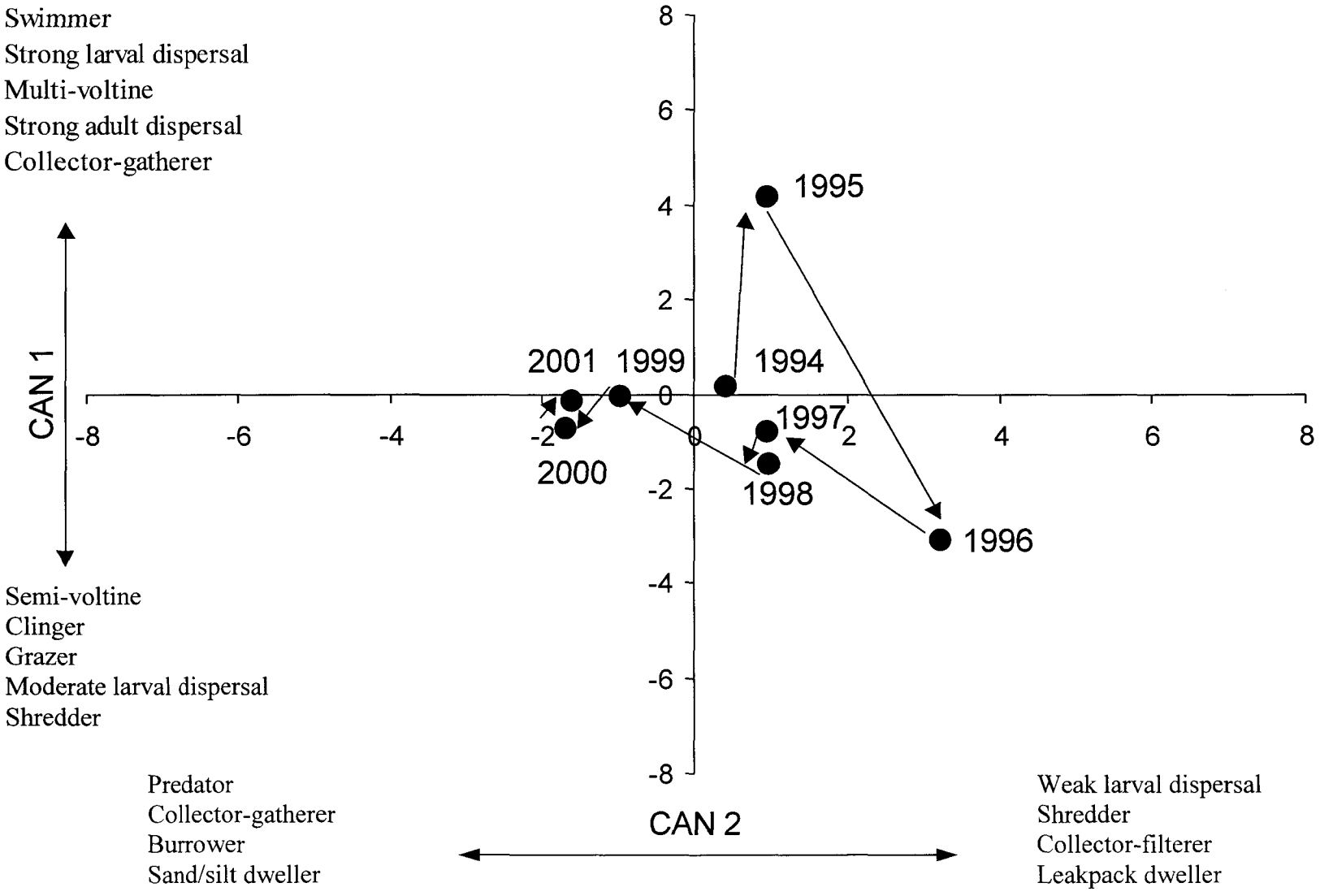
	CAPULIN		FRIJOLES	
TRAIT STATES	CAN1	CAN2	CAN1	CAN2
Collector-gatherer	0.19	0.20	0.44	-0.34
Grazer	0.74	0.57	-0.41	-0.13
Collector-filterer	-0.21	0.01	0.30	0.19
Shredder	0.73	0.06	-0.30	0.20
Predator	0.13	0.65	0.08	-0.34
Univoltine	0.47	0.66	0.14	0.06
Multivoltine	-0.27	-0.01	0.48	-0.02
Semivoltine	0.85	0.06	-0.50	-0.21
Swimmer	0.02	0.07	0.51	-0.09
Attached	-0.25	0.04	0.41	0.07
Burrower	-0.27	0.43	0.05	-0.27
Sprawler	0.53	0.46	-0.26	0.12
Clinger	0.72	0.57	-0.43	-0.19
Weak larval dispersal	0.48	0.65	0.02	0.27
Moderate larval dispersal	0.48	0.41	-0.31	-0.22
Strong larval dispersal	-0.25	-0.17	0.50	-0.10
Weak adult dispersal	0.50	0.20	-0.15	-0.16
Moderate adult dispersal	-0.36	0.24	0.28	0.07
Strong adult dispersal	0.36	0.62	0.45	-0.08
Sediment dweller	-0.31	0.45	0.18	-0.18
Cobble dweller	0.14	0.17	0.04	-0.14
Leakpack dweller	-0.12	-0.06	-0.09	0.15
Sand/silt dweller	-0.09	0.70	-0.01	-0.25
Low drag	0.09	0.04	-0.02	-0.14
High drag	0.35	0.59	0.32	-0.13
Small body size	0.07	0.03	-0.02	-0.12
Large body size	0.42	0.66	0.31	-0.12

LIST OF FIGURES









RESISTANT TRAITS

Habit	***Body Shape***	***Body size***	***Drag***	**TAXA EXAMPLES**
Swimmer*		Large	Low*	Baetidae, Orthocladiinae
Burrower*				*Simulium,Ceratopsyche*
Attached*				*Agabus*
Sprawler	(All)	Medium*	High	*Tricorythodes, Dicranota*
				Chelifera, Tanypodinae
Clinger*		Small	Moderate	Elmidae, *Sweltsa/Triznaka*
				Ephemerella , Glossosomatidae

DECREASING RESISTANCE TO WILDFIRE

RESILIENT TRAITS

Larval dispersal	***Adult dispersal***	***Voltinism***	***Substrate***	***Functional Feeding Group***	**TAXA EXAMPLES**
Strong*		Multi-voltine*	Sand/silt*	Collectors*	Baetidae, *Tricorythodes,Simulium*
	Strong*	Semi-voltine	Sediment*	Predators	*Agabus, Oplonaeschna*
Weak	Moderate*	Uni-voltine*			Glossosomatidae, *Tabanus*
					Rhabdomastix, Dicranota
	Weak*		Cobble*	Grazer*	*Epeorus, Helichus, Lepidostoma*
			Leafpack*	Shredder*	*Amphinemura banksi,* Elmidae

DECREASING RESILIENCE TO WILDFIRE

LIST OF APPENDICES

Appendix 2.1a-b. Presence/absence of 50 (Capulin) or 51 (Frijoles) taxa at 21 "locations" for each canyon, where locations were sampling periods conducted in the same stream segment in each canyon.

Appendix 2.2 – 2.10. Associations between species traits of aquatic insects that convey resistance (habit, body shape, drag, body size) and resilience (larval and adult dispersal ability, voltinism, substrate preferences, functional feeding modes) and environmental variables related to wildfire disturbance (time since fire and peakflow index) and season generated with the fourth-corner problem method with 9999 permutations. Overall model statistics are presented (F, G, and Chi2), as well as correlation (r), chi-squared statistics (D), and significance values (Prob) for each trait state-environmental variable combination. Cells significant at the *a priori* alpha = 0.1 are highlighted in bold. Results for recently (Capulin) and historically (Frijoles) burned canyons are also compared.

APP. 2.1a

CAPULIN (BURNED)	1994		1995			1996	1997			1998			1999			2000			2001		
SPECIES	1	2	1	2	3	1	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Ameletus sp.	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Baetis and Fallceon sp.	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ephemerella sp.	1	1	1	1	1	1	0	0	0	1	0	0	1	1	1	1	0	1	1	0	1
Epeorus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
Nixe and Cinygmula sp.	1	1	1	1	1	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0
Paraleptophlebia sp.	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1
Tricorythodes minutus	0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1
Siphlonurus sp.	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Amphinemura banksi	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	1	0	0	1	1
Capnia sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Sweltsa and Triznaka sp.	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1
Hesperoperla pacifica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoperla sp.	1	1	1	1	1	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1
Pteronarcella badia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agapetus sp.	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0
Glossosoma sp.	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0
Brachycentrus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Hesperophylax sp.	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	0	0
Ceratopsyche sp.	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidostoma sp.	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1
Ochrotrichia sp.	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	0	1	1	0	1	1
Oecetis sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0
Polycentropus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1
Rhyacophila sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tribe Chironomini	0	0	1	0	0	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
Tribe Tanytarsini	1	1	1	1	1	0	1	1	0	1	0	0	1	0	1	0	0	0	0	0	1
Tribe Orthocladiinae	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tribe Tanypodinae	1	0	1	1	0	0	1	1	0	1	0	0	1	1	1	1	1	1	0	1	0
Antocha sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
Caloparyphus sp.	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	1	0	0	1
Chelifera sp.	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1
Dicranota sp.	1	1	1	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	0	0	0
Dixa sp.	1	0	0	0	1	0	1	1	0	1	1	0	1	1	1	0	1	0	0	0	1
Hexatoma sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1
Maruina sp.	1	1	0	1	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	1
Limnophora aequifrons	0	1	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0
Hemerodromia sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	1
Palpomyia sp.	1	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	1	1	0	1
Pedicia sp.	1	0	0	0	0	0	0	1	0	1	1	0	1	1	0	1	1	0	1	0	0
Pericoma sp.	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1
Simulium sp.	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
Tipula sp.	0	1	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	1
Tabanus sp.	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
Rhabdomastix sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1
Oplonaeschna armata	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Argia sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Cordulegaster sp.	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1
Petrophila sp.	1	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0
Agabus sp.	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	0	0	0	0	0	1
Helichus striatus	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1
Narpus concolor	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Optioservus sp.	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	1	1
Zaitzevia parvula	1	1	1	1	1	1	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1

APP. 2.1b

FRIJOLES (UNBURNED)	1994		1995			1996	1997			1998			1999			2000			2001		
SPECIES	1	2	1	2	3	1	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Ameletus sp.	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0
Baetis and Fallceon sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ephemerella sp.	1	0	1	1	1	0	1	0	1	1	0	1	1	1	1	1	0	1	1	0	1
Epeorus sp.	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0
Nixe and Cinygmula sp.	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	1	0	0	1	1
Paraleptophlebia sp.	1	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Tricorythodes minutus	1	1	0	0	1	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	1
Siphlonurus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphinemura banksi	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1
Capnia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Sweltsa and Triznaka sp.	1	1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1
Hesperoperla pacifica	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Isoperla sp.	1	0	1	1	1	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1	0
Pteronarcella badia	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Agapetus sp.	1	0	1	1	0	0	1	1	0	1	1	0	1	1	0	1	0	0	0	0	0
Glossosoma sp.	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	1	1	0	1	0	0
Brachycentrus sp.	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
Hesperophylax sp.	0	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1
Ceratopsyche sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Lepidostoma sp.	1	1	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1
Ochrotrichia sp.	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	0	1	0
Oecetis sp.	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0
Polycentropus sp.	0	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1
Rhyacophila sp.	0	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	0	0	1	0	1
Tribe Chironomini	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tribe Tanytarsini	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0
Tribe Orthocladiinae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tribe Tanypodinae	1	1	0	0	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0	1	1
Antocha sp.	1	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	0	1
Caloparyphus sp.	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	1
Chelifera sp.	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	0	1	1	0
Dicranota sp.	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Dixa sp.	1	0	0	1	1	0	0	1	0	0	1	1	0	1	1	0	0	0	0	1	1
Hexatoma sp.	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1
Maruina sp.	1	1	0	0	0	0	1	0	0	1	1	0	1	1	1	1	0	0	1	0	0
Limnophora aequifrons	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hemerodromia sp.	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palpomyia sp.	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1
Pedicia sp.	1	0	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	0	0	1	0
Pericoma sp.	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Simulium sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tipula sp.	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	1	1
Tabanus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Rhabdomastix sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Oplonaeschna armata	0	1	1	1	0	1	0	1	1	1	1	1	0	0	0	0	1	1	0	1	1
Argia sp.	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0
Cordulegaster sp.	1	1	0	1	1	0	0	1	1	1	1	1	0	1	1	0	1	0	0	0	0
Petrophila sp.	1	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1
Agabus sp.	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Helichus striatus	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0
Narpus concolor	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0
Optioservus sp.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Zaitzevia parvula	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

APP. 2.2		BURNED STREAM						UNBURNED STREAM				
		swimmer	clinger	sprawler	attached	burrower		swimmer	clinger	sprawler	attached	burrower
Years since fire												
	r(i,j)	**-0.0493**	**0.1236**	**-0.0534**	-0.0066	**-0.0445**	*r(i,j)*	0.0111	**-0.0362**	0.0019	-0.0190	**0.0588**
	Prob	0.0413	0.0001	0.0370	0.3986	0.0661	*Prob*	0.3082	0.0431	0.4681	0.1133	0.0094
	F = 2.0532, P = 0.0002						F = 0.6376, P = 0.0580					
Peakflow												
	r(i,j)	**0.0541**	**-0.0597**	-0.0188	**0.0767**	-0.0133	*r(i,j)*	0.0199	-0.0368	0.0125	0.0129	0.0061
	Prob	0.0304	0.0226	0.2595	0.0012	0.3277	*Prob*	0.1786	0.0438	0.2860	0.2101	0.4024
	F = 1.3363, P = 0.0094						F = 0.2227, P= 0.4989					
Season												
	G = 7.4527, P (df = 8) = 0.0208						*G* = 7.1081, P (df = 8) = 0.0017					
	Chi2 = 7.2059, P (df = 8) = 0.0263						*Chi2* = 7.0522, P (df = 8) = 0.0018					
Spring	*D(i,j)*	**+22**	**+61**	43	**-14**	34	*D(i,j)*	23	**+97**	**-40**	29	29
	Moy	17.7081	55.0960	44.9751	20.0046	30.3316	*Moy*	21.6619	78.6477	46.9743	28.0123	26.9827
	Prob	0.0433	0.0927	0.3350	0.0019	0.1432	*Prob*	0.3378	0.0001	0.0163	0.3741	0.2793
Summer	*D(i,j)*	**-16**	61	49	24	**-28**	*D(i,j)*	22	**-81**	**+60**	32	29
	Moy	20.1721	62.7883	51.4495	22.8760	34.6222	*Moy*	24.7539	89.9277	53.7140	31.9879	30.8752
	Prob	0.0540	0.3749	0.2994	0.3815	0.0231	*Prob*	0.1389	0.0174	0.0336	0.6272	0.3037
Fall	*D(i,j)*	15	43	43	**+22**	29	*D(i,j)*	20	**-58**	41	23	23
	Moy	15.1198	47.1157	38.5754	17.1194	26.0462	*Moy*	18.5842	67.4246	40.3117	23.9998	23.1421
	Prob	0.5737	0.1735	0.1297	0.0103	0.1986	*Prob*	0.3232	0.0075	0.4791	0.3626	0.5616

APP. 2.3		BURNED STREAM					UNBURNED STREAM			
		fusiform	flattened	blocky	tubular		fusiform	flattened	blocky	tubular
Years since fire										
	r(i,j)	-0.0250	0.0408	0.0391	-0.0534	*r(i,j)*	0.0092	-0.0150	0.0050	0.0025
	Prob	0.1853	0.0980	0.0724	0.0295	*Prob*	0.3117	0.2280	0.3957	0.4547
	F = 0.7829, P = 0.1399					*F* = 0.0606, P = 0.8648				
Peakflow										
	r(i,j)	0.0378	0.0132	0.0006	-0.0311	*r(i,j)*	-0.0153	0.0064	0.0290	-0.0243
	Prob	0.0936	0.3284	0.5007	0.1355	*Prob*	0.2072	0.3760	0.0632	0.1206
	F = 0.3383, P = 0.5052					*F* = 0.2522, P = 0.3768				
Season										
	G = 4.0873, P (df = 6) = 0.1557					*G* = 3.7213, P (df = 6) = 0.0176				
	Chi2 = 4.1271, P (df = 6) = 0.1478					*Chi2* = 3.7453, P (df = 6) = 0.0171				
Spring	*D(i,j)*	17	28	47	85	*D(i,j)*	**+21**	**+47**	67	97
	Moy	13.3297	31.3527	47.9830	79.0757	*Moy*	15.3376	41.6332	66.7233	92.6440
	Prob	0.0474	0.1949	0.4469	0.1259	*Prob*	0.0003	0.0332	0.5244	0.1758
Summer	*D(i,j)*	11	40	51	81	*D(i,j)*	**-14**	49	75	102
	Moy	15.2315	35.6889	54.8401	90.2741	*Moy*	17.5111	47.6488	76.1470	105.8934
	Prob	0.0263	0.1275	0.1750	0.0334	*Prob*	0.0199	0.3805	0.4225	0.2173
Fall	*D(i,j)*	12	26	46	71	*D(i,j)*	11	**-29**	58	79
	Moy	11.4388	26.9584	41.1769	67.6502	*Moy*	13.1513	35.7180	57.1297	79.4626
	Prob	0.4833	0.4446	0.0973	0.2609	*Prob*	0.1192	0.0072	0.4499	0.5022

APP. 2.4		BURNED STREAM Drag low	moderate	high		UNBURNED STREAM Drag low	moderate	high
Years since fire								
	r(i,j)	0.0321	-0.0074	-0.0316	*r(i,j)*	-0.0021	0.0122	-0.0113
	Prob	0.1417	0.4071	0.1448	*Prob*	0.4594	0.2959	0.2876
	F= 0.3340, P = 0.4816				*F*= 0.0619, P = 0.7963			
Peakflow								
	r(i,j)	**0.0754**	**-0.0794**	-0.0048	*r(i,j)*	0.0129	-0.0238	0.0113
	Prob	0.0040	0.0047	0.4341	*Prob*	0.2746	0.1385	0.2876
	F = 1.8452, P= 0.0153				*F* = 0.1748, P= 0.5203			
Season								
	G = 2.9365, P (df = 4) = 0.1672				*G* = 2.6815, P (df = 4) = 0.0431			
	Chi2 = 2.9998, P (df = 4) = 0.1565				*Chi2* = 2.6640, P (df = 4) = 0.0436			
Spring	*D(i,j)*	88	54	32	*D(i,j)*	101	**+75**	42
	Moy	86.4214	47.3602	34.3338	*Moy*	95.9919	63.2923	42.9947
	Prob	0.4103	0.0639	0.2841	*Prob*	0.1385	0.0009	0.4273
Summer	*D(i,j)*	97	47	34	*D(i,j)*	110	**-62**	52
	Moy	98.6216	54.0501	39.2364	*Moy*	109.7081	72.3844	49.1662
	Prob	0.4075	0.0577	0.0716	*Prob*	0.5179	0.0039	0.1921
Fall	*D(i,j)*	74	41	37	*D(i,j)*	77	53	35
	Moy	73.9570	40.5897	29.4298	*Moy*	82.3000	54.3233	36.8391
	Prob	0.5399	0.5101	0.0101	*Prob*	0.1141	0.4068	0.2930

APP. 2.5		BURNED STREAM Body Size small	medium	large		UNBURNED STREAM Body Size small	medium	large
Years since fire								
	r(i,j)	**0.0433**	0.0073	**-0.0651**	*r(i,j)*	-0.0137	-0.0002	0.0169
	Prob	0.0755	0.4100	0.0111	*Prob*	0.2578	0.5013	0.1999
	F= 1.1049, P = 0.0831				*F*= 0.0999, P = 0.6866			
Peakflow								
	r(i,j)	0.0347	-0.0368	-0.0005	*r(i,j)*	0.0116	**-0.0430**	**0.0359**
	Prob	0.1130	0.1201	0.4908	*Prob*	0.2917	0.0275	0.0311
	F = 0.3820, P= 0.4201				*F* = 0.6989, P= 0.0741			
Season								
	G = 2.5587, P (df = 4) = 0.2149				*G* = 4.5686, P (df = 4) = 0.0027			
	Chi2 = 2.6121, P (df = 4) = 0.2058				*Chi2* = 4.5799, P (df = 4) = 0.0023			
Spring	*D(i,j)*	84	61	29	*D(i,j)*	92	**+86**	40
	Moy	84.4079	53.7159	29.9916	*Moy*	90.3276	69.2902	42.6611
	Prob	0.5076	0.0643	0.4320	*Prob*	0.3866	0.0001	0.1989
Summer	*D(i,j)*	95	54	29	*D(i,j)*	105	**-68**	51
	Moy	96.3659	61.2323	34.3099	*Moy*	103.2442	79.2354	48.7791
	Prob	0.4270	0.0683	0.0499	*Prob*	0.3812	0.0028	0.2465
Fall	*D(i,j)*	74	46	32	*D(i,j)*	74	**-54**	37
	Moy	72.2262	46.0518	25.6985	*Moy*	77.4282	59.4744	36.5598
	Prob	0.3893	0.5387	0.0170	*Prob*	0.2225	0.0871	0.5089

