

Final Report:

**A Natural Experiment Investigating Effects of a Wildfire on
Stream Insect Communities in Bandelier National Monument,
New Mexico**

Submitted by: Nicole MacRury, PhD Candidate

Principle Investigator: Dr. Will Clements

NPS Contact: Brian Jacobs, Bandelier National Monument

ABSTRACT

While the effects of wildfire on stream hydrology and water chemistry are well documented, impacts of wildfire on stream insects are poorly understood. In this research, WE had the unique opportunity to assess the impacts of wildfire and post-fire flashfloods on with a natural experiment, where WE compared benthic invertebrate communities before and after the fire in a burned and a reference stream. Invertebrate communities in both streams were sampled seasonally in two years before, and six years after, the 1996 Dome fire in Bandelier National Monument, New Mexico. WE found that although post-fire floods in the burned stream reduced benthic insect densities to near zero, quick recovery to pre-fire and reference stream densities occurred due to the colonization of *Simulium* black flies, *Baetis* mayflies, and chironomid midges. Taxa richness took longer to recover since more disturbance-sensitive taxa, such as stoneflies and Elmids beetles, were slower to recover during severe post-fire flooding. While invertebrate community composition was similar between the two streams prior to the fire, composition differed dramatically immediately after the fire and did not return to pre-fire or reference composition, even after flooding ceased. Strong negative impacts observed in this study suggest that aquatic insect communities in Bandelier National Monument may be highly susceptible to flashfloods and erosion typically associated with severe canopy fires. Community composition proved to be the most sensitive response in documenting post-fire recovery

INTRODUCTION

The importance of disturbance in shaping benthic community structure is a central tenet in stream ecology (Resh et al. 1988; Reice et al. 1990). Disturbances are discrete events in time that disrupt ecosystem, community, or population structure, as well as change abiotic conditions (White and Pickett 1985). These abiotic changes are outside of the "predictable" range for the system (Resh et al. 1988) and beyond expectations of aquatic organisms given their annual life cycles and habitat (Wallace 1990). Natural disturbances in stream ecosystems are expressed in terms of flow intermittence, predictability, and flood frequency (Poff and Ward 1989); flood magnitude (Quinn and Hickey 1990); and substrate stability (Death and Winterbourn 1995; Townsend et al. 1997). These physical and chemical changes can result in pulse (acute), press (chronic) or ramp (graded) responses in benthic invertebrate communities (Lake 2000). Responses include resistance (magnitude of change) and resilience (time to recovery to pre-disturbance or pre-determined "normal" levels), both of which depend on the existence of survivors, proximity of colonist sources, and taxa-specific dispersal abilities and tolerance to post-disturbance stream conditions (Gray and Fisher 1981; Cushing and Gaines 1989; Boulton et al. 1992).

Single spate and drought events have shown variable and site-specific responses across a wide range of stream habitats (Sheldon 1984; Wallace 1990). Physico-chemical

impacts of spates are usually temporary and "predictable" since they may occur multiple times within an annual flood season. Thus, invertebrate communities have shown mild to moderate pulse responses to spates, where invertebrate taxa were highly resilient (Lake 2000). However, spates that occur outside of the typical flood season, in high gradient areas, or in endorheic spring-fed streams have shown less resistance and longer recovery time (Resh et al. 1988; Cushing and Gaines 1989). Droughts have also resulted in similar dramatic impacts on invertebrate communities due to their gradual and longer-term impacts on aquatic habitat (Resh et al 1988; Lake 2000). More severe watershed-level disturbances have generally resulted in severe impacts and slower community recovery (Niemi et al. 1990; Yount and Niemi 1990; Wallace 1990; Mackay 1992), and thus more distinct press and ramp changes in community resistance and resilience. Clearly, studies on large spatio-temporal scale disturbances hold the greatest potential to explore invertebrate community recovery dynamics in fluvial systems.