APP. 2.6		BURNED STREAM Larval Dispersal Ability				UNBURNED STREAM Larval Dispersal Ability		
		poor	moderate	strong		poor	moderate	strong
Years since fire								
	r(i,j)	-0.0019	0.0127	-0.0194	*r(i,j)*	-0.0071	0.0090	-0.0036
	Prob	0.4750	0.3274	0.1418	*Prob*	0.3706	0.3335	0.2686
	F = 0.1099, P = 0.6743				*F* = 0.0249, P = 0.7633			
Peakflow								
	r(i,j)	**-0.1012**	**0.0742**	**0.0500**	*r(i,j)*	**-0.0450**	**0.0377**	**0.0146**
	Prob	0.0002	0.0048	0.0043	*Prob*	0.0200	0.0380	0.0070
	F = 2.7087, P= 0.0008				*F* = 0.6145, P = 0.0443			
Season								
	G = 1.8859, P (df =4) = 0.1831				*G* = 0.5661, P (df =4) = 0.4156			
	Chi2 = 1.8928, P (df = 4) = 0.1810				*Chi2* = 0.5645, P (df = 4) = 0.4167			
Spring	*D(i,j)*	82	76	16	*D(i,j)*	107	97	14
	Moy	81.3135	72.7977	14.0042	*Moy*	96.6568	91.6221	14.0000
	Prob	0.4816	0.2577	0.0869	*Prob*	0.0152	0.1076	1.0000
Summer	*D(i,j)*	82	82	14	*D(i,j)*	103	105	16
	Moy	92.9232	82.9907	15.9942	*Moy*	110.4835	104.7752	16.0000
	Prob	0.0297	0.4504	0.0952	*Prob*	0.0723	0.5306	1.0000
Fall	*D(i,j)*	80	60	12	*D(i,j)*	80	73	12
	Moy	69.7633	62.2116	12.0016	*Moy*	82.8597	78.6027	12.0000
	Prob	0.0300	0.3323	0.6768	*Prob*	0.3003	0.0891	1.0000

APP. 2.7		BURNED STREAM Adult Dispersal Ability poor	moderate	strong		UNBURNED STREAM Adult Dispersal Ability poor	moderate	strong
Years since fire								
	r(i,j)	**0.0535**	-0.0182	**-0.0566**	*r(i,j)*	-0.0046	0.0103	-0.0111
	Prob	0.0340	0.2696	0.0123	*Prob*	0.4228	0.3198	0.2897
	F= 1.1529, P = 0.0488				*F*= 0.0529, P = 0.8170			
Peakflow								
	r(i,j)	0.0102	**-0.0563**	**0.0730**	*r(i,j)*	-0.0140	-0.0104	**0.0457**
	Prob	0.3529	0.0277	0.0023	*Prob*	0.2549	0.3138	0.0090
	F = 1.6670, P= 0.0135				*F* = 0.6364, P= 0.0849			
Season								
	G = 0.8106, P (df = 4) = 0.7134				*G* = 2.0609, P (df = 4) = 0.1009			
	Chi2 = 0.8089, P (df = 4) = 0.7104				*Chi2* = 2.001, P (df = 4) = 0.1085			
Spring	*D(i,j)*	78	79	17	*D(i,j)*	85	121	12
	Moy	77.4139	72.3344	18.3671	*Moy*	76.2920	110.9822	15.0047
	Prob	0.4953	0.0895	0.3316	*Prob*	0.0206	0.0154	0.0499
Summer	*D(i,j)*	82	75	21	*D(i,j)*	83	123	18
	Moy	88.2632	82.7040	20.9409	*Moy*	87.2523	126.8741	17.1323
	Prob	0.1211	0.0601	0.5876	*Prob*	0.1864	0.2236	0.4093
Fall	*D(i,j)*	72	63	17	*D(i,j)*	61	89	15
	Moy	66.3229	61.9616	15.6920	*Moy*	65.4557	95.1437	12.8630
	Prob	0.1287	0.4514	0.3343	*Prob*	0.1520	0.0913	0.1345

APP. 2.8		BURNED STREAM				UNBURNED STREAM		
		Bi/multi voltine	Uni voltine	Semi voltine		Bi/multi voltine	Uni voltine	Semi voltine
Years since fire								
	r(i,j)	-0.0519	0.0084	0.0513	*r(i,j)*	-0.0087	0.0167	-0.0119
	Prob	0.0164	0.3803	0.0431	*Prob*	0.3136	0.1937	0.2525
	F=1.0946, P = 0.0.0572				*F* = 0.0855, P = 0.6478			
PeakFlow								
	r(i,j)	**0.0671**	**-0.0982**	**0.0555**	*r(i,j)*	**0.0234**	**-0.0431**	**0.0299**
	Prob	0.0023	0.0001	0.0263	*Prob*	0.0902	0.0157	0.0473
	F = 2.4410, P = 0.0007				*F* = 0.5686, P = 0.0572			
Season								
	G = 1.7401, P (df=4) = 0.2888				*G* = 1.4575, P (df=4) = 0.1149			
	Chi2 = 1.7504, P (df = 4) = 0.2855				*Chi2* = 1.4503, P (df = 4) = 0.1163			
Spring	*D(i,j)*	39	113	22	*D(i,j)*	39	141	38
	Moy	36.7043	107.0451	24.3660	*Moy*	39.9874	124.6543	37.6372
	Prob	0.2210	0.1795	0.2317	*Prob*	0.4037	0.0012	0.5248
Summer	*D(i,j)*	40	108	30	*D(i,j)*	47	133	44
	Moy	41.9031	122.2087	27.7963	*Moy*	45.7259	142.4789	43.0539
	Prob	0.2827	0.0111	0.2572	*Prob*	0.3581	0.0522	0.4171
Fall	*D(i,j)*	31	100	21	*D(i,j)*	34	100	31
	Moy	31.3926	91.7462	20.8377	*Moy*	34.2867	106.8668	32.3089
	Prob	0.5161	0.0874	0.5584	*Prob*	0.5350	0.1071	0.3397

APP. 2.9		BURNED STREAM					UNBURNED STREAM			
		sediment	cobble	sand/silt	leafpack		sediment	cobble	sand/silt	leafpack
Years since fire										
	r(i,j)	**-0.0904**	**0.1098**	**-0.0882**	0.0023	*r(i,j)*	-0.01033	-0.0326	0.01247	0.03991
	Prob	0.0008	0.0001	0.0051	0.4640	*Prob*	0.3224	0.067	0.3213	0.0397
	F = 3.4590, P = 0.0001					*F* = 0.3807, P = 0.3433				
Peakflow										
	r(i,j)	0.0566	-0.0035	-0.0273	-0.0319	*r(i,j)*	-0.00221	-0.0211	0.04999	0.00542
	Prob	0.0245	0.4621	0.2264	0.1370	*Prob*	0.4575	0.1713	0.0346	0.4094
	F = 0.6738, P = 0.2499					*F* = 115.59, P = 0.4415				
Season										
	G = 1.8247, P (df = 6) = 0.7084					*G* = 4.1262, P (df = 6) = 0.0641				
	Chi2 = 1.7997, P (df = 6) = 0.7132					*Chi2* = 4.0615, P (df = 6) = 0.0632				
Spring	*D(i,j)*	35	78	10	51	*D(i,j)*	35	**+126**	5	52
	Moy	32.4069	79.1190	9.3377	47.2518	*Moy*	31.9377	108.33	6.6629	55.3481
	Prob	0.2328	0.4480	0.4646	0.1904	*Prob*	0.1513	0.0001	0.2002	0.2050
Summer	*D(i,j)*	36	87	8	47	*D(i,j)*	34	**-117**	8	65
	Moy	36.8906	90.2134	10.6539	54.1502	*Moy*	36.5939	123.807	7.608	63.25
	Prob	0.4540	0.2812	0.1457	0.0469	*Prob*	0.2119	0.0703	0.5307	0.3642
Fall	*D(i,j)*	26	72	10	44	*D(i,j)*	27	**-82**	7	49
	Moy	27.7025	67.6676	8.0084	40.5980	*Moy*	27.4684	92.863	5.7291	47.4019
	Prob	0.3301	0.1832	0.2132	0.2053	*Prob*	0.5071	0.0053	0.2811	0.3746

APP. 2.10		BURNED STREAM						UNBURNED STREAM				
		C-gatherer	C-filterer	Grazer	Predator	Shredder		C-gatherer	C-filterer	Grazer	Predator	Shredder
Years since fire												
	r(i,j)	-0.0232	0.0179	**0.0509**	**-0.0688**	**0.0620**	*r(i,j)*	**0.0484**	**-0.0382**	**-0.0504**	0.0093	0.0114
	Prob	0.2067	0.1998	0.0465	0.0116	0.0255	*Prob*	0.0092	0.0034	0.0199	0.3484	0.2761
	F=1.1841, P = 0.0216						*F* = 0.8016, P = 0.0178					
Peakflow												
	r(i,j)	**0.0641**	**0.0759**	**-0.0471**	-0.0304	**-0.0660**	*r(i,j)*	0.0341	0.0135	-0.0310	-0.0202	0.0010
	Prob	0.0137	0.0003	0.0587	0.1548	0.0186	*Prob*	0.0448	0.1740	0.0985	0.1940	0.4829
	F = 1.8336, P = 0.0013						*F* = 0.3155, P = 0.2693					
Season												
	G = 4.0396, P (df = 8) = 0.2633						*G* = 10.8683, P (df = 8) = 0.0001					
	Chi2 = 4.0249, P (df = 8) = 0.2619						*Chi2* = 10.0564, P (df = 8) = 0.0001					
Spring	*D(i,j)*	51	17	30	59	17	*D(i,j)*	62	26	**+39**	66	**-25**
	Moy	47.7132	17.0051	30.0516	57.3768	15.9687	*Moy*	58.3495	24.6692	28.9640	61.9556	28.3406
	Prob	0.2132	0.6341	0.5552	0.3976	0.4131	*Prob*	0.1437	0.2595	0.0002	0.1792	0.0646
Summer	*D(i,j)*	47	18	39	59	15	*D(i,j)*	**-60**	27	35	66	**+36**
	Moy	54.4408	19.4516	34.2232	65.4930	18.2995	*Moy*	66.6620	28.1826	33.1600	70.8937	32.3604
	Prob	0.0279	0.2588	0.0877	0.0855	0.1188	*Prob*	0.0277	0.2980	0.3178	0.1348	0.0531
Fall	*D(i,j)*	45	16	21	54	16	*D(i,j)*	53	21	**-13**	54	24
	Moy	40.8460	14.5433	25.7252	49.1302	13.7318	*Moy*	49.9885	21.1482	24.8760	53.1507	24.2990
	Prob	0.1355	0.2427	0.0739	0.1420	0.2141	*Prob*	0.1988	0.6052	0.0001	0.4589	0.5411

CHAPTER 3

INSECT COMMUNITY RESPONSES TO AN EXPERIMENTAL DISTURBANCE IN STREAMS ACROSS A GRADIENT OF WILDFIRE HISTORY

ABSTRACT

Wildfire disturbance can alter composition of stream insect communities in burned watersheds, which may impact community resilience to future disturbances. In this research, I compared the impacts of an experimental disturbance on insect communities in streams across a gradient of fire disturbance history. Specifically, I compared resilience among two streams burned in a 1996 wildfire, two streams burned in a 1977 wildfire, and two unburned streams. I compared total density, taxa richness, and community composition on individual cobbles 0, 2, 4, 16, and 42 d after cobbles were physically disturbed (scoured with brushes). I expected communities in recently burned streams to be most resilient to the experimental disturbance due to having a higher proportion of disturbance-tolerant and quick colonizing taxa. Patterns of resilience were related to a gradient of fire history, where insect communities in recently burned streams recovered more quickly than communities in unburned streams. Taxa that were abundant in drift were important colonists in recently burned streams, and in general, taxa with traits that convey resilience (multi-voltinism, strong larval dispersal, generalist feeding strategies) were early colonists in all streams regardless of fire history (i.e. Baetidae and Chironomidae). This study demonstrates that wildfire and post-fire flooding can have lasting effects on community composition, and suggests that post-disturbance communities are more resilient to further disturbance.

INTRODUCTION

Physical disturbances such as changes in intensity, frequency, duration and predictability of hydrologic events (Poff and Ward 1989; Poff 1992), and associated changes in substrate stability (Death and Winterbourn 1995; Townsend et al. 1997a), influence insect communities in streams (Resh et al. 1988; Reice et al. 1990). Community resistance (magnitude of change compared to pre-disturbance communities) to a disturbance depends on the degree to which mortality or displacement of individuals and populations occur (sensu Sousa 1984). Highly resistant communities are comprised of species that can avoid a disturbance (i.e. through emergence) or have physical (i.e. small body size) and behavioral (i.e. use of hyporheic zone) attributes that allow them to utilize in-stream refugia (Palmer et al. 1992; Lancaster and Hildrew 1993; Lake 2000; Lytle 2002). Community resilience (rate of "recovery" to pre-disturbance communities) depends on whether survivors can tolerate post-disturbance conditions, and also on species-specific dispersal abilities given the proximity of colonist sources (Gray and Fisher 1981; Cushing and Gaines 1989; Boulton et al. 1992).

Insect community responses to disturbance are constrained by whether species with necessary recovery mechanisms (population attributes such as life-history, morphological, behavioral traits) have been previously selected for under the historical disturbance regime (Poff and Ward 1990; Poff 1997). Further, the proportion

of species with resilient or resistant traits in a community should correspond to gradients of environmental variation within or among streams (Townsend 1989; Poff and Ward 1990; Poff 1992; Townsend et al. 1997b). For instance, Poff and Allan (1995) found that silt-tolerant fish species that were resource generalists dominated hydrologically unstable streams. Others have found insect taxa with streamlined/flattened bodies and the ability to attach to substrate (conveying resistance), and with strong larval or adult mobility, small size, and generalist resource use (conveying resilience), in streams where flooding was more recent and severe (Townsend et al. 1997b; Chapter 1; Chapter 2). These studies fit predictions that species with strong recovery mechanisms dominate communities in disturbance-prone environments (Resh et al. 1988; Reice et al. 1990; Poff 1992).

If communities in disturbance-prone streams have more species with resistant and resilient traits compared to those in historically stable streams, these communities should also show faster recovery after further disturbance. However, testing this hypothesis has often proven difficult. Gradients of historical disturbance regimes are often too subtle to produce strong variation in community composition (Feminella 1996) or in resistant and resilient trait representation in communities among streams (Rosser and Pearson 1995; Miller and Golladay 1996). Disturbance histories that include large-scale or severe perturbations (e.g. Scrimgeour et al. 1988; see reviews in Yount and Niemi 1990; Niemi et al. 1990; Chapter 1) create stronger environmental gradients and thus more variation in community structure. In particular, wildfires and post-fire flooding alter insect communities (Rinne 1996; see Gresswell 1999 for review; Chapter 1) such that composition shifts from specialist to generalist taxa (Minshall et al. 1997), and from

longer-lived taxa with weak dispersal abilities to multi-voltine taxa with strong dispersal abilities (Chapter 1; Chapter 2). Given increases in taxa with strong recovery mechanisms in recently burned streams, community resilience to further disturbance should correspond to a gradient of fire disturbance history.

Two large-scale wildfires (the 1977 La Mesa and 1996 Dome fires) on the Pajarito Plateau, north central New Mexico, provided an excellent opportunity to compare communities in streams that differ in fire history. These wildfires resulted in multiple 100-year flash flood events, followed by dampened but elevated floods for up to three years in burned streams (Veenhuis 2002). Major alterations to stream channel and bed substrate (Reneau et al. 1999; Cannon and Reneau 2000) and severe impacts on insect communities (> 98 % reduction in total density) were documented after these floods in a stream burned in the Dome fire (Chapter 1). Further, marked changes in composition (Chapter 1) and trait representation (Chapter 2) between pre- and post-fire communities were documented in the same burned stream. In this study, I compared communities associated with cobble substrate across streams that differed in post-fire recovery time. Specifically, I compared communities in two streams burned in 1996, in two streams burned twenty years prior (1977), and in two unburned streams (no history of fire in the 1900's). I also tested whether community resilience to an experimental disturbance corresponded to this wildfire history gradient.

Previously, I demonstrated that taxa with resistant and resilient traits were early colonists in a burned stream after the 1996 Dome fire, while taxa with poorly resistant or

resilient traits did not recover (Chapter 2). Patterns between post-fire recovery time and resilience traits in Chapter 2 were used to predict representation of resilient traits in cobble-associated communities along a gradient of fire history. Specifically, I expected a higher proportion of strong larval dispersers and thus higher drift rates in recently burned streams compared to unburned streams. I also predicted that recently burned streams would have taxa that were multi-voltine, generalist feeders (i.e. collectors), and strong adult dispersers. In contrast, communities in unburned streams were expected to have taxa with weaker dispersal abilities, semi-voltine lifecycles, and specialist feeding strategies. Given predicted differences in representation of resilient traits, I expected that resilience of total insect density, taxa richness, and community composition to experimental disturbance would increase from unburned to recently burned streams.

STUDY SITE DESCRIPTION

This study was conducted in streams that drain six canyons of the Pajarito Plateau located in Bandelier National Monument and Santa Fe National Forest, near Los Alamos, New Mexico (Figure 3.1). The Pajarito Plateau was created when pyroclastic ashflows from pre-historic volcanic eruptions left tuff deposits up to 300 m thick along the east flank of the Sierra de los Valles. Currently, the Plateau slopes towards the Rio Grande River in a series of canyons and mesas that have been carved into the rheolitic tuff by erosion. Riparian vegetation in these canyons consists primarily of Western box elder (*Acer negundo*), narrowleaf cottonwood (*Populus angustifolia*), alder (*Alnus oblongifolia*), and ponderosa pine (*Pinus ponderosa*). The six streams in this study are first order in size and are spring fed at high elevations (2500-3500 m), have perennial

reaches at mid-elevations (2000 -2500 m), have no perennial tributaries, and are typically disconnected from the mainstem of the Rio Grande River by ephemeral reaches (with the exception of the stream in Frijoles canyon). The six streams differed in length of perennial reaches and average baseflow (Table 3.1).

The Plateau has a semiarid mountain climate, with mean annual precipitation ranging from 33-46 cm. Hydroclimatology (sensu Poff and Ward 1989) for all Pajarito Plateau canyons are snowmelt driven in mid-spring and show flashy responses to monsoonal precipitation events in summer. Localized and intense convectional thunderstorms occur from July through September and contribute more than half of the annual rainfall (Purtymun and Adams 1980). These storms can result in flash floods in one Pajarito stream but not in adjacent streams. Flash floods occur when in-stream sediment dams are created from erosion during intense rain events and then break, releasing large volumes of stored water downstream. While the monsoon season creates spatial and intra-seasonal variation in peakflows among Pajarito canyons, inter-annual differences in streamflow are driven by winter snowmelt and spring precipitation from large-scale frontal storms. Cyclic El Niño climate events bring increased spring and summer precipitation approximately every four years (Andrade and Sellers 1988). Thus, changes in baseflow across years are more similar among canyons.

Wildfire has played a central role in the Pajarito Plateau ecosystem. High-frequency, low-intensity fires have been replaced by low-frequency, high-intensity canopy fires due to increases in fuel load through fire suppression and grazing (Touchan

et al. 1996). The six streams in this study differ along a gradient of wildfire history (Table 3.1). The La Mesa fire of 1977 burned 62 km^2 on the eastern side of Plateau, including Frijoles canyon and portions of Alamo canyon (Figure 3.2). The 1996 Dome fire burned over 65 km^2 of the Pajarito Plateau, including several middle canyons (Capulin and Sanchez). Despite differences in spatial extent and intensity, the La Mesa and Dome fires resulted in similar 100-year flash floods events that scoured the entire perennial segments of Frijoles and Capulin streams (Cannon and Reneau 2000; Veenhuis 2002). Historical (before 1900's) severe flood events in Plateau streams have also been found to correspond to wildfires (McCord 1996). At the time of this study, northeastern (Guaje) and southwestern (Cochiti) canyons had not been burned in a wildfire or severely flooded during the 1900's.

METHODS

I selected two streams burned in 1996 (Capulin and Sanchez, hereafter referred to as C1996 and S1996), two streams burned in 1977 (Alamo and Frijoles, referred to as A1977 and F1977), and two unburned streams (Guaje and Cochiti, referred to as G1900 and C1900). Five study sites between 2000 and 2500 m elevation were located in five separate riffles in the perennial segment of each stream. These sites were selected in a random-stratified manner from all potential riffles that had cobble substrate and were at least 50 m apart. Physicochemical measurements were collected at each site at least once during the study. Measurements included conductivity (μS), pH, alkalinity and hardness (as mg/L CaCO3), temperature (C°), dissolved oxygen (mg/L; Winkler Titration Kit),

current velocity (m/s), substrate composition (relative % of sand, cobble, and boulder substrate), and stream depth (cm) at each site. Current velocity and depth were taken at three points on a randomly placed transect across each riffle. Substrate composition of experimental sites was qualitatively assessed by visual inspection, using the same observer to reduce bias between sites.

In late May 1999, 20 cobbles that were similar in size (fist-sized), shape (rounded) and texture (smooth with minimal pockmarking) were collected from each of the five study sites in each stream. For the flood disturbance treatment, each cobble was scoured with a stiff wire brush to reduce periphyton biomass and to remove insects. Any remaining insects were removed with forceps. I wrapped each cobble in aluminum foil and then estimated surface area from the foil weight with an independently determined weight-to-surface area regression (Reice 1980). To expand the spatial scale of the disturbance and to reduce immediate sources of colonists, I removed all non-experimental cobbles and physically disturbed smaller substrate (i.e. sand) within 4-m^2 patches of streambed (Figure 3.3). This disturbance was modeled after a post-fire flash flood of 2.8 m^3/s (approx. 2–yr. flood; Veenhuis 2002) that I observed in a burned canyon. During this flood, high sediment loads and flood stages between 0.5 -1.0 m tumbled and scoured large substrates (i.e. boulders), and insects and algal biomass were greatly reduced on cobbles immediately following the flood (N. K. M. Vieira, unpublished data).

Scoured cobbles were numbered with a yellow (non-toxic) water-resistant crayon and were arranged into 4 x 5 grids in the center of each of these 4-m^2 disturbed areas

(Figure 3.3). Cobbles in each of the grids were assigned to the following "time since disturbance" treatments: 2, 4, 16, or 42 days of colonization. On each day, I randomly sampled one cobble from each row per grid (n = 4 cobbles per grid; n = 20 per stream). I sampled grids, and rows within the grid, moving in a downstream to upstream direction to minimize disturbance to unsampled grids or rows. To determine community composition on naturally occurring cobbles among canyons, I also selected four cobbles near each of the five grids (n = 20 per stream) both before (t = 0 d) and after (t = 43 d) the experiment. Naturally occurring cobbles were randomly selected from all cobbles that were minimally imbedded such that at least 75% of their surface area was exposed to streamflow. Communities on 0-d natural cobbles were compared to communities on experimental cobble samples to determine recovery after the manipulated disturbance. Communities on experimental cobbles at 42 d were also compared to communities on natural 43-d cobbles.

To collect natural and experimental cobbles, an individual cobble was placed in a 250-μm dipnet located immediately downstream and then transferred to a bucket. This sampling technique largely collected insects on a cobble, but also sampled insects associated with sediments and detritus underneath cobbles. Insects were removed with a soft-bristle brush and forceps, elutriated into a 250-μm sieve, and preserved in vials with 80% ethanol. After sampling, experimental cobbles were placed back in their grid position to maintain a constant cobble density throughout the remainder of the study. These cobbles were marked with a non-toxic red crayon to avoid re-sampling. The study was terminated on July 15, 1999 before the summer monsoon season.

To investigate drift as a colonist source, I collected three drift samples (500- μm mesh) for one hour after dusk (8:15 p.m. - 9:15 p.m.) in each stream. Mean drift rates were calculated to determine the abundance of insects drifting into experimental sites. Since the total number of drifting insect colonists was deemed more relevant to community resilience than a per volume density of insects, drift rates were not adjusted by stream discharge. Drift samples were collected before t = 0 d with the exception of G1900, which could not be sampled until t = 43 d. All invertebrate samples were sorted by order, and then identified to the lowest taxonomic resolution possible with a dissection microscope.

Statistical Analysis

Statistical analyses were conducted with use of SAS/STAT statistical software (SAS Institute 1996). Significance of statistical tests was interpreted based on an *a priori* alpha level of 0.05. Descriptive statistics were generated to compare mean physical and chemical characteristics among streams, and to compare mean total insect density, densities for each insect taxa, and taxa richness among "time since disturbance" treatments within streams. Individual cobbles were used to calculate descriptive statistics to best reflect variation among sample units. This was considered appropriate since the experimental disturbance was applied to, and the "time since disturbance" treatment was randomly allocated to, individual cobbles. As an extra measure to check that cobble sizes

were similar between canyons, I employed a one-way analysis of variance (ANOVA) model to test the main effects of stream on cobble surface area. I also investigated relationships between cobble surface area and both total insect density and taxa richness for each canyon with Pearson product-moment correlation coefficients. Assumptions for parametric tests were checked with residual plots and with diagnostic tests (Ott 1993).

I employed canonical discriminant analysis (CDA) to compare representation of resilient population attributes on natural 0-d cobbles among canyons. CDA is a descriptive, dimension-reducing multivariate technique that constructs linear combinations of independent variables (species traits) to maximize separation between pre-assigned groups (canyons). For this study, I chose traits that were a) previously associated with recovery in a burned stream (Chapter 2), b) appropriate for communities on cobbles, and c) associated with resilience to hydrologic disturbance. These traits included larval and adult dispersal, voltinism, and functional feeding modes. Taxa associated with silt and erosional sediments (Chapter 2), but which also utilize cobbles, were coded as "silt tolerant". Resistant traits were not considered since I removed all insects on experimental cobbles at the beginning of the study (thus resistance = 0 for all streams). Trait representation was expressed as a proportion to better compare streams. Analyses were conducted using both the proportion of individuals (# of individuals with a trait/total insect density) and the proportion of taxa (# of taxa with a trait/taxa richness).

To investigate resilience of community composition to the experimental disturbance, I calculated the proportional change ($[X_{0mean} - X_i] / X_{0mean}$) in total insect

density and taxa richness compared to levels on natural 0-d cobbles (X_{0mean}) for each cobble at each sample period "i" (experimental cobbles: i = 2, 4, 16, 42; natural cobbles i = 43). Mean proportional changes (± 1SE) were plotted to visually compare responses across streams at the same scale. Resilience was also measured by comparing changes in community composition after the experimental disturbance for each stream with the following proportional similarity index (PSI) (Wolda 1981):

$$PSI = 1 - 0.5*(\sum | p_{0i} - p_{ti} |) \qquad \text{(Eq. 1)}$$

where p_{0i} and p_{ti} are the relative proportions of total abundance (p) for each species (i) at t = 0 d and for all times "t" = 2, 4, 16, 42, 43. For each stream, proportions at t = 0 (p_{0i}) were expressed as a single mean density for each species calculated across all natural cobbles, while p_{ti} proportions were densities of each species on each individual cobble. PSI scores range from 0 (no species in common) to 1 (identity and relative abundance of species are identical).

I employed mixed- effects nested ANOVA's with repeated measures to investigate whether total insect density, taxa richness, and PSI measures differed across time treatments, fire history, and canyons nested within fire history. I also included two-way interactions and random effects of grids nested within canyons and fire history in all models. To better meet the assumption of independence of error terms (Ott 1993), data from individual cobbles were averaged for each grid and grids were considered as replicates. This conservative sample size (n = 5 per canyon per sample period) accounted

for the fact that while individual cobbles received the experimental treatment, adjacent cobbles were close enough in proximity for their communities to interact. Since sample periods (days) were repeated measures at the grid level, a correction for autoregression was performed in all models.

To investigate the importance of drifting insects on community resilience, I compared mean drift abundance, taxa richness, and % Baetidae using descriptive statistics. I also graphically compared relative densities of dominant taxa (taxa that represented > 5% of total density) on 0-d natural cobbles to dominant taxa on 2-d experimental cobbles and in drift samples. To compare differences in community composition between cobbles and drift, I calculated PSI values between 0-d and 2-d cobbles and between 2-d cobbles and drift samples. Due to the different sampling techniques and sample sizes between cobbles and drift samples, I calculated a single mean density for each taxa across all 0 d or 2 d cobbles (n = 16-20), and across all drift samples (n = 3). I used these overall means to calculate a single PSI value (lacking variability estimates) to represent 0 d, 2 d, and drift samples.

RESULTS

In total, 720 cobbles were sampled throughout the study. Mean densities for each taxa on experimental and natural cobbles for all streams are presented in Appendix 3.1a-f. Sample sizes for statistical analysis ranged from 16 - 20 cobbles per sample period per stream (see Appendix 3.1a-f) because a few sample were lost. Cobble surface area

varied little (mean = 0.04 m^2 and SD = 0.007 m^2) and was similar among streams (overall ANOVA model $F_{df=5} = 2.19$; $P = 0.0886$). Cobble surface area was not significantly correlated with total insect density or taxa richness for any of the six streams or for any sample period within each stream (Pearson product-moment correlation coefficients r = -0.18 to 0.10; all $P > 0.20$).

Physical and chemical characteristics varied among streams, but did not show clear differences along a fire history gradient. Point estimates of water temperature showed a slight trend with fire history, where streams burned in 1996 were warmest, streams not burned since 1900 were coolest, and temperatures for streams burned in 1977 were intermediate (Table 3.2). Conductivity and % cobble substrate were highest in recently burned streams, but varied among the other four streams irrespective of fire history (Table 3.2). For instance, conductivity was higher in streams with longer perennial reaches (F1977 and C1900) compared to streams with shorter perennial reaches or lower baseflow (A1977 and G1900) (Table 3.2). Percent cobble substrate corresponded with geographic location of the canyons, where southwestern canyons (C1900, S1996, and C1996) had higher, middle canyons (F1977 and A1977) had intermediate, and the canyon farthest to the northeast (G1900) had the lowest percent cobble substrate. Percent sand and depth were lowest in S1996 and A1977, the two most intermittent streams, but were higher in streams with longer perennial reaches (C1990, F1977, and C1996) (Table 3.2). Point estimates of DO, pH, stream velocity, and width were similar across streams.

One-way ANOVA revealed that total insect density on natural cobbles collected at 0 d differed significantly among canyons ($F_{df=105} = 39.77$; $P < 0.0001$), but did not show a consistent trend with fire history. Cobble densities for C1900, S1996, and C1996 were similar and were significantly higher than densities on G1900 and F1977 cobbles, and densities were lowest for A1977 (Figure 3.4). Taxa richness on natural 0-d cobbles also differed among canyons ($F_{df=105} = 61.14$; $P < 0.0001$) and showed a general trend along a fire history gradient, where S1996 and C1996 had low richness, and G1900 and C1900 canyons had higher richness (Figure 3.4).

CDA conducted with taxa densities revealed that trait representation on natural cobbles at 0 d differed among streams (Wilks' Lambda: $F_{df=65} = 17.24$; $p < 0.0001$). The first two canonical variables explained 89.7 % of the total variation in representation among streams. The first canonical variable (CAN1) explained 62.9 % of the variation ($F_{df=65} = 17.24$; $p < 0.0001$) and distinguished recently burned streams from those burned in 1977 or before 1900 (Figure 3.5a). Multi-voltine individuals with strong larval dispersal and generalist feeding preferences dominated recently burned streams and were positively correlated with CAN1, while uni-voltine individuals with weak larval dispersal and specialist feeding strategies represented the other four streams and were negatively correlated with CAN1 (Table 3.3). CAN2 explained 26.8 % of the total variation among streams ($F_{df=48} = 10.39$; $p<0.0001$) and separated F1977 and C1900 from A1977 and G1900 (Figure 3.5a). Proportions of individuals that were semi-voltine, silt tolerant, and grazers were higher in C1900 and F1977 and were negatively correlated with CAN2 (Table 3.3). The positive CAN2 direction primarily described trait representation in

A1977 and G1900 (higher proportion of weak or strong adult dispersers, predators, and silt-intolerant individuals) (Table 3.3).

CDA conducted with the number of species with each trait (Wilks' Lambda: $F_{df=65} = 15.94$; $p < 0.0001$) showed similar differences in trait representation among streams. The first two canonical variables (CAN1 and CAN2) explained 87.6 % of the total variation in representation. CAN1 explained most (75.7%) of the variation ($F_{df=65} = 17.24$; $p < 0.0001$) and distinguished recently burned streams in the positive direction from all other streams in the negative direction (Figure 3.5b). Recently burned streams had a higher proportion of taxa with multi-voltinism, strong larval dispersal, and silt tolerance, while other streams had uni-voltine taxa with weak adult and larval dispersal, silt-intolerance, and specialist feeding strategies (Table 3.3). CAN 2 explained 11.9% of the variation between streams ($F_{df=48} = 8.62$; $p < 0.0001$) and separated F1977 and C1900 from A1977, G1900, and C1996 (Figure 3.5b). C1996 and A1977 had a higher proportion of grazing taxa with strong adult dispersal compared to F1977, which had more collector-gatherer taxa or semi-voltine taxa (Table 3.3).

Total insect density varied significantly across time treatments and across canyons with different fire histories, but also differed between canyons within fire history (Table 3.4; see Appendix 3.1a-f). Both fire history and canyon interacted with time treatments to influence densities (Table 3.4). Examining proportional changes in densities revealed that unburned streams (G1900, C1900) showed the highest reduction after 2 d and the slowest recovery (by 42 d) (Figure 3.6). Recently burned streams (S1996, C1996)

showed less reduction and faster recovery, where 0-d levels were exceeded on 2-d cobbles (Figure 3.6). Proportional reductions in total insect density differed between streams burned in 1977 (A1977 and F1977) and did not show intermediate resilience (Figure 3.6). F1977 showed no proportional reduction and thus the highest resilience among all streams, while A1977 showed reductions more similar to reduction in unburned streams. Recovery time for A1977 was intermediate, where densities were similar to 0-d densities by 16 days. Densities of 42-d experimental cobbles were similar to (or exceeded) natural 0d densities compared to 43 d natural cobbles in all streams except G1900.

Taxa richness showed a similar correspondence between resilience and wildfire history. Changes in richness were significantly related to time since the experimental disturbance, fire history, canyons nested within fire history, and all two-way interactions (Table 3.4). Recently burned streams (S1996 and C1996) showed the least proportional reduction in number of taxa at 2 d and recovered to richness on natural cobbles around 16 d (Figure 3.7). Unburned streams (G1900 and C1900) showed higher reductions in taxa richness at 2 d and recovered by 42 d (C1900) or did not recover (G1900) (Figure 3.7). Resilience was again variable for streams burned in 1977, where F1977 showed a similar reduction at 2 d and recovery rate compared to recently burned streams (Figure 3.7). A1977 showed a much higher reduction in richness and a recovery rate similar to G1900. By 42 d, taxa richness matched or exceeded richness observed on natural cobbles (43 d) in all streams except G1900.

Resilience in community composition on cobbles was also related to fire history. PSI was significantly related to time since the experimental disturbance, fire history, canyons nested within fire history, and all two-way interactions (Table 3.4). Community composition in recently burned streams showed the least change (approximately 10%), and thus the highest resilience, compared to other streams (Figure 3.8). Streams burned in 1977 and unburned streams responded similarly and showed a more dramatic change (50 - 62%) in composition on cobbles compared to 0 d composition. For all streams, PSI for cobbles at sample periods 2, 4, 16, 42, and 43 d showed similar deviations from initial community composition, and experimental cobbles did not demonstrate recovery by 42 d (Figure 3.8).

Total abundance and taxa richness of drift samples differed among streams and corresponded to a gradient of fire history. In general, streams burned in 1996 had higher drift rates, especially C1996 (Table 3.5). Baetidae (primarily *Baetis tricaudatus* Dodds) individuals accounted for 86-89% of total drifting insects. F1977 also had a high number of insects drifting per unit time, but Baetidae only comprised 37% of the drift (Table 3.5). C1900, A1977, and G1900 showed lower total drift abundance and lower percent Baetidae in drift. Taxa richness in drift samples did not correspond to fire history, where richness was higher in C1996, F1977, and C1900 and lowest in G1900, A1977 and S1996 (Table 3.5).

Drift composition was most important for community resilience in recently burned streams. Taxa that were dominant on C1996 and S1996 cobbles at 0 d, such as

baetids and chironomids, remained dominant on 2-d cobbles and were also dominant taxa in drift (Figure 3.9). Thus, community composition at 2 d was similar to both drift samples and 0-d cobbles in C1996 and S1996 (Table 3.5). For F1977, composition at 2 d appeared to be a mixture of dominant taxa at 0 d and drifting taxa, while A1977 composition at 2 d appeared to be more similar to 0 d than drift composition (Figure 3.10; Table 3.5). Streams not burned since 1900 showed a similar pattern (Figure 3.11), where composition on 2-d cobbles was more similar to composition on 0-d cobbles than composition in drift (Table 3.5). In streams not burned in 1996, taxa that were uncommon in drift samples increased (i.e. *Cinygmula* sp. and *Agapetus* sp.) or remained similar (*Sweltsa* sp.) in proportion at 2 d compared to 0 d. Conversely, many taxa found in drift samples were still lower in proportion or absent after two days, including *Dixa* sp., *Epeorus* sp., *Simulium* sp., elmid beetles, and *Hesperoperla pacifica* Banks. Taxa such as *Ceratopsyche* sp., *Hesperophylax* sp., *Pteronarcella badia* Hagen, and *Ephemerella* sp. were not in drift and decreased in streams where they occurred.

DISCUSSION

Insect community responses to an experimental disturbance differed in streams across a gradient of wildfire history. Total insect density and taxa richness responses showed higher resilience in streams severely burned in the 1996 Dome fire compared to unburned streams. Furthermore, community composition in recently burned streams changed little in response to the experimental disturbance, while compositional changes

in unburned streams were more pronounced. Differences in rates and composition of drift contributed to differences in resilience among streams. Drift rates in recently burned streams were an order of magnitude higher than rates in unburned streams, and taxa found in drift directly contributed to recolonization after the experimental disturbance. In contrast, drift rates were lower in unburned streams, and taxa in drift did not explain recolonization patterns. Thus, differences in community resilience between recently burned and unburned streams, and the relative contribution of drift towards resilience, corresponded to differences in wildfire history.

My findings lend support to the hypothesis that community responses to a unit disturbance will vary among streams having different disturbance histories (Resh et al. 1988; Poff 1992). Other researchers have also found higher resistance and resilience to experimental disturbance in disturbance-prone streams. For instance, Rosser and Pearson (1995) suggested that recent scouring floods facilitated high resilience of community composition to experimental disturbance due the presence of taxa with strong colonization abilities. Similarly, Matthaei et al. (1997) attributed high resilience after an experimental flood disturbance to the fact that insect communities were shaped by a historically harsh and unpredictable disturbance regime. Specifically, communities included insect taxa with strong dispersal abilities through drift, allowing for quick recovery. In an observational study, Miller and Golladay (1996) found that communities in harsher intermittent streams were more resistant to spates and drying than communities in more stable perennial streams. In my study, drift contributed to higher resilience in

both total insect density and community composition responses in streams with a more recent history of wildfire.

In contrast to community resilience in recently burned and unburned streams, resilience in streams burned in 1977 did not follow a gradient of wildfire history. Instead of showing intermediate resilience, resilience in Frijoles was similar, or even higher, than resilience observed in recently burned streams. Resilience in Alamo was always more similar to resilience observed in unburned streams. Although these streams were similar in wildfire history, differences in burn severity and spatial extent of burns may have been responsible for unexpected patterns of resilience. For instance, Frijoles canyon was intensely burn over 50 percent of its watershed in 1977, and also experienced 100-year flashfloods in post-fire years (Veenhuis 2002). A smaller portion of Alamo canyon was moderately burned in both the 1977 and 1996 fires, and severe post-fire floods were not documented after either fire (Purtyman and Adams 1980; N. K. M. Vieira, personal observation). Further, communities in the three streams that experienced intense burn and post-fire flooding in the last 30 years (Capulin, Sanchez, and Frijoles) had the highest drift rates and resilience compared to streams that have not been severely burned or flooded in over 100 years. Thus, post-fire flood history, as well as wildfire history, may have influenced community resilience to experimental disturbance.

Representation of resilient species traits in cobble communities generally corresponded to a gradient of wildfire history and further explained high resilience in recently burned streams. Communities in streams burned in the 1996 Dome were largely

comprised of individuals with resilient attributes such as strong larval dispersal, multi-voltinism, or generalist feeding strategies (i.e. Baetidae, Orthocladiinae, and *Simulium* sp.). In contrast, communities in unburned streams had more individuals with weak larval dispersal, specialist feeding strategies (i.e. shredder *Amphinemura banksi* Baumann and Gaufin) stoneflies, grazing heptageniid mayflies) and semi-voltine lifecycles (i.e. several stonefly taxa, elmid beetles). Correspondingly, total insect density was highly resilient to experimental disturbance in recently burned streams and less resilient in unburned streams. Trait representation based on the proportion of taxa with a particular trait showed similar results, with the exception that recently burned streams had more taxa tolerant to silt and sediment. Other trait-based studies on stream insects (Richards et al. 1997; Townsend et al. 1997b) and fish (Poff and Allan 1995) have found higher representation of taxa with strong larval and adult mobility, short generation times or multi-voltinism, generalist resource use, and silt-tolerance in streams with less hydrologic stability.

Proportions of taxa with resilient attributes partially explained why differences in community resilience between canyons burned in 1977 and unburned canyons did not always correspond to a fire history gradient. Frijoles and Cochiti, the two streams with higher baseflow and longer perennial reaches, had a higher representation of collector-gatherer and silt-tolerant taxa compared to Guaje and Alamo. Silt-tolerance may convey resilience by allowing taxa to persist on hand-placed cobbles that are embedded in recently disturbed (and more readily entrained) substrate (i.e. in the 4-m^2 patches). Also, taxa that were strong colonists (i.e. Baetidae and Chironomidae) contributed to high

resilience to experimental disturbance in these two streams, despite being at low densities on natural cobbles. However, taxa with attributes that are not considered resilient (i.e. weak adult dispersal and larval dispersal, specialist feeding strategies) also recolonized disturbed cobbles. For instance, the grazer *Cinygmula* sp. increased in Alamo and Guaje, and pupae of the grazer *Agapetus* sp. increased in Cochiti, as early as 2 d after the disturbance. In general, drift rates, taxa richness in drift, insect densities on natural cobbles, and representation of resilient traits likely interacted to drive differences in resilience between these four streams.

Small-scale experimental studies have been successfully employed to address hypotheses about community responses to disturbance in streams (i.e. Reice 1985; Robinson and Minshall 1986; Boulton et al. 1988; Rosser and Pearson 1995). However, it is unclear as to how well responses to experimental disturbances can be generalized to predict responses to natural disturbances (Resh et al. 1988; Lake 1990). In two studies where effects of experimental "floods" and real floods are compared, community responses differed. Matthaei et al. (1997) found that colonization rates and patterns after an experimental disturbance in 9-m^2 patches of substrate were similar to rates and patterns observed after a 5-yr flood at the same sites. In contrast, Brooks and Boulton (1991) found than communities after an experimental disturbance in 0.25 m^2 substrate patches differed in recovery rates and faunal composition compared to communities after a flood in a temporary Australian stream. Townsend (1989) suggested than experimental studies may merely reflect insect "redistribution" rather than true recolonization after a large-scale disturbance. Therefore, small-scale experimental disturbances may be less

appropriate for predicting community recovery patterns after natural disturbances (Lake 1990) that alter physical habitat (Niemi et al. 1990; Mackay 1992) and reduce in-stream refugia and colonist sources (Yount and Niemi 1990).