Increasing numbers of unnaturally intense wildfires in the western US (Van Wagner 1983) have provided unique opportunities to investigate recovery and recolonization patterns of aquatic communities after a watershed-level disturbance. Multiple, co-occurring changes in water chemistry, hydrology, and stream morphology in burned watersheds have been associated with wildfires (see Rieman and Clayton 1997; and Gresswell 1999 for reviews). For example, increases in temperature (Royer and Minshall 1997), phosphorous and nitrogen levels (Spencer and Hauer 1991), sediment transport (Troendle and Bevenger 1996), flooding (Novak and White 1989), and organic material losses (McIntyre and Minshall 1996) have been documented from days to

decades post-fire. Thus physico-chemical changes related to wildfire translate into a range of disturbances with varying levels of severity, spatial extent, and longevity.

Impacts of these fire-associated disturbances on stream insect communities have been extremely varied, ranging from positive effects on abundance and diversity to severe and long-term reductions in diversity and changes in taxonomic composition (see review in Gresswell 1999). Stronger impacts on invertebrate communities and slower recovery times were observed in small order streams or when post-fire flooding occurred (La Point et al. 1983; Rinne 1996; Minshall et al. 1997). Functional recovery patterns in response to wildfires have received little attention. However, Minshall et al. (1997) found an increase in trophic generalist invertebrates and opportunistic species, such as collector-gathering chironomids and *Baetis* mayflies, but observed decreases in scrapers, such as sensitive heptageniid mayflies, for several years after the 1988 fires in Yellowstone National Park. As with most large-scale disturbance studies, observations on community recovery were made "after-the-fact" and without comparisons to pre-fire data.

Recent wildfires in north central New Mexico present a unique opportunity to examine effects of fire disturbance on streams and benthic insect communities. In 1996, an intense canopy fire burned over 65 km² of the Pajarito Plateau, including several western canyons of Bandelier National Monument, NM. Eastern canyons, which are otherwise similar in geomorphology and physico-chemical stream characteristics, were not burned. Since a monitoring study was conducted in a burned and unburned canyon before the fire (Stevens 1996), WE was able to compare the chemical, hydrological, and

ecological effects of the 1996 Dome Wildfire with a before-after control-impact (BACI) design (Stewart-Oaten et al. 1986). Our main objectives were to assess abiotic impacts of the fire and associated negative effects on stream insect communities; to monitor post-fire resistance and resilience of invertebrate communities in the burned canyon; and to relate taxa-specific population responses to community recolonization patterns.

STUDY SITE DESCRIPTION

This study was conducted in two streams located in Capulin and Frijoles canyons of Bandelier National Monument, New Mexico. The 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 1.1). 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. The Monument is 132 km² and ranges in elevation from 3111 m at the Caldera rim of Cerro Grande to 1590 m at the Rio Grande River valley. The Plateau has a semiarid mountain climate, with mean annual precipitation ranging from 33-46 cm. Wildfire has played a central role in this arid ecosystem, where high frequency low-intensity fires have been replaced by low frequency high-intensity canopy fires (Touchan et al. 1996). Both Capulin and Frijoles watersheds have been burned in the last thirty years (Figure 1.2). In June 1977, the La Mesa Fire burned the eastern half of Bandelier National Monument (including Frijoles). In April 1996, the Dome Fire burned 66.8 km² of the Monument (including Capulin canyon).

Capulin and Frijoles watersheds are approximately similar in drainage area (51 km²); stream order (spring-fed 1st order streams with no permanently wetted tributaries); permanency (perennial reaches from 1500-3000m); gradient (3-4% at lower elevation and 6-7% at higher elevations), and base flow (0.02 - 0.03 m³/s). Although Frijoles was burned in the 1977 La Mesa fire, invertebrate communities were similar to Capulin communities prior to the 1996 Dome fires (Pippin and Pippin 1980, 1981; Stevens 1996). Riparian vegetation in both canyons consists primarily of box elder, narrowleaf cottonwood, alder, and ponderosa pine. Annual hydrographs for all Pajarito Plateau canyons are snowmelt driven in mid-spring and show flashy response to precipitation in summer. Inter-annual differences are driven mostly by winter and spring precipitation from cyclonic storms, while summer rainfall during the monsoon season creates spatial and intra-seasonal variation. Localized and intense convectonal thunderstorms occur from July through September and contribute more than half of the annual rainfall (Purtymun and Adams 1980).