Patterns of community recovery after my small-scale (4-m^2) experimental disturbance, which simulated a 2-yr flood event, were only loosely similar to patterns observed following 100-yr flood events associated with the 1996 Dome fire (Chapter 1). Multivoltine taxa with strong larval drift propensities and generalist feeding strategies (i.e. Baetidae, Chironomidae) recolonized quickly following both post-fire floods and the experimental disturbance. Taxa with weaker larval dispersal or specialized resource use (i.e. heptageniids, *Ceratopsyche* sp., elmid beetles, and *A. banksi*) were greatly reduced by post-fire flashfloods and were also lower in density on experimental cobbles. These patterns corresponded to general patterns observed after other hydrologic disturbances (see reviews in Neimi et al., 1990; Niemi and Yount 1990; Lake 2000). However, further extrapolation between these studies is complicated by differences in spatiotemporal scales within which disturbances and population recovery mechanisms operate (Fisher 1990; Poff and Ward 1990; Poff 1992). For instance, *Agapetus* sp. and *Cinygmula* sp. quickly recolonized experimental cobbles (i.e. larvae likely crawled from nearby undisturbed substrate), but took several years to recolonize flooded reaches in a burned stream via aerial dispersal. In general, voltinism and adult dispersal likely contributed more strongly to inter-annual recovery patterns after post-fire floods (Chapter 1; Chapter 2) than to the daily recovery patterns observed in this study. Others have found high community resilience to severe floods in flashy desert streams due to timing of

emergence and adult dispersal (Gray and Fisher 1981; Grimm and Fisher 1989; Boulton et al. 1992; Lytle 2002).

Comparing responses to experimental disturbances along a disturbance regime gradient is useful in that responses can be interpreted in light of historical influences shaping communities (Resh et al. 1988; Poff 1992). In this study, I found that communities in recently burned streams were more resilient to a small-scale experimental disturbance due to the fact that prior flood disturbance favored taxa with resilient attributes. To my knowledge, this is the only study testing community responses to experimental disturbance in streams that differ in wildfire disturbance. However, observational studies have shown that composition of stream insect communities corresponds with fire history (Roby 1989) and other measures of wildfire disturbance. For instance, Minshall et al. (1997) found lower community resilience to wildfire in small order streams that had a larger percentage of their watersheds burned in the 1988 Greater Yellowstone Area fires. Lawrence and Minshall (1994) found that stream insect diversity correlated with higher intensity burns and distance of the burn from the stream channel, where streams with greater disturbance were lower in diversity. Strong environmental gradients created by wildfire and post-fire disturbances in burned streams have been largely overlooked as a template against which to compare community responses to disturbance.

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Table 3.1. Stream characteristics and wildfire history for six study streams, Bandelier National Monument and Santa Fe National Forest, near Los Alamos, NM. Records marked with an asterisk are estimated from maps and personal observations during the study. All streams have a gradient between 3 - 7%. Specific locations of study reaches can be found in Figure 3.2.

Year of most recent fire	Canyon	Drainage Area (km^2)	Perennial length (%)*	Baseflow (m^3/s)	Percent of Watershed Burned in Fires
1996					
	Capulin	51	70%	0.04	6% in 1977 La Mesa Fire, 90% in 1996 Dome Fire
	Sanchez	20	<40%	0.02	50%* in 1996 Dome Fire
1977					
	Frijoles	51	>90%	0.06	58% in 1977 La Mesa fire
	Alamo	50	40%	0.02	22% in 1977 La Mesa Fire, 20% in 1996 Dome Fire
< 1900					
	Guaje	50*	60%	0.03	none at time of study
	Cochiti	65*	80%	0.04	none at time of study

Table 3.2. Means (and standard deviations) for physical and chemical characteristics for six study streams across a gradient of fire history in Bandelier National Monument and Santa Fe National Forest, near Los Alamos, NM.

Physicochemical measures	1996 DOME FIRE				1977 LA MESA FIRE				NO FIRE SINCE 1900			
	Sanchez		Capulin		Frijoles		Alamo		Guaje		Cochiti	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
ph	7.7	0.5	8.3	0.1	8.1	0.2	8.2	0.2	7.6	0.6	7.8	0.5
Temperature (C)	14.2	4.2	13.8	5.5	12.9	3.5	12.1	4.2	10.1	3.6	11.9	3.7
Conductivity (u ohms)	141.7	21.7	174.2	17.8	120.0	14.1	114.2	24.3	90.0	16.5	132.3	10.9
Dissolved Oxygen (mg/L)	8.3	0.7	8.7	0.5	8.6	0.5	8.6	1.2	9.3	0.5	8.1	0.6
Hardness (mg/L as CaCO3)	40.0	6.0	51.4	7.5	27.9	11.8	50.0	5.6	24.0	0.1	36.0	5.7
Alkalinity (mg/L as CaCO3)	38.0	7.2	64.7	9.1	43.9	17.7	55.0	8.5	32.7	3.1	52.5	4.9
Width (m)	1.5	0.7	1.7	0.4	1.7	0.3	1.3	0.5	1.5	0.4	1.2	0.4
Depth (cm)	7.0	3.5	8.2	1.8	11.3	2.6	6.7	2.9	8.8	2.7	11.2	3.3
Velocity (m/s)	0.3	0.1	0.3	0.1	0.3	0.1	0.3	0.3	0.3	0.1	0.3	0.1
% Boulder Substrate	7.6	9.8	3.3	4.3	2.1	2.9	4.1	5.8	0.7	2.3	1.3	2.8
% Cobble Substrate	29.3	12.4	27.3	11.9	14.8	12.0	18.0	12.0	13.3	11.2	21.1	10.1
% Sand Substrate	25.7	11.7	46.7	13.7	51.9	17.2	33.6	13.9	41.5	13.5	44.5	13.7

Table 3.3. Summary of canonical discriminant analysis for six study streams varying in fire history, near Los Alamos, NM. Correlations between species traits and the first two canonical variables (CAN1 and CAN2) are presented for analyses conducted with either the proportion of individuals, or the proportion of taxa, with each trait. Further detail regarding traits can be found in the text and in Chapter 2. All univariate P-values for traits <0.001.

	Prop. of Individuals		Prop. of Taxa	
SPECIES TRAITS CONVEYING RESILIENCE	**CAN1**	**CAN2**	**CAN1**	**CAN2**
Collector -gatherer	0.85	0.04	0.07	-0.54
Grazer	-0.71	-0.31	-0.67	0.43
Collector-filterer	-0.08	0.31	0.34	0.29
Shredder	-0.65	-0.17	-0.64	-0.10
Predator	-0.39	0.37	0.18	0.07
Uni-voltine	-0.90	0.33	-0.90	0.26
Multi-voltine	0.97	0.02	0.93	-0.06
Semi-voltine	-0.35	-0.68	-0.28	-0.49
Weak larval dispersal ability	-0.68	-0.30	-0.75	0.14
Strong larval dispersal ability	0.98	0.17	0.83	0.02
Weak adult dispersal ability	0.51	0.41	-0.79	-0.05
Strong adult dispersal ability	-0.50	0.50	0.10	0.59
Silt-tolerant	-0.39	-0.44	0.72	-0.18
Silt-intolerant	0.43	0.35	-0.77	0.14

Table 3.4. Results for mixed-effects nested ANOVA models (Type III SS) testing main effects of colonization time (time), fire history (fire), canyons nested within fire history categories (canyon(fire)), and relevant two-way interactions on insect community responses after an experimental disturbance conducted in six study streams near Los Alamos, NM. See text for further detail on statistical analysis.

Response	Parameters	Statistics		
		df	F	P
Total Insect Density	Time	5	88.7	<0.0001
	Fire	2	102.1	<0.0001
	Canyon(fire)	3	104.5	<0.0001
	Fire*Time	10	7.9	<0.0001
	Canyon(fire)*Time	15	5.1	<0.0001
Taxa Richness	Time	5	82.1	<0.0001
	Fire	2	200.9	<0.0001
	Canyon(fire)	3	123.6	<0.0001
	Fire*Time	10	9.1	<0.0001
	Canyon(fire)*Time	15	3.3	0.0001
PSI	Time	5	49.9	<0.0001
	Fire	2	328.9	<0.0001
	Canyon(fire)	3	29.1	<0.0001
	Fire*Time	10	5.5	<0.0001
	Canyon(fire)*Time	15	2.6	0.0018

Table 3.5. Mean (and standard deviations) for drift samples characteristics (n=3) in six streams differing in wildfire history (burned in 1996, 1977, or prior to 1900) near Los Alamos, NM. PSI (proportional similarity index) values (see text for details) are presented for comparisons between community composition on experimental cobbles at t = 2 days versus drift composition and composition on natural undisturbed cobbles at t = 0 d.

Fire	Canyon	Total Abundance		Taxa Richness		% Baetidae		T=2 vs Drift	T=2 vs T=0
		Mean	SD	Mean	SD	Mean	SD	PSI	PSI
1996	CAPULIN	729.0	312.7	15.0	1.2	89.0	3.1	0.88	0.91
	SANCHEZ	138.0	138.0	7.0	1.7	86.0	0.3	0.93	0.92
1977	ALAMO	38.0	9.1	9.0	2.5	22.0	10.3	0.40	0.50
	FRIJOLES	138.0	33.2	13.0	1.0	37.0	9.4	0.54	0.55
<1900	COCHITI	57.0	29.1	11.0	3.5	39.0	8.3	0.52	0.61
	GUAJE	65.1	38.2	7.5	0.7	64.0	33.4	0.37	0.62

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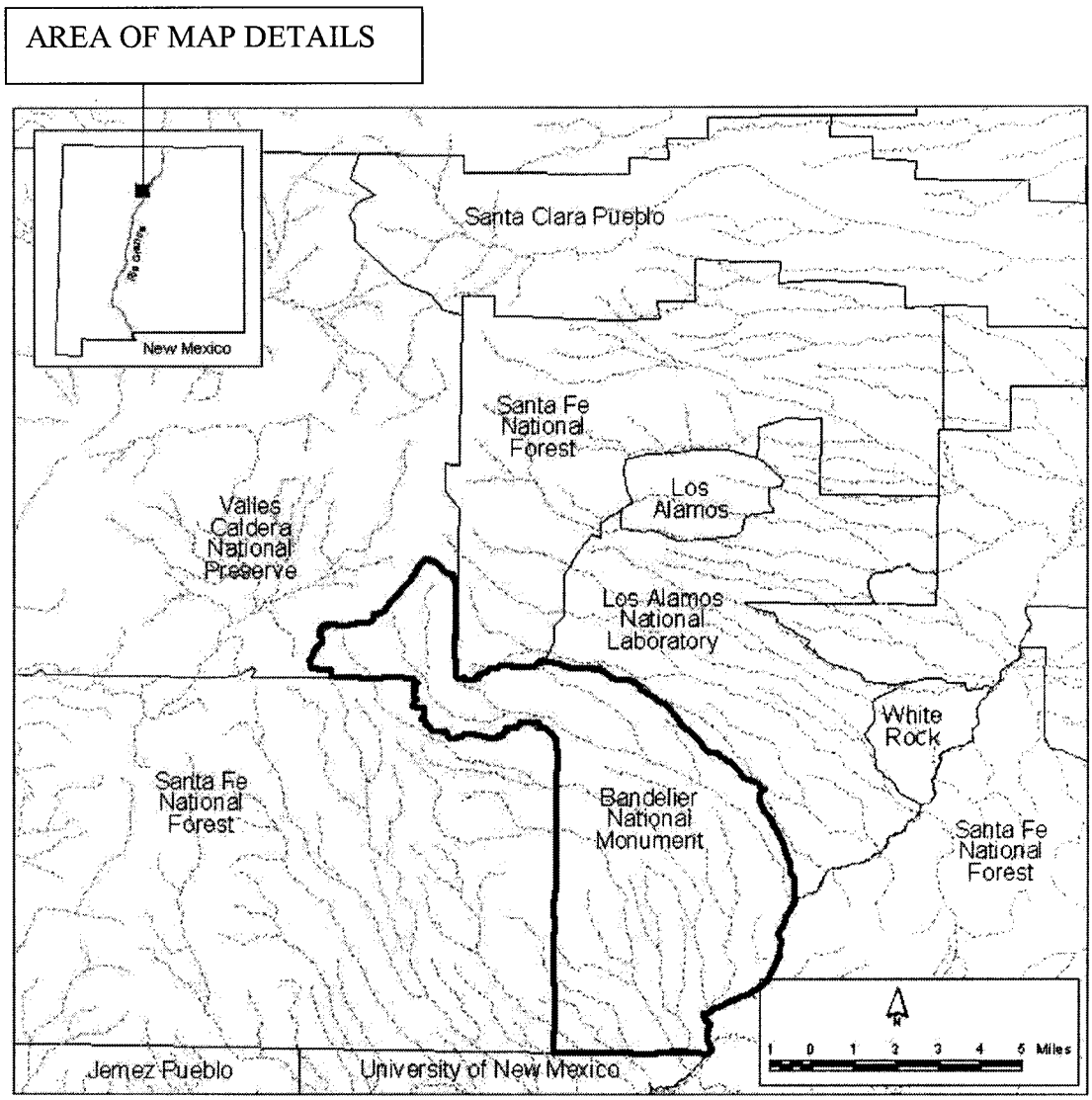
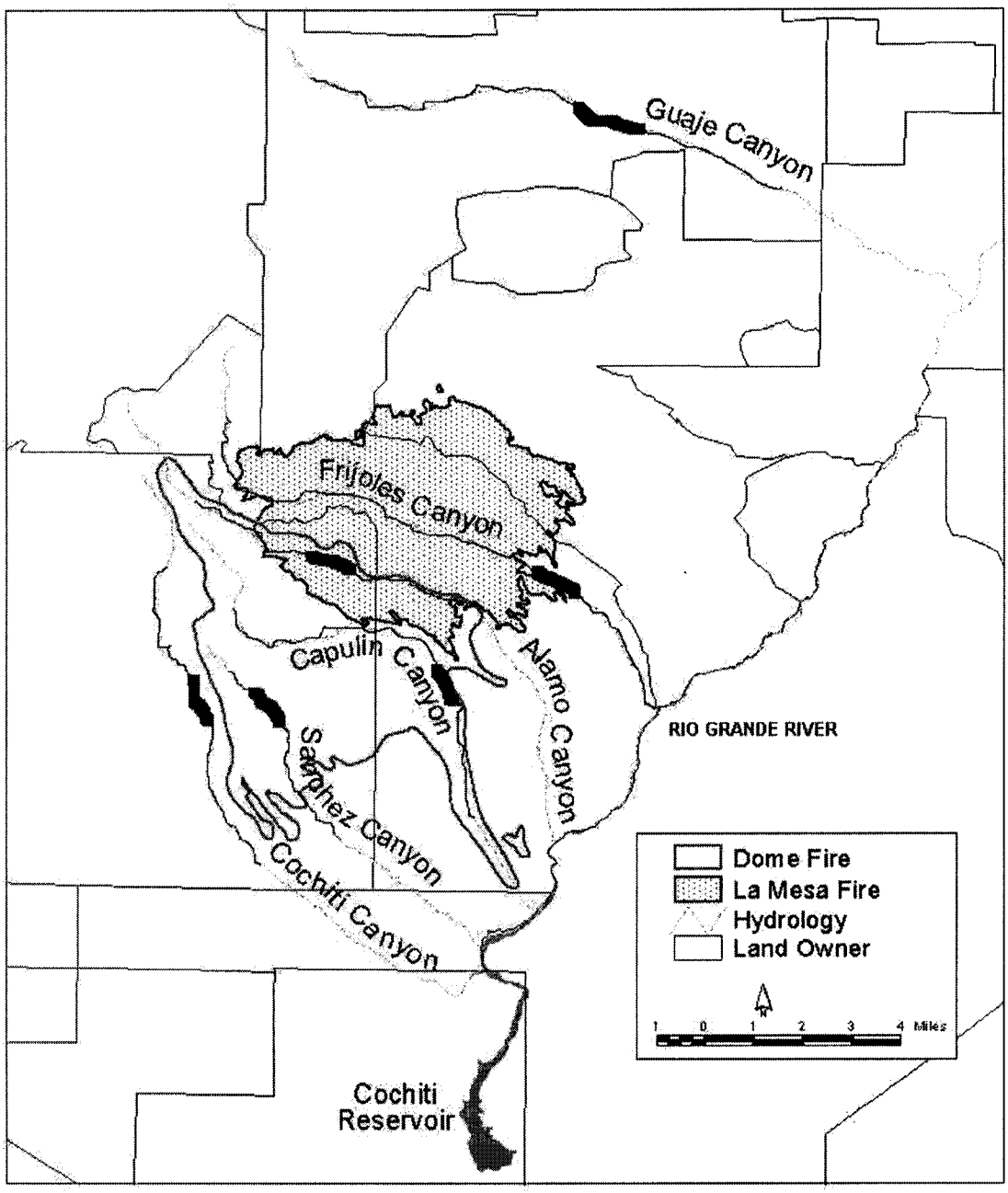
Figure 3.8. Mean (± 1SE) changes in proportional community similarity (PSI; see text for details) on cobbles after an experimental disturbance compared to communities on undisturbed cobbles at 0 d in six streams that span a gradient of wildfire history (burned in 1996, 1977, or prior to 1900). Sample sizes for each time period range from 16-20 (see Appendix 3.1).

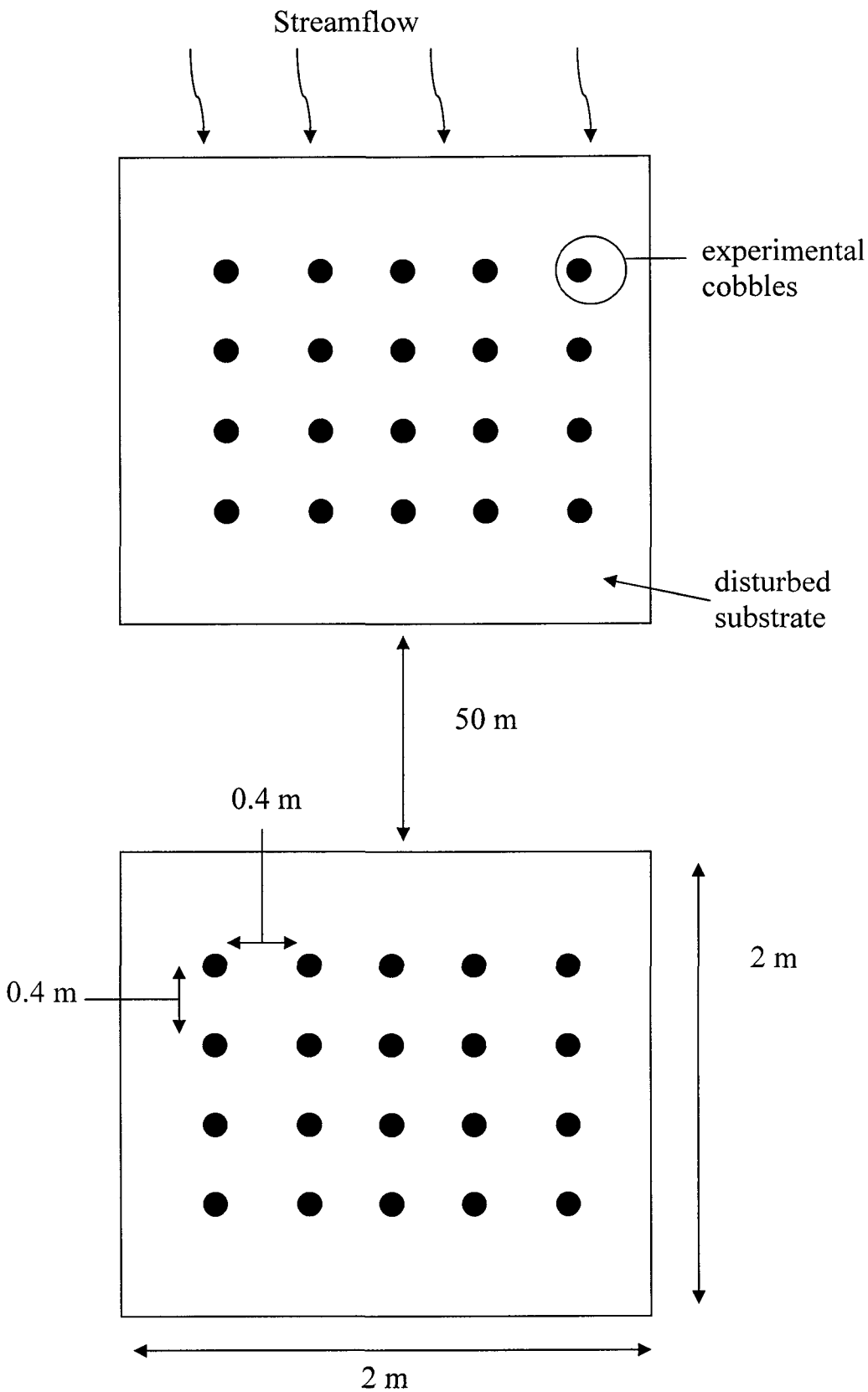
Figure 3.9. Mean relative proportions of dominant insect taxa (>5% of total density) in two canyons burned in the 1996 Dome fire (Capulin and Sanchez; near Los Alamos, NM) before (0 d) and 2 d after an experimental flood disturbance on cobbles, and in drift samples.

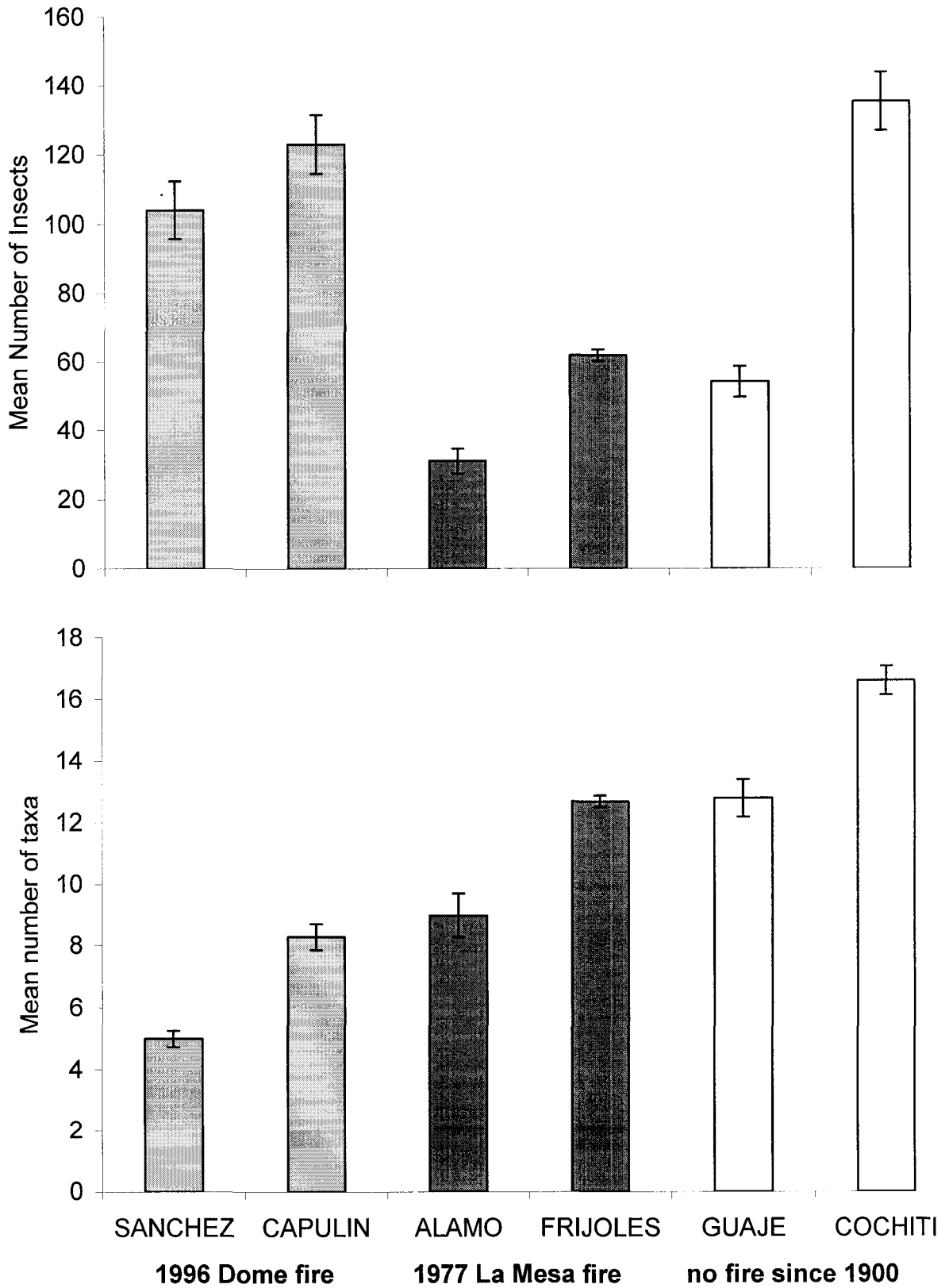
Figure 3.10. Mean relative proportions of dominant insect taxa (>5% of total density) in two canyons burned in the 1977 Dome fire (Frijoles and Alamo; near Los Alamos, NM) before (0 d) and 2 d after an experimental flood disturbance on cobbles, and in drift samples.

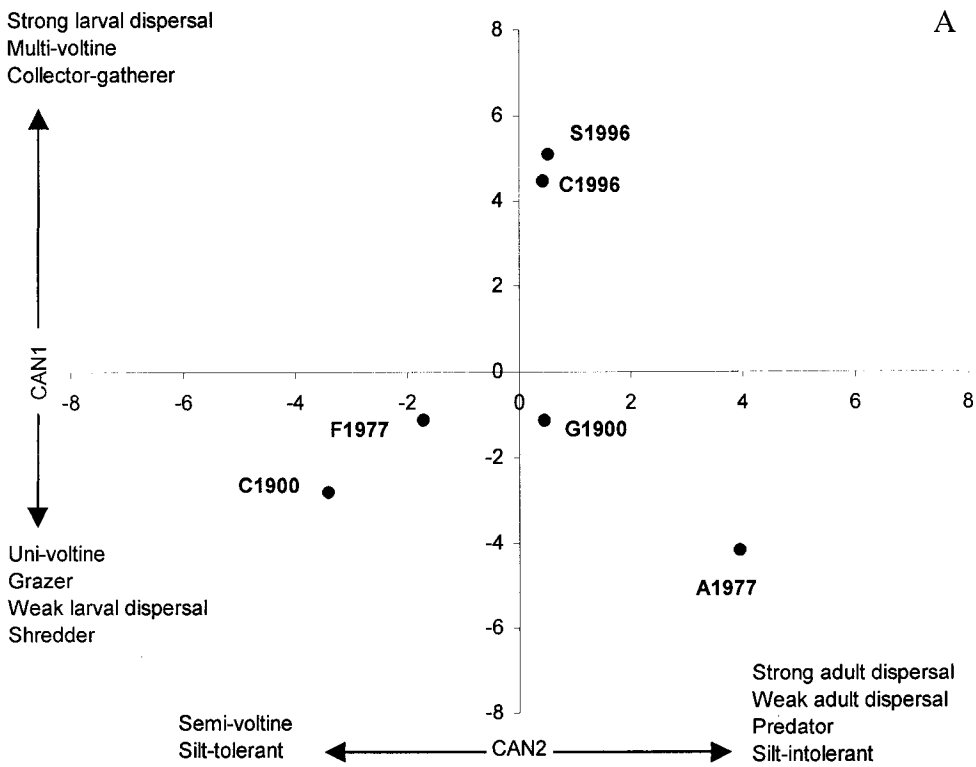
Figure 3.11. Mean relative proportions of dominant insect taxa (>5% of total density) in two canyons not burned since in the 1900's (Guaje and Cochiti; near Los Alamos, NM) before (0 d) and 2 d after an experimental flood disturbance on cobbles, and in drift samples.