METHODS

WE compared chemical, hydrological, and benthic insect community characteristics between Frijoles and Capulin canyons in three seasons per year for two years prior to the Dome Fire (1994 - 1995) and six years after the fire (1996 - 2001). Three 50 m reaches at least 100 m apart and at approximately 2000 m elevation were sampled in each canyon as part of a separate study prior to the Dome fire (Stevens 1996; Figure 1.2). The same reaches were sampled in post-fire years and sampling schedules

and techniques were consistent throughout the pre- and post-fire sampling dates. Stream peakflow data were collected from a USGS stream gage in Frijoles (gage: 08313350), USGS partial gages in Capulin (J. Veenhuis, USGS, unpublished data), and our personal observations of floods and post-flood debris lines. Annual and monthly precipitation data were collected from the nearest National Climate Data Center station in Los Alamos, NM (station: 295084). Since daily discharge and local daily precipitation data for years 1994 - 2001 were not available for Capulin canyon, only total rainfall and peakflow estimates could be summarized and compared.

On each sampling date, water temperature (°C), conductivity (uS), pH, and dissolved oxygen (Winkler Titration kit; mg/L) were measured in each reach (n = 3 per canyon). Water samples (1 L) were collected from each reach, chilled on ice, and transported to the laboratory. WE analyzed water samples for 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 sent to the USFS Laboratory, Ft. Collins, CO for anion and cation analysis. After filtration through a 0.45 um 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). Stream velocity (m/s) and depth (cm) were measured in the thalweg of each reach. To collect benthic macroinvertebrates, three Surber samples (standard 0.0929 m² area; 750- μ m mesh) were taken in riffles of each reach (n = 9 per canyon). Riffles were sampled within each reach, but WE intentionally excluded large boulders or woody debris. Since the same Surber sampler and sampling

protocol were used for pre-fire samples, before and after fire samples were directly comparable. Benthic invertebrates were preserved in 70% ethanol in the field, transported to the laboratory, and sorted and identified with a dissection microscope to taxonomic levels (genus or tribe) reported in the pre-fire study (Stevens 1996). Taxa richness, overall density, and relative taxa densities were calculated.

Statistical Analysis

Descriptive statistics were generated for physico-chemical data to characterize conditions at each sampling date in each canyon. Temporal patterns of changes in invertebrate taxa richness and density were compared graphically with means and 95% confidence intervals for each sample date. Statistical differences between Capulin and Frijoles samples at each sample date were assessed with two-sample Student t-tests with unequal variance. When assumptions of parametric statistics were not met with transformations, non-parametric Wilcoxon Rank Sum tests were conducted. Linear regression analysis was used to relate monthly peak flows to total monthly rainfall. To increase sample size and to incorporate peak flows that occurred before and after both the 1977 La Mesa and 1996 Dome fires, data for Capulin and Frijoles canyons were combined for the regression analysis.

To describe changes in taxa composition after the Dome fire, WE conducted a canonical discriminant analysis. This descriptive, dimension reducing technique constructed linear combinations of the response variables (taxa-specific abundances) to

maximize separation (discriminate) between the following pre-assigned groups: pre-fire (1994-1995), early post-fire (1996 - 1997), intermediate post-fire (1998-1999), and late post-fire (2000 and 2001) for each canyon (8 total groups). Individual Surber samples taken within each time bracket were used as replicates for each group, and abundance data were transformed to reduce variability in statistical analyses and to better meet parametric requirements. Taxa that were low in abundance or did not meet normal-distribution requirements were combined by Family or Order. Sample sizes for each discriminated group were Capulin 1994-1995 (n = 45); Frijoles 1994-1995 (n = 54); Capulin and Frijoles 1996-1997 (n = 36 each); Capulin and Frijoles 1998-1999 (n = 54 each); and Capulin and Frijoles 2000-2001 (n = 27 each).