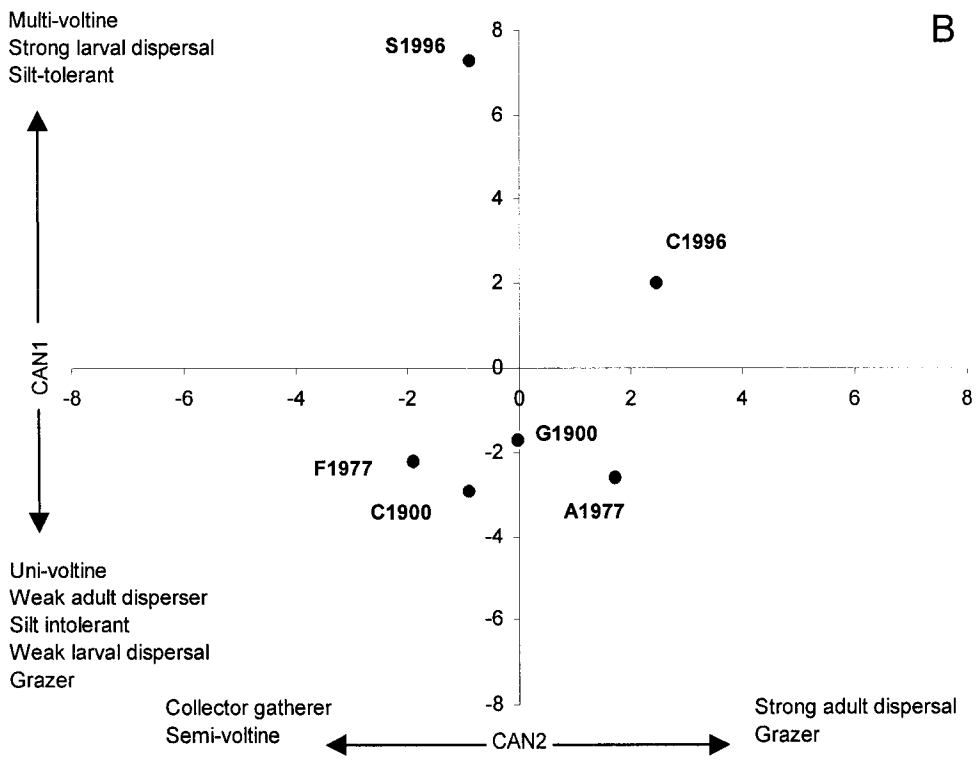


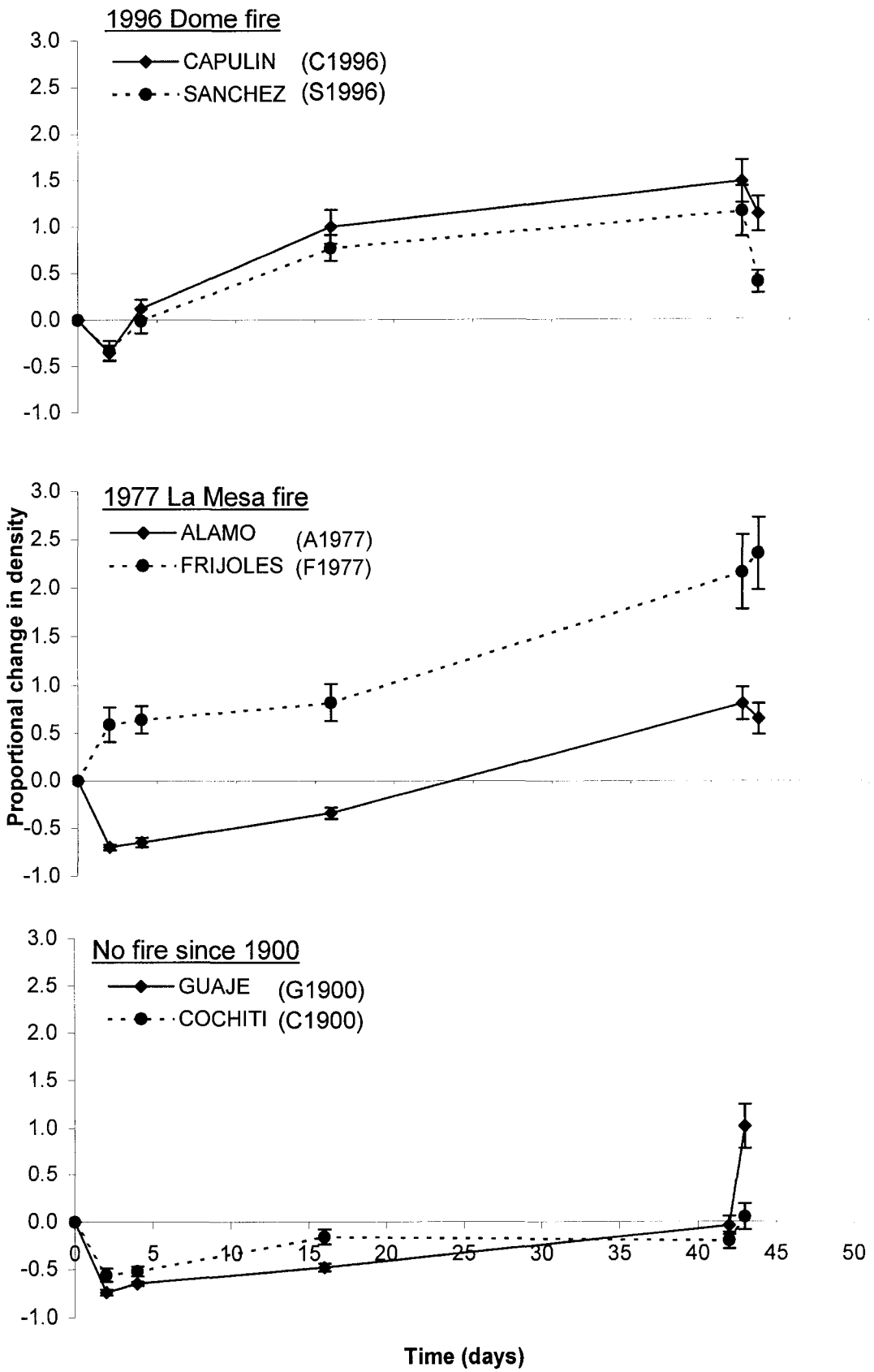


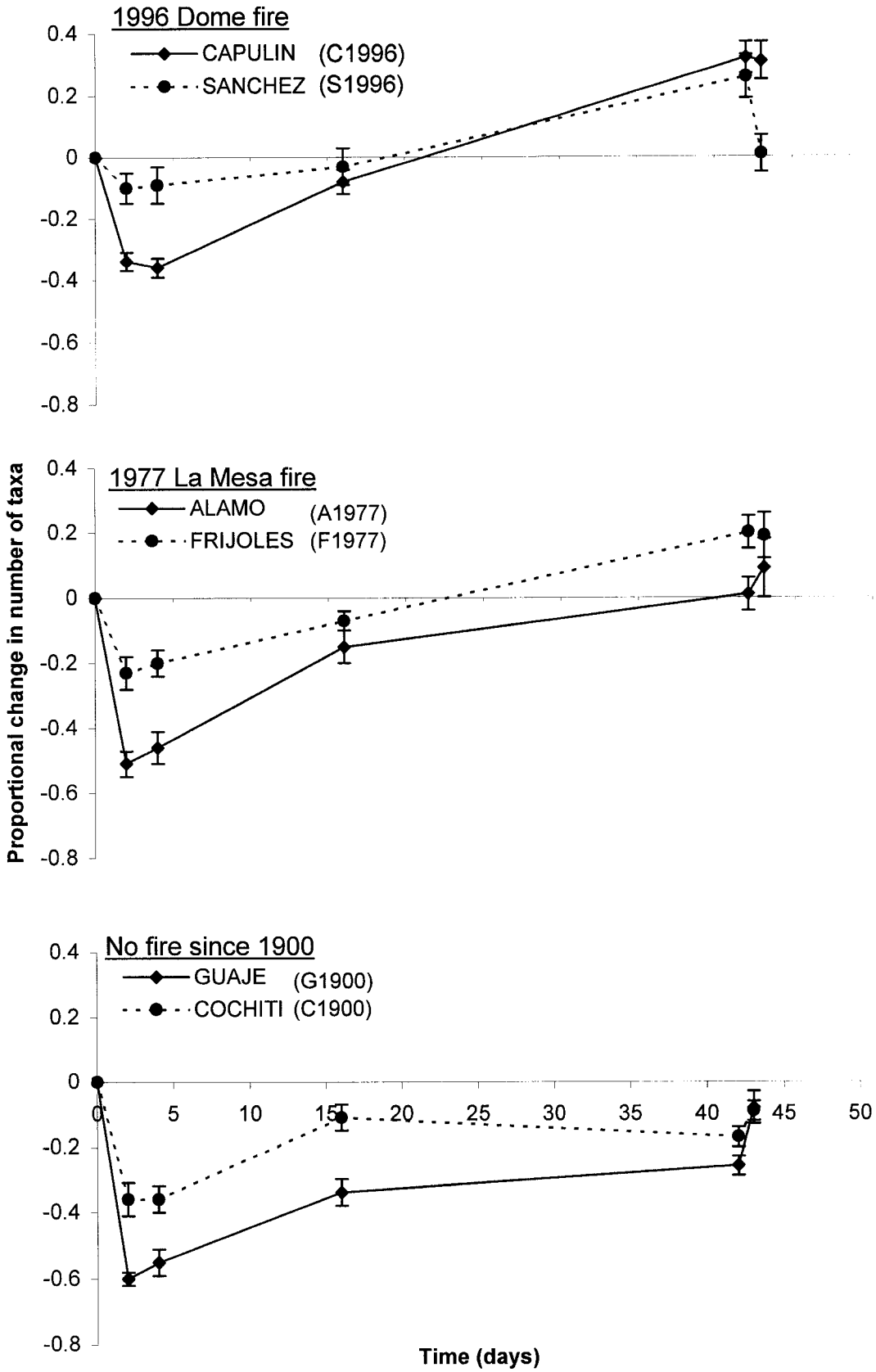


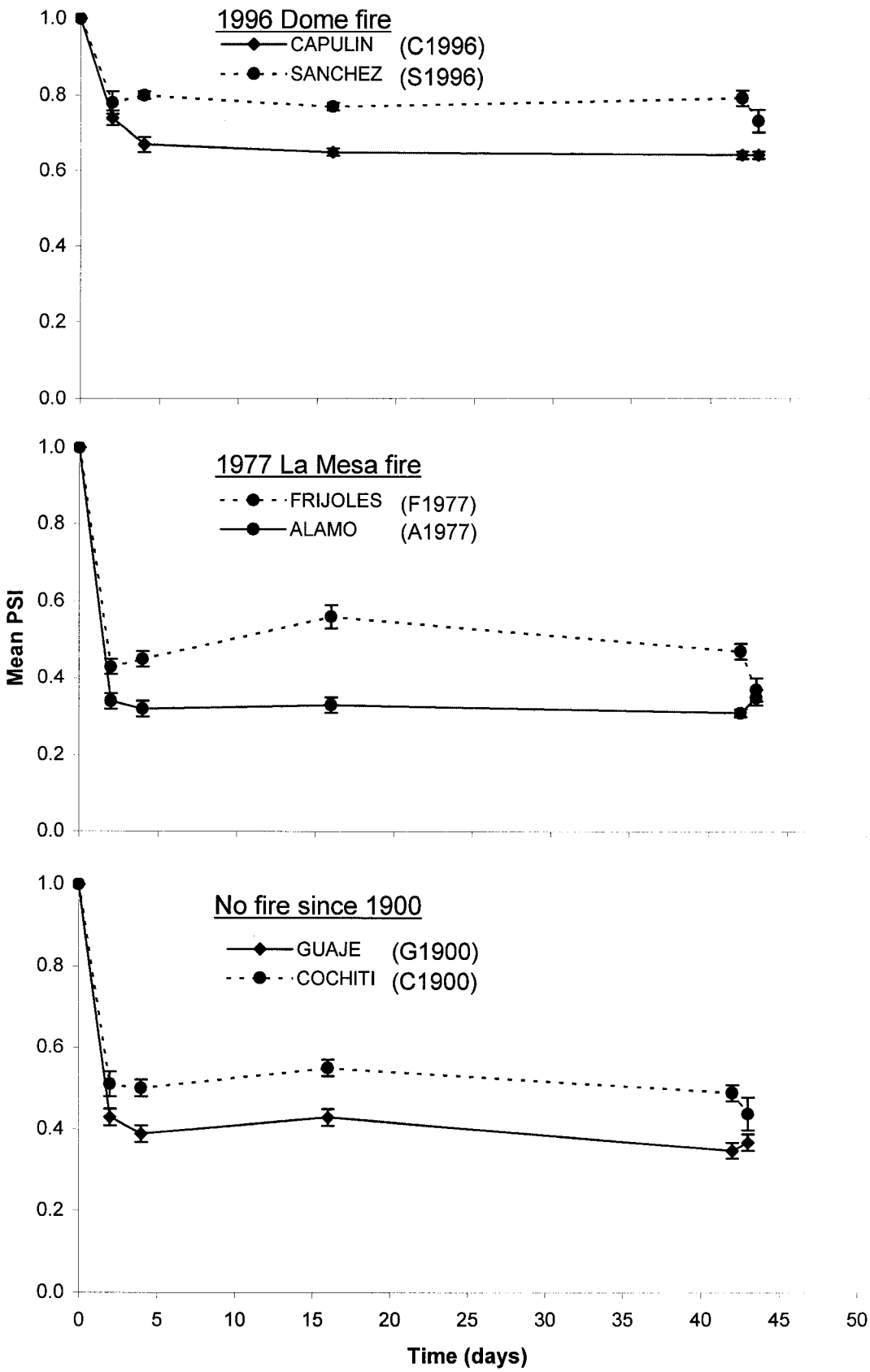


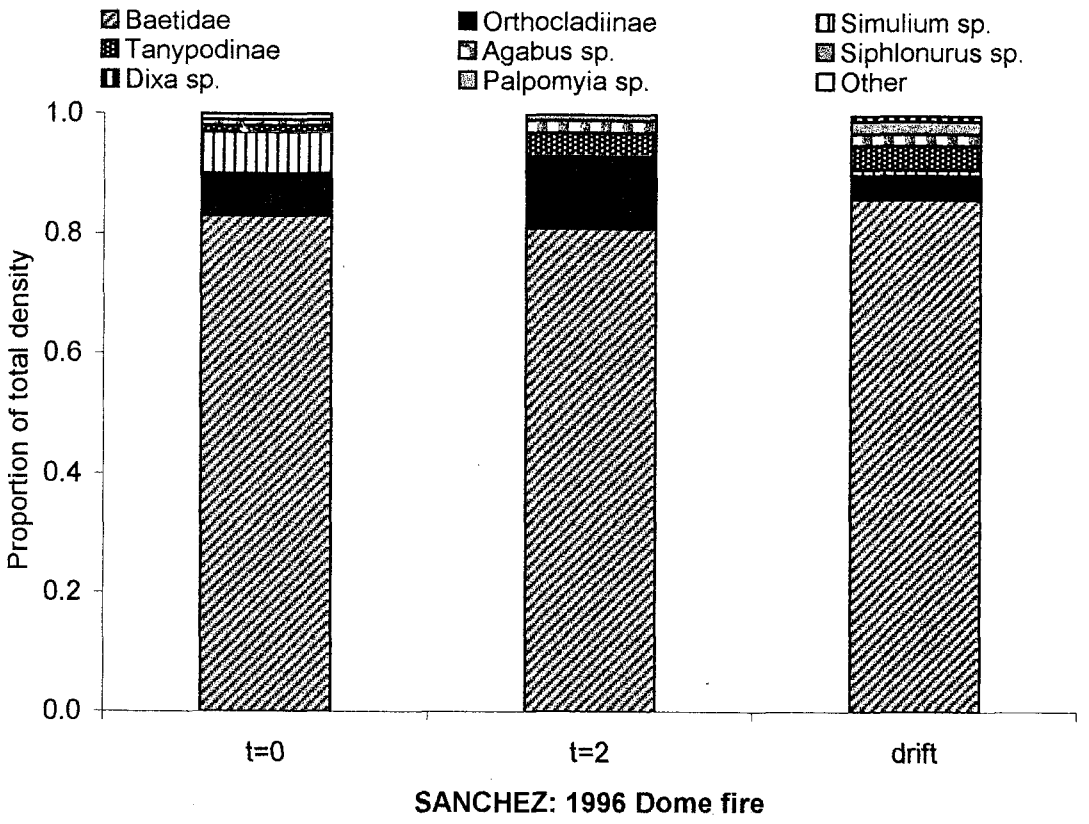












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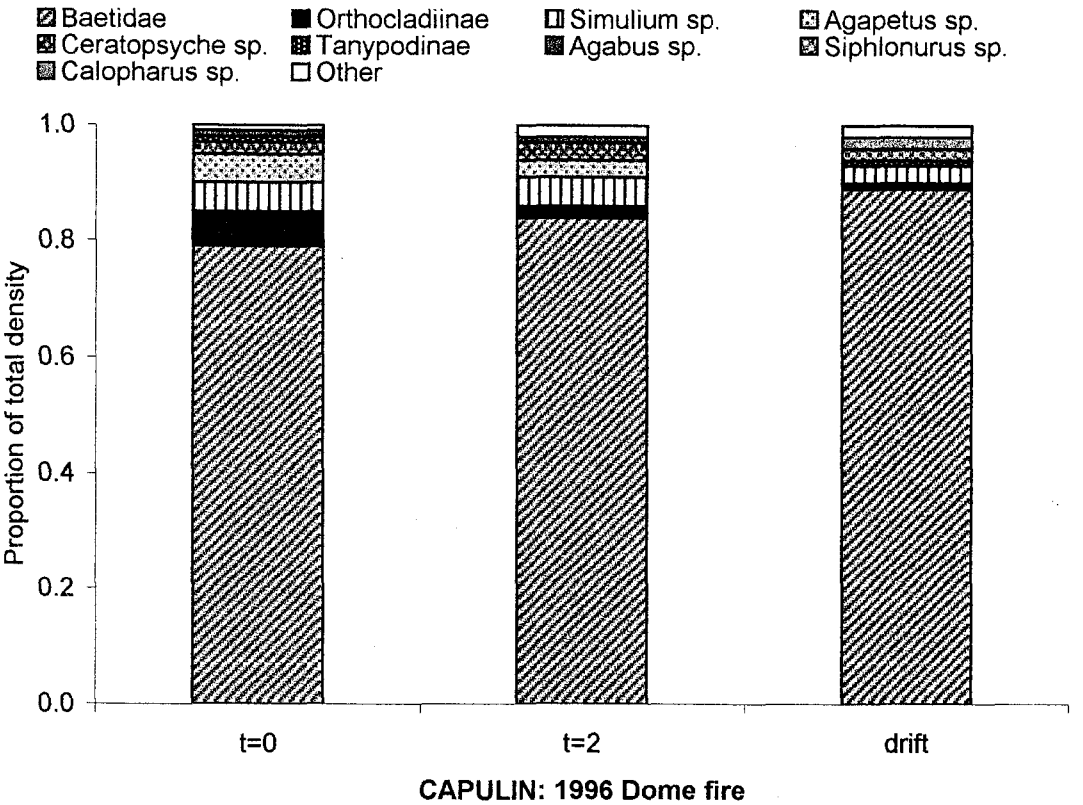
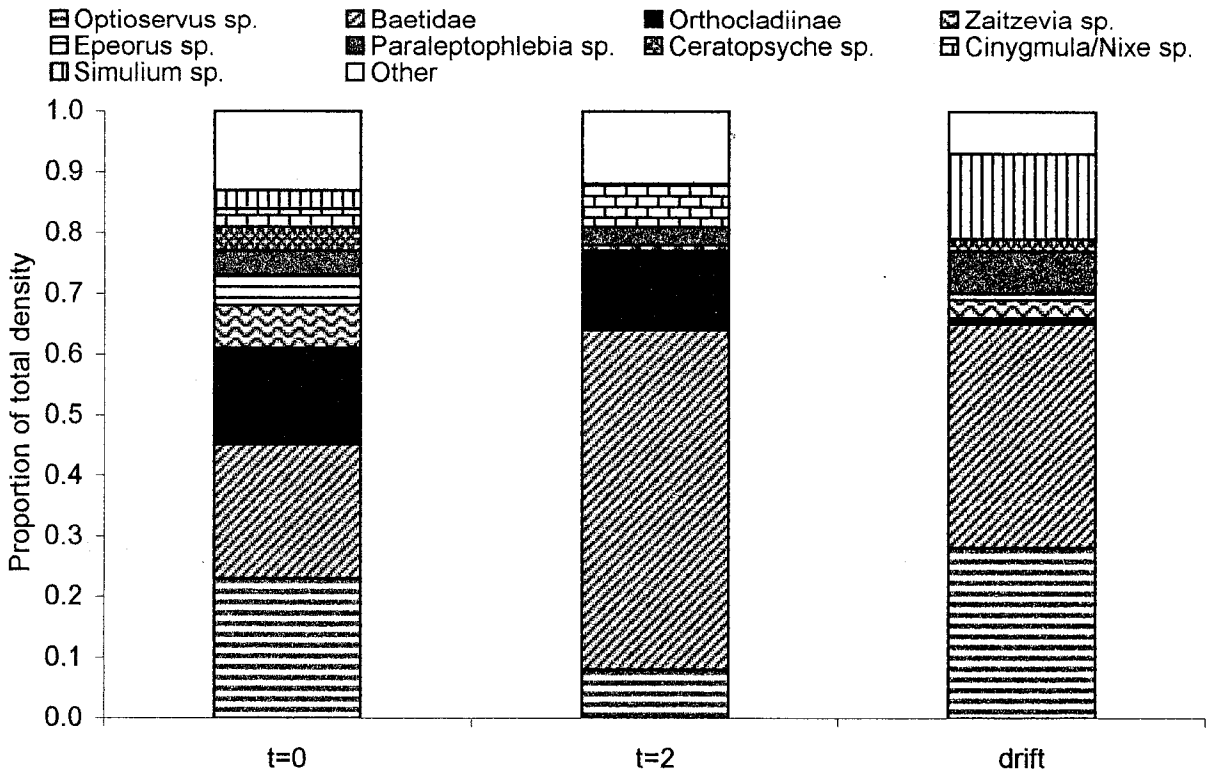
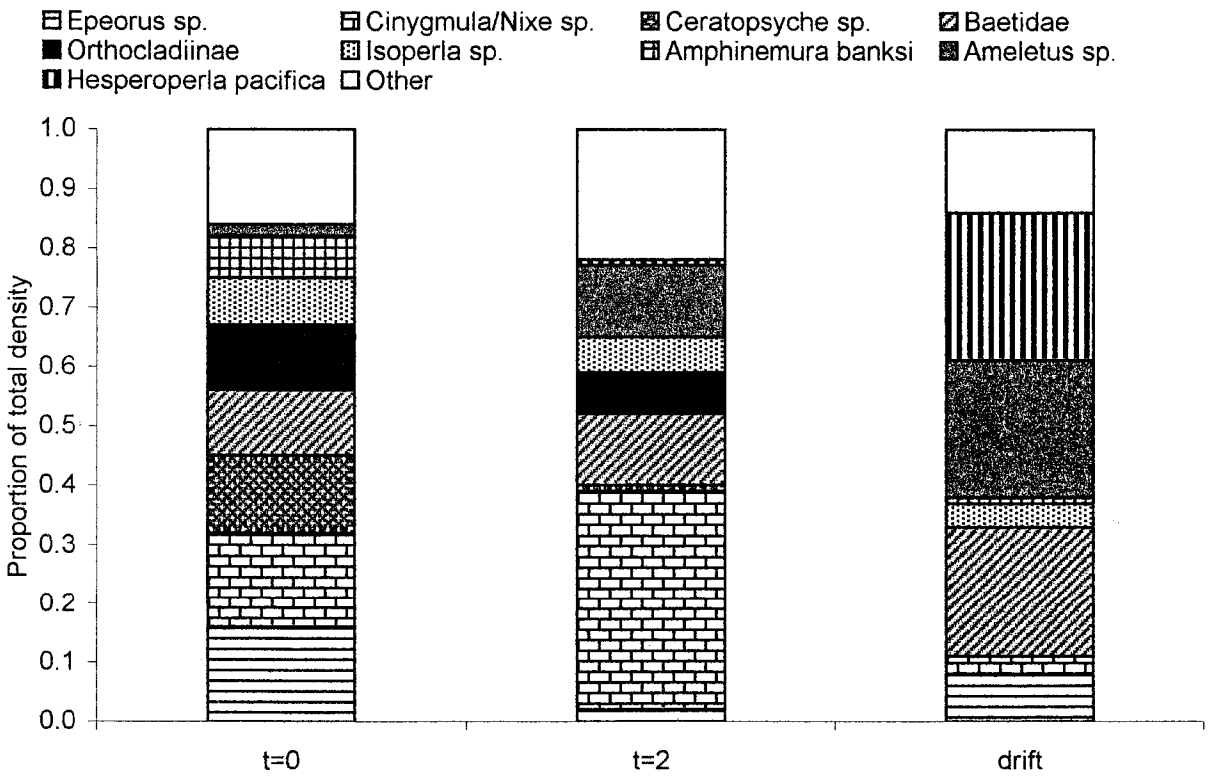


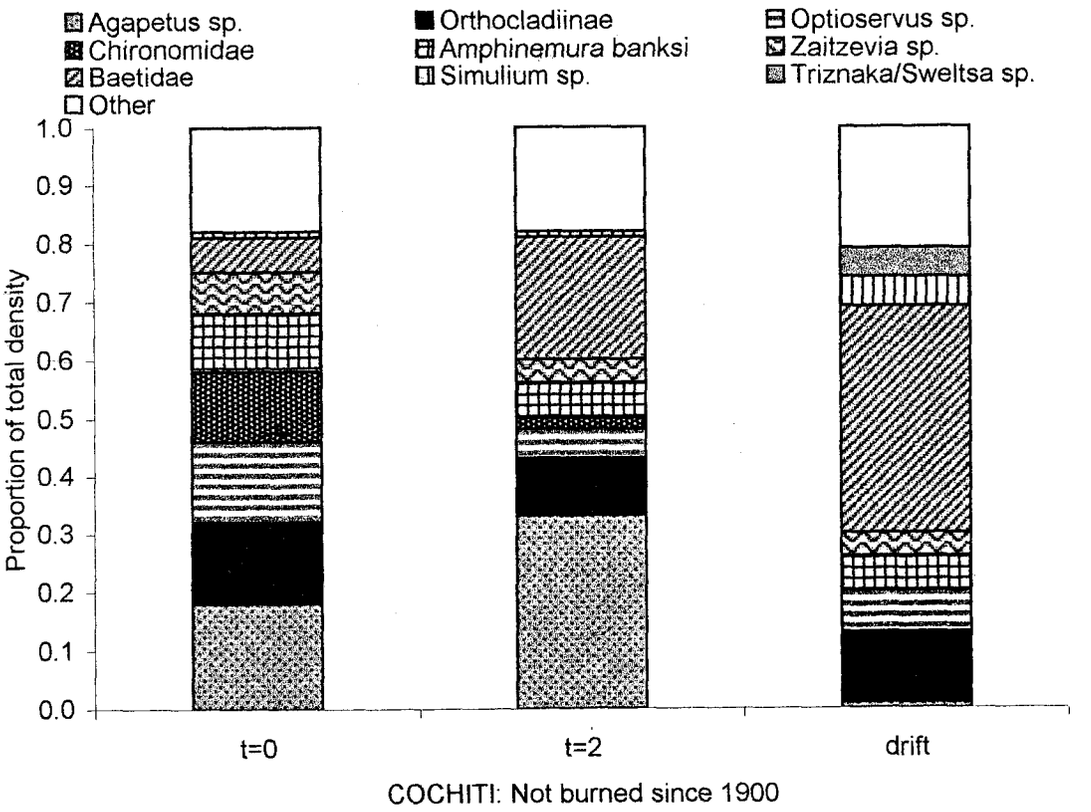
CAPULIN: 1996 Dome fire



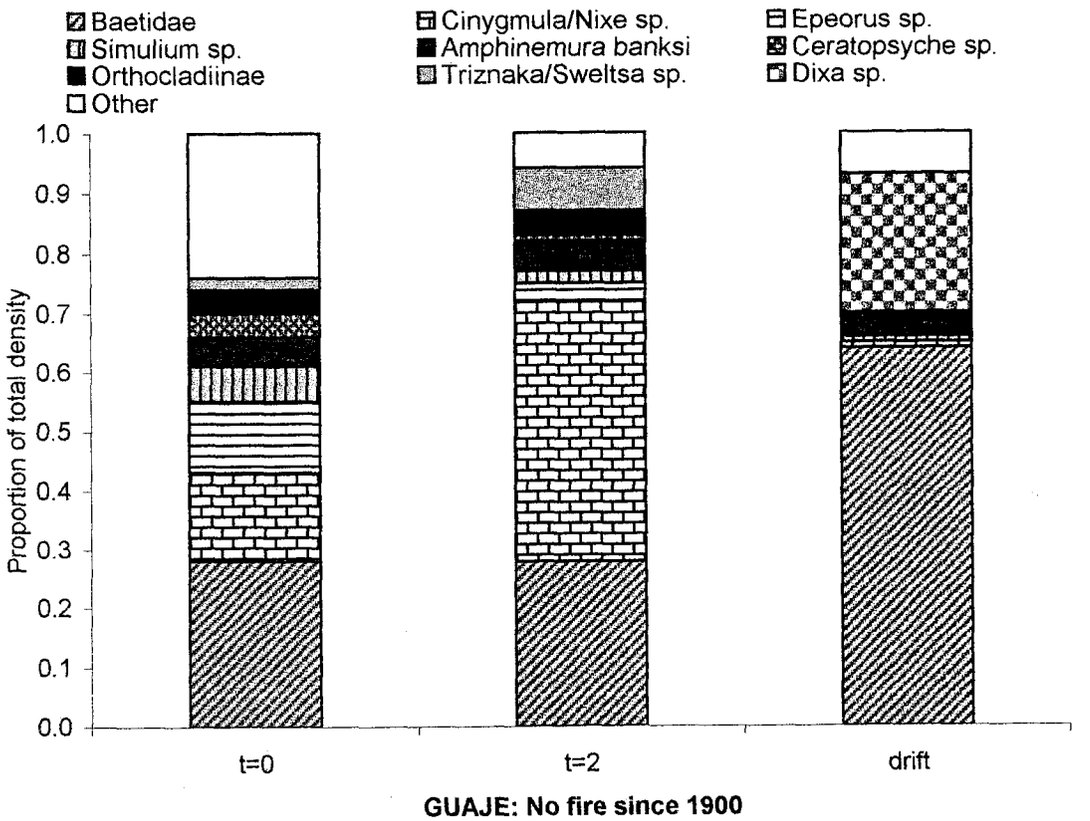
FRIJOLES: 1977 La Mesa fire



ALAMO: 1977 La Mesa fire



COCHITI: Not burned since 1900



GUAJE: No fire since 1900

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Appendix 3.1 a-f. Mean densities on cobbles (and standard deviations) for all taxa at each time point after (2, 4, 16, and 42 d) an experimental disturbance. Densities on natural cobbles collected at 0 d and 43 d are also reported. Only taxa that comprised more than 1% of total density in any canyon are presented. Total densities and taxa richness means are also presented.

APP 3.1a	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Capulin Taxa	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ameletus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Baetidae (small)	63.9	29.1	56.8	31.1	116.1	48.1	208.8	96.6	232.6	81.9	184.6	77.2
Baetis tricaudatus	32.1	10.4	10.8	10.0	11.1	13.4	13.0	16.8	3.2	1.7	3.6	3.3
Ephemerella sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.3	0.9	0.0	0.0	0.0	0.0
Epeorus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Nixe/Cinygmula sp.	0.5	0.9	0.1	0.5	0.1	0.2	1.1	1.3	1.1	1.3	0.6	1.2
Paraleptophlebia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7	0.0	0.0	0.0	0.0
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	1.0	0.5	1.0
Siphlonurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphinemura banksi	0.1	0.3	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0
Capnia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sweltsa/Triznaka sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hesperoperla pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isoperla sp.	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.0	2.0	1.1	3.6	2.5
Pteronarcella badia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agapetus sp.	5.0	3.2	5.2	8.8	5.5	5.7	6.0	3.6	2.9	2.7	2.8	3.5
Brachycentrus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.8	1.7
Hesperophylax sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratopsyche sp.	2.3	3.3	2.0	3.3	0.5	0.9	0.4	0.6	28.8	26.0	23.8	19.6
Lepidostoma sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycentropus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhyacophila sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microcaddisfly sp.	0.0	0.0	0.2	0.4	0.4	0.8	2.9	2.8	1.1	1.1	0.4	0.9
Chironominae	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tanytarsini	0.0	0.0	0.1	0.2	0.2	0.4	0.1	0.2	0.0	0.0	0.0	0.0
Orthocladiinae	7.4	6.2	2.3	3.4	1.9	1.6	5.2	4.1	10.7	6.2	8.8	7.5
Tanypodinae	1.1	1.7	0.0	0.0	0.0	0.0	0.5	1.0	0.4	0.6	0.3	0.7
Antocha sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.8
Calopharus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5
Chelifera sp.	0.4	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	0.4	0.8
Dicranota sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.5	0.2	0.6
Dixa sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maruina sp.	0.7	1.4	0.1	0.2	0.0	0.0	0.4	0.9	1.8	3.4	8.2	11.1
Palpomyia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.2	0.4	0.0	0.0
Simulium sp.	7.4	16.9	2.5	3.5	2.4	3.1	6.6	10.2	18.5	30.2	22.4	24.9
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0
Tabanus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.3	0.6	0.2	0.4	0.0	0.0	0.2	0.5	0.1	0.3	0.5	0.9
Agabus sp.	0.8	1.1	0.3	0.7	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Optioservus sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Zaitzevia sp.	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	16	na	20	na	20	na	20	na	18	na	18	na
DENSITY	122.9	34.0	80.3	44.3	138.0	54.6	245.7	97.7	304.9	119.3	262.1	96.9
TAXA RICHNESS	8.3	1.7	5.3	1.2	5.2	1.1	7.4	1.6	10.6	1.9	10.5	2.1

APP. 3.1b	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Sanchez Taxa	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Ameletus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Baetidae (small)	73.1	36.5	52.2	46.5	93.3	57.1	170.3	66.5	181.7	100.4	121.6	63.0
Baetis tricaudatus	13.3	9.0	9.5	9.8	3.0	3.0	3.7	3.1	9.2	10.1	8.4	9.5
Ephemerella sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Epeorus sp.	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0
Nixe/Cinygmula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Paraleptophlebia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.0
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Siphlonurus sp.	0.2	0.7	0.1	0.2	0.2	0.4	0.2	0.4	0.0	0.0	0.1	0.3
Amphinemura banksi	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Capnia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sweltsa/Triznaka sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hesperoperla pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isoperla sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pteronarcella badia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agapetus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brachycentrus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hesperophylax sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6
Ceratopsyche sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	8.4	16.2	3.6	7.0
Lepidostoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Polycentropus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Rhyacophila sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microcaddisfly sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4	0.1	0.3
Chironominae	0.1	0.5	0.3	0.6	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.3
Tanytarsini	0.2	0.5	0.0	0.0	0.1	0.2	0.0	0.0	0.2	0.5	0.0	0.0
Orthocladiinae	7.1	6.3	5.5	3.2	3.5	2.3	6.6	6.0	9.3	10.1	8.8	11.7
Tanypodinae	0.9	1.0	1.5	1.8	1.6	2.0	2.9	2.6	1.1	1.3	2.1	2.3
Antocha sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calopharus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.1	0.3
Chelifera sp.	0.1	0.2	0.0	0.0	0.1	0.2	0.1	0.2	0.2	0.7	0.0	0.0
Dicranota sp.	0.1	0.3	0.0	0.0	0.1	0.2	0.1	0.3	0.0	0.0	0.3	0.6
Dixa sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maruina sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	2.2	0.1	0.3
Palpomyia sp.	0.0	0.0	0.2	0.5	0.1	0.3	0.0	0.0	0.1	0.2	0.1	0.3
Simulium sp.	8.1	19.1	0.1	0.3	0.3	0.6	0.1	0.3	12.1	25.3	0.1	0.3
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tabanus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Agabus sp.	0.5	0.8	0.6	0.8	0.3	0.6	0.5	0.5	0.2	0.5	0.1	0.3
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Optioservus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3
Zaitzevia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
N	20	na	20	na	20	na	20	na	18	na	16	na
DENSITY	103.8	34.3	69.8	53.3	102.5	58.7	184.6	66.4	224.4	120.4	145.8	51.9
TAXA RICHNESS	5.0	1.1	4.5	1.1	4.6	1.2	4.9	1.4	6.3	1.4	5.1	1.3

APP. 3.1c	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Frijoles Taxa	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ameletus sp.	0.5	1.1	1.6	1.5	0.9	1.2	0.7	0.7	0.0	0.0	0.0	0.0
Baetidae (small)	4.9	8.4	49.2	37.3	55.5	29.5	23.0	14.3	64.2	58.3	33.9	45.5
Baetis tricaudatus	8.7	4.3	8.8	6.0	9.3	8.1	11.5	8.0	5.3	6.7	6.1	5.0
Ephemerella sp.	0.0	0.0	0.1	0.2	0.0	0.0	0.3	0.7	0.9	1.8	1.3	1.4
Epeorus sp.	2.8	3.4	0.1	0.5	0.2	0.4	0.1	0.2	0.0	0.0	0.0	0.0
Nixe/Cinygmula sp.	1.5	2.1	5.9	5.0	7.5	3.2	16.9	9.1	17.5	12.9	9.3	8.2
Paraleptophlebia sp.	2.1	2.4	3.1	3.2	2.6	2.1	3.1	2.6	2.7	2.7	1.2	1.8
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.7	0.2	0.4
Siphlonurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphinemura banksi	1.8	2.0	3.2	3.6	3.1	2.6	4.3	4.3	5.2	6.5	3.1	5.4
Capnia sp.	0.3	0.8	0.9	1.7	0.2	0.4	0.1	0.3	0.0	0.0	0.1	0.3
Sweltsa/Triznaka sp.	0.5	0.6	0.2	0.5	0.6	0.8	1.4	1.5	1.3	1.5	0.7	0.9
Hesperoperla pacifica	0.4	0.5	0.2	0.5	0.3	0.6	0.5	1.0	0.6	0.7	0.9	1.0
Isoperla sp.	0.7	0.8	0.7	0.9	0.5	0.7	0.5	0.8	0.8	1.2	0.2	0.4
Pteronarcella badia	0.4	1.1	0.1	0.3	0.1	0.2	0.3	0.8	0.3	1.2	0.0	0.0
Agapetus sp.	0.4	0.6	0.2	0.4	0.5	1.2	0.4	0.5	0.1	0.3	0.2	0.4
Brachycentrus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.9	0.4	0.8
Hesperophylax sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3
Ceratopsyche sp.	2.2	1.8	0.1	0.3	0.2	0.4	0.1	0.3	11.4	16.0	5.8	6.9
Lepidostoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3
Polycentropus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0
Rhyacophila sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2
Microcaddisfly sp.	0.2	0.4	0.1	0.3	0.1	0.2	0.6	1.2	0.5	1.0	1.4	1.9
Chironominae	0.7	0.8	0.1	0.3	0.0	0.0	0.1	0.2	26.6	32.4	93.4	89.5
Tanytarsini	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.3	0.0	0.0	0.0	0.0
Orthocladiinae	11.4	10.0	9.7	7.4	10.7	7.5	18.2	18.9	11.3	12.9	9.3	5.3
Tanypodinae	0.3	0.9	3.0	5.0	0.5	0.8	0.7	1.0	0.9	1.1	0.9	1.0
Antocha sp.	1.0	1.6	0.0	0.0	0.0	0.0	1.7	3.0	7.6	7.3	8.2	9.5
Calopharus sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7
Chelifera sp.	0.2	0.6	0.1	0.2	0.0	0.0	0.1	0.3	0.8	1.2	0.9	1.9
Dicranota sp.	0.1	0.2	0.2	0.4	0.2	0.4	0.4	0.8	0.6	0.9	0.4	0.7
Dixa sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.2	0.5
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maruina sp.	0.2	0.4	0.2	0.4	0.0	0.0	0.0	0.0	2.4	9.6	0.4	1.2
Palpomyia sp.	0.2	0.4	0.1	0.2	0.0	0.0	0.0	0.0	0.1	0.3	0.1	0.2
Simulium sp.	2.1	4.2	0.1	0.2	0.3	0.6	0.5	1.1	2.6	3.4	1.6	2.8
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2
Tabanus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agabus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.0
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2
Optioservus sp.	14.3	9.8	9.7	14.0	8.0	9.4	24.8	26.8	28.4	19.3	23.1	21.6
Zaitzevia sp.	4.1	4.9	1.3	2.0	0.8	1.1	2.9	2.5	2.6	3.0	3.5	2.8
N	17	na	20	na	20	na	20	na	18	na	17	na
DENSITY	61.8	25.0	98.4	51.0	101.7	39.4	112.9	51.8	196.2	100.4	207.7	94.4
TAXA RICHNESS	12.7	2.8	10.0	2.7	10.4	2.5	12.1	1.9	15.6	2.8	15.4	3.6

APP. 3.1d	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Alamo Taxa	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ameletus sp.	0.3	0.6	0.9	0.8	1.3	2.1	1.0	1.4	0.1	0.5	0.1	0.2
Baetidae (small)	0.3	0.7	0.0	0.0	0.1	0.5	0.0	0.0	0.3	0.6	1.0	1.3
Baetis tricaudatus	3.3	3.6	1.2	1.8	0.9	1.3	0.2	0.4	0.4	0.9	0.5	1.1
Ephemerella sp.	0.9	0.9	0.2	0.5	0.4	0.7	0.3	0.6	0.0	0.0	0.3	0.8
Epeorus sp.	4.9	4.1	0.4	1.0	0.6	1.3	0.6	1.5	0.1	0.2	0.1	0.2
Nixe/Cinygmula sp.	3.6	2.6	3.3	2.0	3.4	3.1	4.6	2.6	9.3	4.4	5.4	5.8
Paraleptophlebia sp.	0.2	0.4	0.0	0.0	0.1	0.3	0.2	0.5	0.2	0.6	0.1	0.3
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.7	0.5	0.9
Siphlonurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphinemura banksi	2.7	3.1	0.0	0.0	0.2	0.4	0.8	1.2	0.6	1.2	1.1	1.5
Capnia sp.	0.1	0.5	0.1	0.2	0.1	0.2	0.1	0.3	0.0	0.0	0.1	0.2
Sweltsa/Triznaka sp.	0.3	0.5	0.4	1.0	0.7	1.1	1.9	2.1	0.8	1.2	0.2	0.4
Hesperoperla pacifica	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isoperla sp.	2.6	3.3	0.6	0.8	0.5	0.7	1.1	1.5	0.6	1.0	3.1	3.4
Pteronarcella badia	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7
Agapetus sp.	0.0	0.0	0.5	0.9	0.6	0.9	3.3	4.0	11.9	11.0	9.9	8.8
Brachycentrus sp.	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.0	0.0	0.3	0.6	0.3	1.0	0.1	0.3	0.0	0.0	0.0	0.0
Hesperophylax sp.	0.3	0.8	0.2	0.4	0.5	1.4	0.5	0.8	0.2	0.4	0.1	0.3
Ceratopsyche sp.	4.0	3.6	0.2	0.4	0.1	0.2	0.2	0.7	0.9	1.7	1.7	3.4
Lepidostoma sp.	0.1	0.3	0.1	0.2	0.1	0.2	0.2	0.4	0.1	0.3	0.2	0.4
Polycentropus sp.	0.1	0.2	0.1	0.2	0.1	0.3	0.4	0.7	0.3	0.7	0.4	1.0
Rhyacophila sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Microcaddisfly sp.	0.3	0.6	0.0	0.0	0.0	0.0	0.1	0.3	0.6	0.9	2.9	6.3
Chironominae	0.1	0.3	0.0	0.0	0.0	0.0	0.2	0.5	8.1	9.8	3.4	5.8
Tanytarsini	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.3	1.0	0.5	1.1
Orthocladiinae	3.4	2.4	0.6	0.8	0.4	0.7	1.4	1.4	13.3	10.1	10.9	9.0
Tanypodinae	0.3	0.8	0.1	0.3	0.2	0.4	1.3	1.5	3.8	4.6	1.9	2.0
Antocha sp.	0.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Calopharus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Chelifera sp.	0.1	0.2	0.1	0.2	0.0	0.0	0.0	0.0	0.2	0.5	0.9	1.4
Dicranota sp.	0.1	0.2	0.0	0.0	0.2	0.4	0.0	0.0	0.2	0.4	0.6	0.8
Dixa sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.2	0.6
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Maruina sp.	2.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	3.2	5.5
Palpomyia sp.	0.1	0.2	0.2	0.5	0.0	0.0	1.6	2.3	1.4	1.6	0.8	1.2
Simulium sp.	0.2	0.5	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.3	0.1	0.5
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2
Tabanus sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0
Agabus sp.	0.0	0.0	0.0	0.0	0.1	0.2	0.2	0.4	0.1	0.2	0.1	0.3
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Optioservus sp.	0.1	0.3	0.0	0.0	0.0	0.0	0.2	0.4	0.6	1.3	0.3	0.6
Zaitzevia sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
N	18	na	20	na	19	na	20	na	18	na	17	na
DENSITY	30.5	14.9	9.2	4.0	10.8	7.4	20.4	8.8	56.1	22.8	51.2	19.8
TAXA RICHNESS	9.7	2.9	4.9	1.7	5.4	2.1	8.6	2.2	10.1	2.1	10.9	3.6

APP. 3.1e	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Cochiti Taxa	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ameletus sp.	0.1	0.3	0.0	0.0	0.1	0.3	0.1	0.3	0.0	0.0	0.0	0.0
Baetidae (small)	1.3	1.6	7.9	11.0	8.9	8.3	18.0	15.7	25.0	21.1	54.2	49.5
Baetis tricaudatus	6.6	4.9	4.9	3.2	4.5	3.0	3.0	3.0	1.1	1.2	2.4	3.6
Ephemerella sp.	2.7	2.0	0.4	0.6	0.7	1.0	0.5	1.0	1.2	1.6	1.4	1.5
Epeorus sp.	1.7	1.5	0.6	0.9	0.7	1.1	1.2	1.3	0.3	0.8	1.1	2.4
Nixe/Cinygmula sp.	1.3	1.7	0.7	0.9	1.4	1.9	7.2	3.6	3.8	2.6	3.0	4.3
Paraleptophlebia sp.	3.3	3.0	1.1	2.0	2.0	1.6	2.0	1.5	1.1	1.0	1.3	2.0
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Siphlonurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphinemura banksi	14.4	9.6	3.8	3.8	5.1	4.7	9.1	7.4	2.6	2.6	6.0	4.2
Capnia sp.	0.1	0.3	0.0	0.0	0.2	0.5	0.1	0.2	0.0	0.0	0.1	0.2
Sweltsa/Triznaka sp.	0.5	0.9	0.1	0.3	0.2	0.4	1.3	0.9	1.3	1.8	0.3	0.6
Hesperoperla pacifica	0.1	0.2	0.0	0.0	0.1	0.2	0.3	0.9	0.0	0.0	0.2	0.4
Isoperla sp.	0.5	0.6	0.2	0.4	0.1	0.5	0.9	1.0	1.6	1.3	1.9	1.9
Pteronarcella badia	1.0	1.7	0.3	0.8	0.0	0.0	0.4	1.1	0.3	0.8	0.1	0.2
Agapetus sp.	25.0	20.8	22.0	23.6	23.9	21.7	34.8	21.9	20.4	15.2	16.0	16.3
Brachycentrus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.1	0.2	0.2	0.5	0.0	0.0	0.1	0.3	0.0	0.0	0.1	0.3
Hesperophylax sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceratopsyche sp.	4.1	2.7	0.5	0.6	1.5	1.6	2.3	2.3	3.2	1.6	13.9	27.8
Lepidostoma sp.	3.9	4.9	4.0	4.2	3.9	3.3	2.2	2.4	0.6	0.8	0.7	1.2
Polycentropus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.4
Rhyacophila sp.	1.2	1.3	0.0	0.0	0.1	0.2	0.4	0.6	0.2	0.6	0.8	1.4
Microcaddisfly sp.	0.1	0.3	0.1	0.2	0.0	0.0	0.1	0.3	1.6	1.7	1.2	1.9
Chironominae	17.3	14.8	1.5	1.8	0.2	0.4	2.1	2.0	2.6	2.5	4.2	6.5
Tanytarsini	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.0	0.0	0.0	0.0	0.0
Orthocladiinae	18.2	9.9	5.3	4.4	3.9	3.3	8.2	6.4	4.7	3.2	9.1	7.6
Tanypodinae	0.8	1.4	0.2	0.6	0.2	0.5	0.4	0.5	0.3	1.0	0.3	0.6
Antocha sp.	1.9	1.6	0.1	0.3	0.2	0.4	0.1	0.2	0.7	1.0	4.4	6.7
Calopharus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	3.2
Chelifera sp.	0.9	0.8	0.1	0.2	0.1	0.5	0.3	0.5	0.0	0.0	0.1	0.3
Dicranota sp.	0.1	0.2	0.1	0.2	0.1	0.2	0.1	0.3	0.6	1.0	0.2	0.7
Dixa sp.	0.1	0.5	0.0	0.0	0.1	0.2	0.2	0.4	0.8	2.5	0.0	0.0
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2
Maruina sp.	0.6	1.6	0.1	0.5	0.0	0.0	0.0	0.0	0.1	0.2	4.4	11.2
Palpomyia sp.	0.1	0.3	0.1	0.2	0.0	0.0	0.0	0.0	0.1	0.2	0.5	1.8
Simulium sp.	0.7	1.9	0.4	0.6	0.6	1.5	0.3	1.0	0.0	0.0	1.0	1.9
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tabanus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Agabus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Optioservus sp.	17.3	11.3	2.4	3.1	4.0	5.3	13.9	12.8	25.0	28.6	8.6	5.0
Zaitzevia sp.	9.2	8.7	1.8	2.4	2.9	3.3	3.3	3.1	8.9	10.4	3.7	2.6
N	20	na	17	na	20	na	20	na	18	na	19	na
DENSITY	134.6	38.4	58.8	36.8	65.2	29.1	112.8	48.3	108.3	51.8	142.0	82.1
TAXA RICHNESS	16.6	2.1	10.9	3.3	11.0	2.7	15.1	3.0	14.2	2.4	15.4	2.5

APP. 2.1f	0	Days	2	Days	4	Days	16	Days	42	Days	43	Days
Guaje Taxa	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Ameletus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2
Baetidae (small)	8.2	5.8	0.6	0.9	0.4	0.9	0.3	0.6	3.7	8.8	31.8	32.3
Baetis tricaudatus	7.6	4.5	3.6	3.0	3.4	2.3	4.6	2.2	3.4	2.5	6.9	3.7
Ephemerella sp.	0.4	0.9	0.0	0.0	0.1	0.3	0.2	0.4	1.1	1.8	1.4	2.5
Epeorus sp.	5.6	4.1	0.3	0.7	0.9	1.0	0.6	1.1	0.2	0.4	0.2	0.7
Nixe/Cinygmula sp.	7.3	4.3	6.4	4.0	8.6	3.4	6.4	3.4	4.4	2.7	4.6	3.0
Paraleptophlebia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Tricorythodes sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Siphlonurus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Amphinemura banksi	2.7	1.8	0.6	0.6	0.4	0.8	1.2	1.4	1.7	2.7	1.8	2.6
Capnia sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sweltsa/Triznaka sp.	1.3	1.7	0.8	1.0	2.1	1.7	2.0	2.0	2.4	2.3	1.7	1.6
Hesperoperla pacifica	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Isoperla sp.	0.3	0.5	0.1	0.2	0.2	0.5	0.4	0.8	0.1	0.2	1.1	0.9
Pteronarcella badia	1.5	1.5	0.0	0.0	0.1	0.2	0.3	0.6	0.1	0.3	0.4	1.0
Agapetus sp.	0.1	0.2	0.0	0.0	0.0	0.0	3.9	4.5	21.0	14.1	25.1	14.3
Brachycentrus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Glossosoma sp.	0.4	0.6	0.2	0.4	0.5	1.0	0.0	0.0	0.0	0.0	0.4	1.2
Hesperophylax sp.	0.1	0.2	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Ceratopsyche sp.	2.1	2.1	0.1	0.3	0.1	0.5	0.3	0.8	0.3	0.4	1.3	1.6
Lepidostoma sp.	1.7	2.2	0.1	0.3	0.6	0.8	1.5	1.6	4.3	2.9	2.0	4.1
Polycentropus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhyacophila sp.	2.4	7.4	0.0	0.0	0.0	0.0	0.1	0.3	0.1	0.5	0.6	1.1
Microcaddisfly sp.	0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0
Chironominae	1.9	2.9	0.2	0.5	0.0	0.0	0.2	0.4	0.2	0.5	0.9	1.2
Tanytarsini	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Orthocladiinae	2.0	2.3	0.5	0.6	0.6	1.1	3.7	3.6	4.6	2.9	22.5	19.5
Tanypodinae	0.1	0.2	0.0	0.0	0.1	0.2	0.1	0.3	0.1	0.2	0.1	0.2
Antocha sp.	0.7	1.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.8	2.4
Calopharus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chelifera sp.	0.3	0.4	0.0	0.0	0.1	0.2	0.0	0.0	0.1	0.2	0.4	0.9
Dicranota sp.	0.1	0.3	0.0	0.0	0.1	0.2	0.1	0.2	0.1	0.2	0.2	0.6
Dixa sp.	0.0	0.0	0.0	0.0	0.1	0.2	0.1	0.2	0.0	0.0	0.2	0.5
Hexatoma sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Maruina sp.	1.7	3.1	0.1	0.3	0.0	0.0	0.3	0.4	0.1	0.2	0.0	0.0
Palpomyia sp.	0.1	0.2	0.1	0.2	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Simulium sp.	3.3	6.3	0.2	0.4	0.4	0.7	0.3	0.6	0.2	0.4	0.7	2.1
Tipula sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2
Tabanus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oplonaeschna sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Agabus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Narpus sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Optioservus sp.	1.6	2.3	0.3	0.6	0.4	0.7	1.1	1.7	3.4	2.9	3.3	3.2
Zaitzevia sp.	0.5	1.6	0.0	0.0	0.0	0.0	0.7	1.4	0.1	0.3	0.4	1.1
N	20	na	19	na	20	na	20	na	20	na	20	na
DENSITY	53.9	20.5	13.4	7.0	18.8	5.6	28.2	8.8	51.8	23.5	109.2	53.5
TAXA RICHNESS	12.8	2.7	5.0	1.8	5.9	2.3	8.6	2.2	9.6	1.8	12.0	2.9

APPENDIX A

COLONIZATION AND GROWTH OF A SHREDDER STONEFLY, *PTERONARCELLA BADIA* HAGEN, ON BURNED CONIFEROUS AND DECIDUOUS DETRITUS

ABSTRACT

Wildfires can reduce both quantity and quality of detrital inputs into streams by removal or change of riparian vegetation, and also by increased flushing from post-fire floods. These changes may have negative impacts on detritivorous insects, especially shredders that specialize on coarse organic material. In this study, I conducted an *in situ* experiment to compare leaf breakdown rates of four detritus treatments: burned and unburned deciduous leaves (*Populus deltoides*), and burned and unburned coniferous needles (*Pinus ponderosa*). I also conducted experiments to compare colonization and growth of the shredder stonefly, *Pteronarcella badia* Hagen, on these detritus treatments. Microbial respiration and levels of carbon, nitrogen, and lipid were measured to compare nutritional quality of the detritus treatments. Breakdown rates and microbial respiration were highest on unburned deciduous leaves and lowest on burned pine needles. In spite of these differences, colonization of *P. badia* was similar across treatments. A microcosm experiment revealed that *P. badia* also grew similarly on all treatments, despite differences in nutritional quality. My study suggests that moderate burning of riparian vegetation, both deciduous and coniferous, does not alter nutritional content or leaf structure enough to negatively impact growth to *P. badia* shredders. Instead, export of high quality detritus during post-fire floods may have stronger negative impacts on detritivores.

INTRODUCTION

Heterotrophic energy sources are the primary energy pathway in lotic systems in low-order woodland streams (Allan 1995). Terrestrial organic matter inputs are an important food source for invertebrate detritivores, who play an important role in both function and structure of aquatic food webs. Functionally, detritivores are responsible for up to 25 percent of leaf litter degradation in streams (Petersen and Cummins 1974; see review in Allan 1995). Not surprisingly, experimental removal of detritivorous invertebrates has resulted in lower decomposition rates of terrestrial organic matter (Wallace et al. 1982). Further, shredder detritivores break down coarse organic matter (CPOM) into finer matter (FPOM), thereby making FPOM available to collectors (Cummins et al. 1973; Short and Maslin 1977; Wallace and Webster 1996). Thus, changes in quantity, quality, or timing of terrestrial litter inputs as a result of disturbance may negatively impact detritivore populations (Rounick and Winterbourn 1983) and result in bottom-up effects on aquatic food webs (Wallace et al. 1997).