To determine whether post-fire community composition returned to pre-fire composition, a second exploratory canonical discriminant analysis was conducted with only Capulin taxa. Each sample year was designated as a group (1994 - 2001; 8 groups) and all Surber samples within each year were treated as replicates. Samples sizes for discriminated yearly groups were 1994 (n = 18); 1995 (n = 27); 1996 (n = 9); 1997 - 2000 (n = 27 each); and 2001 (n = 9). Taxa that were low in abundance, or did not meet parametric statistical assumptions, were combined by Family or Order to create a normalized response variable. To compare individual taxa responses, mean abundance and 95% CI's were calculated for all taxa in Capulin and Frijoles that comprised over 1% of the total number of invertebrates recorded in each canyon throughout the study. Recolonization patterns of key taxa that were identified in canonical discriminant

analysis with Capulin only were compared graphically with means and 95% confidence intervals.

RESULTS

Dissolved oxygen was above 8 mg/L for all sample times in both canyons except for 1996 samples, where both canyons were only between 5.5 and 6.5 mg/L (Stevens 1996). Hardness, alkalinity, and conductivity in Capulin were more than three times higher in 1996 compared to pre-fire levels, but were only slightly higher than pre-fire conditions by May 1997 (Appendix 1.1). Similar changes in water chemistry were not observed in Frijoles. Temperature and pH were similar both before and after the fire in Capulin, and similar to values in Frijoles. In contrast, anions and cations increased dramatically in Capulin immediately after the fire, but remained slightly elevated above both pre-fire and Frijoles concentrations until May 2001 (Figure 1.3). Along with increases in alkalinity and hardness, moderate increases in Ca^+ , Mg^+ , K^+ , and SO_4^- in Capulin were responsible for increases in total dissolved solids (Figure 1.4).

Point measurements of width and thalweg depth changed little and were similar between canyons throughout the study (width range: 1.5 - 2.3 m and depth range: 10-20 cm). Stream velocity was also similar between canyons, and showed similar inter-annual fluctuations in both canyons (Appendix 1.1). However, evidence of flood-induced scouring and aggradation, stream widening, and channel shifting was observed in Capulin 1996 samples indicating major reach- and segment-level changes (personal observation;

Reneau et al., in review; Cannon and Reneau, in review). Physical changes were better associated with annual peak flows, which were similar in Capulin and Frijoles prior to the Dome fire, but increased considerably in Capulin after the fire (Figure 1.5). In the year of the Dome fire, estimated peak flows during the monsoon season increased several orders of magnitude in Capulin canyon. Based on debris lines and direct observations, flood stages in 1996 were estimated at a peak of 2-3 m. In following years, peak flows dampened but were still an order of magnitude higher than average in Capulin until 1999. This pattern was similar to the pattern observed in Frijoles after the 1977 La Mesa Fire (Figure 1.5). Total monthly precipitation was not a significant predictor of monthly peak flows in Capulin and Frijoles before or after the Dome and La Mesa fires (adjusted- $R^2 = 0\%$, $P_{\text{model}} = 0.67$; Appendix 1.2).

Insect densities in Capulin and Frijoles were similar prior to the Dome fire (Figure 1.6). In the first post-fire sampling event in July 1996, densities decreased to only a few individuals in Capulin samples, while little deviation from pre-fire trends was observed in Frijoles. Capulin densities rebounded in spring 1997 due to colonization of *Simulium* sp. (56% of total density), Orthocladinae (22% of total density), and *Baetis* sp. (17% of total density, but were severely reduced again in October after the 1997 monsoon season. Capulin and Frijoles densities were similar in pre-fire samples and in 1998-2001, although Capulin densities were slightly higher and more variable in May 1998 (t-test: $p = 0.075$) and October 1999 (t-test: $p = 0.125$). Dense patches of *Simulium* sp. and *Baetis* sp. were responsible for increases in May 1998, while Orthocladinae, *Ceratopsyche* sp., and *Isoperla* sp. were responsible for increases in October 1999.