Reduced inputs of detritus have been observed following disturbances that alter terrestrial-aquatic ecotones, including agricultural land use (Delong and Brusven 1993; Townsend et al. 1997), logging practices (Webster et al. 1990; Bilby and Bisson 1992),

prescribed fire treatments (Britton 1990), and wildfire (McIntyre and Minshall 1996; Minshall et al. 1997). Forestry practices and wildfire can further alter in-stream retention of detritus through increased streamflow, removal of debris dams, and loss of woody debris inputs (Bilby 1981; Minshall et al. 1997). Along with detritus quantity, prescribed fire and wildfires can also reduce quality of detritus due to increased charcoal content (Minshall et al. 1997) and moderate to long-term changes in riparian vegetation species (Britton 1990).

Unnaturally intense and destructive wildfires are becoming more common in North American conifer forests and shrublands (Van Wagner 1983, 1988), where high-frequency, low-intensity fires have been replaced by low-frequency, high-intensity canopy fires (Touchan et al. 1996). Impacts of a wildfire on riparian vegetation, and also on stream communities, vary depending on the fire's intensity (Lawrence and Minshall 1994; Gresswell 1999). Studies documenting the impact of post-fire changes in quantity and quality of detritus on invertebrate communities have been largely descriptive. Reductions in both terrestrial detritus inputs and in-stream retention as a result of fire have been correlated with shifts in invertebrate community composition from shredder and collector-gatherer dominated communities to more generalist herbivore-detritivore feeders after a wildfire (Molles 1982; Mihuc et al. 1996; Chapter1). Only one experimental study has been conducted to compare the nutritional content of burned and unburned detritus, and to assess the ability of invertebrate taxa to grow on burned detritus (Mihuc and Minshall 1995). They found that only generalist detritivores and generalist detritivore-herbivores in a burned stream could grow on naturally burned detritus.

Mihuc and Minshall (1995) showed that more insect taxa grew on unburned versus burned detritus, and also found that deciduous detritus showed higher microbial conditioning than coniferous detritus. However, these authors did not specifically compare growth on burned deciduous versus burned coniferous detritus. In this study, I conducted an *in situ* field experiment to compare breakdown rates, microbial activity, and nutritional content of burned and unburned detritus from two sources: cottonwood leaves (*Populus deltoides*; hereafter referred to as leaves) and ponderosa pine needles (*Pinus ponderosa*; hereafter referred to as needles). I also compared colonization of a common invertebrate shredder in western streams, *Pteronarcella badia* Hagen stoneflies, on these four leafpack treatments. Finally, I conducted a laboratory experiment in stream microcosms to compare growth of *P. badia* on burned and unburned leaves and needles. I hypothesized that microbial activity and nutrient content, and thus growth and colonization of *P. badia*, would be highest on unburned leaves, intermediate for unburned needles and burned leaves, and lowest on burned needles.

METHODS

Field experiment

Cottonwood leaves and ponderosa pine needles were gathered just prior to abscission and dried at 56°C for 24 h. Half of the needles and leaves were burned in a K.H. Huppert muffle furnace to simulate a fire. Modifying the 100% burn treatment as

described by Mihuc and Minshall (1995), I burned materials at 450°C until materials were blackened but still structurally intact (approximately 1 min.). This treatment achieved a light-moderate burn, where 35-50 % of the surface area of a leaf or needle was blackened and left a charcoal residue when touched (but did not immediately break apart). I chose this less severe burn treatment (compared to Mihuc and Minshall 1995) so that the detritus maintained its structural integrity when subjected to streamflow and would be available as coarse particles to shredders. Also, this burn level simulated burned detritus collected in the field after an intense canopy fire in a Pajarito Plateau Stream, near Los Alamos, NM (N. K. M Vieira, unpublished data). Each of four detritus treatments, burned and unburned deciduous leaves and pine needles, were weighed into 8-g dry weight samples on an electronic precision balance (model BP110S, Satorius Co., Edgewood, NY). Artificial leafpacks were constructed by placing leaves or needle samples in 2.27-kg citrus bags (Cady Bag Co., Pearson, GA) with 5 x 5 mm mesh openings. Leakpacks were transported in plastic Ziplock® bags to prevent leaf or needle loss prior to the study.

Ninety-six leafpacks (24 per treatment) were placed in a riffle at 2320 m elevation in the Cache La Poudre River, Colorado, on October 22, 1999. A maximum of 10 leafpacks, including at least two from each detritus treatment, were randomly allocated to each of ten wooden racks and tethered with 36-cm cable ties. Racks were placed in two rows (n=5 each) in the center of the riffle, perpendicular to the current and at 0.5 m depth. Leafpacks were collected after 27 and 50 d (n = 12 per treatment). On each date, leafpacks were sampled in a stratified random fashion, where at least one of each

treatment was sampled from each rack. Leafpacks (including invertebrates) were collected with a 250 μm dipnet, placed in large Ziplock® bags filled with stream water, and transported in coolers to the laboratory.

All invertebrates were removed from each leafpack and preserved in 90% ethanol, and *P. badia* individuals were counted. However, for the 27-d leafpacks, a random sample of live *P. badia*, stratified across leafpacks from all four detritus treatments, were counted on each leafpack and then transferred to a stream microcosm to be used in later feeding experiments. After invertebrates were removed, leafpacks collected after 27 and 50 d were rinsed with water, dried at 56°C for 24 h, and weighed to the nearest 0.1 mg obtain final dry mass. For 50-d samples, 1-g of leaves or needles were randomly selected from five leafpacks from each treatment and pooled for nutritional analysis. A LECO CHN-1000 Carbon Hydrogen Nitrogen analyzer was used to measure percent carbon and percent nitrogen (an indication of proteins) values. Total lipid or % solvent extract was removed from the sample with chloroform-methanol extraction.

To compare microbial colonization across detritus treatments, I measured microbial respiration by monitoring reductions in dissolved oxygen. Water for the experiment was obtained from Horsetooth Reservoir, Fort Collins, CO and was filtered (0.45 μm) to remove organics and other microbes. Three leaves or needles from each treatment were randomly picked from 50-d leafpacks before they were dried and weighed, and each leaf and needle was randomly allocated to each of 12, 50-ml beakers (n = 3 per treatment). Four additional beakers, two with unburned leaves and two with

burned needles, were used to track changes in oxygen levels in order to determine when to terminate the study (range-finding to prevent 100% oxygen loss). Two beakers without detritus were included to account for microbial activity in the reservoir water. At time zero, dissolved oxygen (mg/L) was measured in each beaker (Yellow Springs, OH model 52 oxygen meter). Beakers were then sealed with Parafilm® to prevent exchange with atmospheric oxygen, placed on magnetic stir-plates to maintain water circulation, and incubated at 6°C. After 18 h, DO was measured again and wet-weights (g) of leaves or needles in each beaker were recorded.

Microcosm experiment

Live *P. badia* (length: mean = 47.6 mm, SD = 1.89 mm) from 27-d unburned pine and leaf treatments were transferred to stream microcosms and allowed to acclimate for 24 h without food at the Stream Research Laboratory, Colorado State University, Fort Collins, CO. Microcosms were oval (76 x 46 x 14 cm) flow-through fiberglass tanks with a water volume of 13-L and a current of 30 cm/s generated by a paddle wheel. Unfiltered water was supplied from Horsetooth Reservoir and microcosms were housed in a greenhouse to provide natural light regimes. Four cages were randomly allocated to each of ten microcosms. Cages were square Tupperware® containers (15.5cm x 11cm x 11cm) with 6-cm diameter holes cut into each side. Holes were covered by 250-μm mesh to allow water flow but prevent escape of detritus or *P. badia*. Within each microcosm, each detritus-burn treatment was randomly allocated to one of the four cages (n=10 cages per treatment). Leaves and needles in the detritus treatments were covered with 1-mm

mesh and a cobble was used to anchor the mesh and to provide cover for *P. badia*. *Pteronarcella badia* individuals were measured for length with digital calipers and three individuals were randomly assigned to each of the 40 cages. Length was used as an indicator for growth instead of dry mass to more easily obtain before and after measurements on live insects. *Pteronarcella badia* were allowed to feed for 12 d, after which organisms were re-measured. To determine microbial conditioning of detritus treatments, microbial respiration was measured with leaves and needles used in the microcosm experiment and run for 13 h.

Statistical analysis

For comparisons of colonization across treatments, *P. badia* abundances on 27 d and 50 d leafpacks were adjusted to the remaining leafpack dry mass at the time of collection (no. individuals / g leafpack mass remaining). Decomposition after 27 d and 50 d was calculated as the percent loss of dry mass relative to the initial dry mass. Microbial respiration was calculated as the percent loss in DO (mg/L/g detritus) after being adjusted for DO changes in water-only beakers. Total growth was calculated as the percent change in length of individual stoneflies relative to the mean initial length of the three stoneflies in each cage.

All statistical analyses were conducted with use of SAS/STAT statistical software (SAS Institute 1996). I compared leaf decomposition, colonization and growth of *P. badia*, and microbial respiration across treatments with means and 95% confidence

intervals. I employed ANOVA and Tukey's HSD comparisons of means to assess differences among the four treatments and to investigate block effects due to microcosm and position of wooden racks in the stream. All independent variables and all two-way interactions were originally included in a global ANOVA model. However, if variables were highly insignificant ($p > 0.5$) they were removed for a collapsed model of burn treatment, detritus type, and burn * type interactions. Assumptions of normality and heterogeneity and independence of errors were checked with diagnostic tests available in SAS, and appropriate transformations were performed (Ott 1993).

RESULTS

Conditions in the Poudre River at the beginning of the colonization study were the following: 4.6 °C, 10.6 mg DO/L, 7.3 pH and 50 μS conductivity. In general, cottonwood leafpacks lost a higher percentage of their original mass compared to pine needle leafpacks after both 27 d and 50 d (Table 4.1). Unburned cottonwood leaves showed the highest loss of 48.8% while burned pine showed the lowest loss of 24.4%. For each treatment, total percent loss was similar between 27-d and 50-d samples ($p_{model} = 0.7988$; $df_{model} = 95$). There were no significant block effects due to location in the stream. A collapsed two-way ANOVA model, with 27 d and 50 d samples combined, revealed that burn treatment, detritus type, and the treatment x type interaction contributed to differences in decomposition (all $p < 0.0001$; $df_{model} = 95$). Total percent loss was disproportionately higher for unburned leaves, followed by burned leaves, and then burned and unburned needles (Figure 4.1).

In contrast to leafpack decomposition rates, I did not find a difference in number of *P. badia* colonizing burned and unburned leaves and needles (Figure 4.1). There was no significant difference in colonization between 27 d and 50 d, among wooden racks, or between any treatment (ANOVA: $p_{model} = 0.6911$ and $df_{model} = 95$; log-transformed data). However, a trend existed where colonization was slightly higher on pine needles, especially on unburned pine needles (Table 4.1).

In both respiration studies (18 hr and 13 hr tests), the first measure of dissolved oxygen levels in range- finding beakers indicated that enough time had passed to detect differences in oxygen levels between treatments. Therefore, oxygen levels were measured in all beakers (range- finding and treatment beakers) at the same time. This allowed for range-finding beakers to be added as additional replicates for the unburned leaf and burned pine treatments (n = 5 for these two treatments). Microbial respiration was higher on leaves compared to needles in both experiments (Table 4.2), and there was no significant difference between experiments ($p_{model} = 0.3584$; $df_{model} = 31$; log-transformed data). A collapsed ANOVA model, with both experiments combined, showed differences between burn treatments and detritus types ($p < 0.0001$ for both factors; $df_{model} = 31$), but no significant interaction ($p = 0.5813$; $df_{model} = 31$). Microbial respiration was highest on unburned leaves, followed by burned leaves, and lowest on unburned and burned needles (Figure 4.1).

Although burned leaves and needles were notably different in texture and color than unburned organic material, and microbial respiration was lower on burned material, nutritional analysis indicated similar chemical makeup between burned and unburned treatments within each detritus type (Table 4.3). However, there was a notable difference between needles and leaves. Burned and unburned needles were higher in lipids and carbon, but lower in nitrogen, compared to leaves.

Physical and chemical conditions during the microcosm experiment were the following: 11.7 °C, 7.7 mg DO/L, 7.7 pH and 60 uS conductivity. Nine *P. badia* died from unknown reasons and were thus excluded from analysis. *P. badia* grew an average of 1.4 mm in length (approximately 20% of their initial length) over 12 d on all treatments (Figure 4. 1). Relative growth rates were similar regardless of detritus type or burn treatment and there was no significant block effects due to microcosm (ANOVA: $p_{model} = 0.9211$ and $df_{model} = 39$; Figure 4.1).

DISCUSSION

I found clear differences in leafpack decomposition between burn treatments and detritus types, where total percent losses of leafpack mass ranged between 20 - 50%. Decomposition rates of burned detritus treatments were slower compared to unburned treatments of similar detritus types (i.e. leaves or needles), especially for deciduous leaves. Also, detritus treatments comprised of pine needles showed slower decomposition compared to treatments with deciduous leaves. For all detritus treatments,

I observed little difference in percent loss of leafpack mass between 27 and 50 d, indicating that decomposition rate slowed considerably after 27 d. Decomposition rates for unburned cottonwood leaves (0.01 day^{-1}) and pine needles (0.005 day^{-1}) were slightly faster than rates published in previous studies for related plant species (see review in Allan 1995).

Differences in chemical and structural makeup between treatments likely contributed to differences in decay rates between leaves and needles. For instance, others have shown that pine needles have longer decomposition half-lives than deciduous leaves due to their waxy cuticle and rigid structure (Webster and Benfield 1986). My burned and unburned detritus also differed in structure and texture, where burned needles and leaves were more brittle, and the cuticle was reduced or absent on burned needles (T. Barnes, Colorado State University, personal observation). However, a difference in burned and unburned decomposition was only found for deciduous leaves. Further, leafpacks with unburned leaves lost more mass than those with burned leaves, even though burned leaves were more brittle and thus more susceptible to mechanical breakdown via streamflow. Thus, structural changes due to burn treatments did not likely influence differences in leafpack decomposition in this study.

Microbial activity likely contributed to differences in leafpack decomposition among treatments. Differences in microbial oxygen consumption between burned treatments, and between needles and leaves, were very similar to patterns observed for leafpack decomposition. Unburned leaves showed the highest percent loss of mass and

the highest microbial respiration, while burned needles showed lower percent losses and the lowest microbial activity. Other studies have shown similar positive correlation between litter breakdown and conditioning, especially with fungal colonization (Webster and Benfield 1986). Similar to my study, Mihuc and Minshall (1995) found lower microbial activity on needles versus deciduous leaves. Microbial activity may be lower on needles because the cuticle inhibits fungal colonization (Barlacher et al. 1978). I also found that microbial activity was lower on burned materials, similar to the findings of Mihuc and Minshall (1995), who found lower fungal colonization on burned CPOM. While fungal colonization may likely have contributed to decomposition differences in this study, I did not distinguish fungal versus bacterial respiration.

Feeding and other activities of detritivores contribute up to 25% of decomposition of detritus in experimental leafpacks (Petersen and Cummins 1974). Shredders prefer detritus that has been conditioned (Arsuffi and Suberkropp 1985), especially if conditioning has increased nitrogen (protein) or lipid content (Kaushik and Hynes 1971; Cargill et al. 1985). Thus, positive correlations between decomposition rates and total shredder densities (Fabre and Chavet 1998) or detritivore feeding preferences (Cargill et al. 1985) have been observed. In contrast, I did not find a relationship between decomposition rates and densities of *P. badia*, the dominant shredder on leafpacks in terms of biomass (N. K. M. Vieira, Colorado State University, unpublished data). Colonization was very similar across burn treatments and detritus types, and no obvious trends were observed across either factor. Nelson (2000) also found little correspondence between leaf breakdown rates and densities of the nemourid shredder *Zapada cinctipes*

Banks in metal impacted streams. Boulton and Lake (1992) only found a correlation between total shredders and benthic organic material in riffle habitats, and this relationship varied widely with season. In my study, leafpacks may not have been in the stream long enough to detect effects of detritivore activity on decomposition.

Associations between detritivore densities and detritus mass alone do not demonstrate how detritivores utilize leafpacks; feeding activity and growth must be documented to assess whether detritus is a viable food source or merely a substrate for colonization. Previous studies have shown higher growth rate of invertebrates on conditioned versus unconditioned detritus (Sutcliffe et al. 1981; Lawson et al. 1984) and on detritus with higher microbial respiration (Ward and Cummins 1979). However, in my feeding experiment, *P. badia* grew similarly on all treatments, regardless of differences in microbial respiration. *P. badia* in my experiment may have been able to grow on proteins in leaves and lipids in needles, since both nutrients have been cited as important food resources for macroinvertebrates (Short et al. 1980; Cargill et al. 1985). Also, *P. badia* may have utilized the microbes rather than the detritus itself. My respiration studies confirmed that burned detritus was at least colonized by low densities of microbes, which may have been enough to provide adequate food for *P. badia* for the short duration of the feeding experiment.

In contrast to my findings, Mihuc and Minshall (1995) found that 10 of 11 taxa could not grow on 100% burned detritus, and cited low lipid and protein content, as well as low microbial densities, as potential explanations. However, they also found greater

reductions in microbial colonization on 100 % burned treatments and greater differences in protein and lipids due to burning. I found that 100% burned material disintegrated into fine particulate matter when in contact with streamflow (N. K. M. Vieira, unpublished data), and thus used a less severe burn treatment similar to the 35% natural burn also tested in Mihuc and Minshall (1995). In their study, naturally burned material showed slightly higher bacterial colonization than the 100% burned material. Further, Mihuc and Minshall (1995) found that three generalist detritivore taxa could grow on this conditioned 35% burn detritus, including the nemourid stonefly *Zapada columbiana* Claasen. In general, while more severely burned material is much lower in nutritional quality, light to moderately burned CPOM detritus is more similar to unburned detritus in nutritional value. Lightly burned detritus is also more available to shredders due to better structural integrity and thus slower mechanical breakdown from streamflow.

Changes in quality and quantity of terrestrial litter inputs after a fire should impact shredders that specialize on course organic inputs from riparian habitats more than collector detritivores. Mihuc and Minshall (1995) experimentally demonstrated that moderately burned (35%) detritus was an adequate food source for several generalist detritivores, but not for the specialist shredders *Oligophlebodes sigma* Milne (Trichoptera) and *Ephemerella infrequens* McDunnough (Ephemeroptera). However, in the field, Minshall et al. (1997) did not find obvious reductions in shredders, despite high charcoal content of detritus in burned streams. My microcosm experiment shows that moderately burned leaves and needles may still provide food to some shredder taxa such

as pteronarcid stoneflies. Thus, changes in food quality may not have strong influences on detritivore populations in burned streams.

Changes in food quantity due to reduced retention from post-fire flooding may be more important than reduced food quality in burned streams (Britton 1990; McIntye and Minshall 1996; Minshall et al. 1997). I documented severe reductions or complete removal of shredder taxa (primarily Plecoptera: Nemouridae and Diptera: Tipulidae) following the 1996 Dome Fire and multiple post-fire 100-year flood events in burned Pajarito Plateau streams, near Los Alamos, NM (Chapter 1; Chapter 3). Recolonization success of these taxa remained low until post-fire flashfloods abated (Chapter 1). In contrast, the shredders *P. badia* and *Amphinemura banksi* (Baumann and Gaufin) quickly recolonized another Pajarito stream burned in the 2000 Cerro Grande fire, despite severe burning and flushing of detritus during severe post-fire floods (Vieira and Clements 2003). Unburned stream reaches upstream were able to provide a source of both colonists and detritus. Thus, it is unclear as to whether shredder populations were influenced by changes in detritus resources, or by the interactions between recolonization abilities and availability of refugia (Chapter 2). Understanding the relative importance of changes in food quantity and quality, versus other physico-chemical impacts of fire, will aid in determining management and protection scenarios for riparian zones in fire-prone watersheds.

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Table A.1. Mean percent loss of dry mass of leafpacks consisting of burned and unburned ponderosa pine needles and deciduous cottonwood leaves, and mean number of *Pteronarcella badia* colonizing these treatments. Leafpacks were allowed to condition and breakdown for 27 d or 50 d in the Cache la Poudre River, Colorado. Initial dry-mass of each leafpack was 8-g. (N = 12).

		Percent loss of leakpack biomass				**Number of P. badia**			
		Burned		Unburned		Burned		Unburned	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Detritus Type	Days in Stream								
Leaves	27	38.57	5.62	47.60	1.89	9	3.83	8	4.50
	50	34.37	2.73	48.83	2.91	9	4.94	5	1.77
Needles	27	24.39	8.66	24.58	8.56	8	4.75	10	8.67
	50	25.38	14.68	25.03	3.18	10	6.17	10	9.67

Table A.2. Mean oxygen use (% reduction of $mgO_2/L/g$-detritus) of microbes on burned and unburned ponderosa pine needles and deciduous cottonwood leaves in two independent trials. Leaves and needles were conditioned for 27 d in Trial 1 and 50 d in Trial 2.

		Burned			Unburned		
Detritus Type	Trial	N	Mean	SD	N	Mean	SD
Leaves							
	1	3	40.5	12.2	5	64.7	10.6
	2	3	38.5	21.8	5	93.1	30.0
Needles							
	1	5	16.3	4.6	3	32.6	4.9
	2	5	9.8	7.5	3	25.8	5.4

Table A.3. Nutritional analysis of burned and unburned ponderosa pine needles and cottonwood leaves conditioned for 50 d in the Cache la Poudre River, Colorado. Percent solvent extract represents both nutritive and non-nutritive lipids.

Detritus Type	Burn Treatment	% Solvent Extract	% Carbon	% Nitrogen
Leaves	Unburned	3.8	42.8	2.0
	Burned	4.1	48.4	1.9
Needles	Unburned	12.1	51.6	1.2
	Burned	10.6	55.7	1.4

LIST OF FIGURES