Seasonal density patterns varied by year, but were generally high in spring samples and lower in fall samples. Post-fire seasonal patterns in Capulin were similar to patterns observed in Frijoles for all years except 1997.

Taxa richness in Capulin was more severely impacted than total density (Figure 1.7). Although taxa richness in Capulin was similar to or slightly lower than Frijoles before the fire, richness in Capulin dropped to a mean of two taxa in July 1996, well below the slight decrease observed in Frijoles. Taxa richness remained significantly below pre-fire Capulin and post-fire Frijoles measures until May 1999 (t-test: $p = 0.104$). In October 1999 and July and October 2000, taxa richness was higher in Capulin (t-test: $p = 0.005$, $p = 0.0308$, and $p = 0.002$, respectively), but by May 2001, taxa richness was similar between Frijoles and Capulin (t-test: $p = 0.556$). Inter-annual seasonal patterns were similar to those observed for invertebrate abundance. Similar to seasonal patterns observed for insect densities, taxa richness was generally higher in spring and lowest in fall. Capulin patterns tracked patterns observed for Frijoles with the exception of July 1997, and October 1999 and 2000 samples.

Densities of dominant (>1% of total insect densities combined across years) taxa differed between Capulin and Frijoles and varied widely across years and seasons within years (see Appendix 1.3). Therefore, some taxa needed to be grouped by Family or Order to meet parametric assumptions in canonical discriminant analysis (Table 1.1). Canonical discriminant analysis clearly separated post-fire Capulin samples from pre-fire Capulin samples and all Frijoles samples with three canonical variables (89.5%

variability explained). The first canonical variable explained 60.3% of the variation, while the second and third explained 21.3% and 7.9%, respectively.

Canonical variable-1 generally distinguished all post-fire Capulin samples, and separated immediate post-fire Capulin samples from late post-fire Capulin samples (Figure 1.8). To a lesser degree, it separated pre-fire Frijoles and Capulin samples from post-fire Frijoles samples. Frijoles was separated from Capulin due to its greater abundance of elmids beetles and *Amphinemura* sp., and due to the lack of *Brachycentrus* sp., *Pteronarcella* sp. in Capulin (Table 1.1). In contrast, glossosomatids, rare dipterans (primarily *Palypomia* sp. and *Dixa* sp.), Odonata (*Oplonaeschna* sp.), and *Simulium* sp. were more abundant in Capulin, especially in late post-fire years. Canonical variable-2 separated pre-fire Capulin and Frijoles samples, and distinguished pre-fire Capulin samples from immediate post-fire samples (Figure 1.8). Higher densities of Odonata and Glossosomatids, and to a lesser degree *Ceratopsyche* sp. and heptageniids, were found in pre-fire and late post-fire Capulin samples compared to Frijoles (Table 1.1). *Simulium* sp. separated early from late post-fire samples in Capulin.

Multivariate analysis for Capulin canyon alone revealed more distinct annual patterns in the post-fire community recovery trajectory. Some taxa were combined into Family or Order groups to meet normality requirements (Table 1.2). Canonical discriminant function analysis clearly separated pre-fire, immediate post-fire, and post-fire recovery samples with three canonical variables (87.2% variability explained). The

first canonical variable explained 50.2% of the variation, while the second and third explained 30.7% and 6.3%, respectively.

Canonical variable-1 generally distinguished all post-fire Capulin samples from pre-fire samples (Figure 1.9). Densities of *Simulium* sp., as well as rare Diptera, Chironomidae, and other Ephemeroptera (primarily *Trichorythodes* sp.), were higher in post-fire samples (Table 1.2). Conversely, densities of elmids, *Amphinemura* sp. Heptageniids, and *Lepidostoma* sp. decreased in post-fire samples. Canonical variable-2 separated early post-fire samples (1996-1998) from later post-fire samples, and to a lesser degree, from pre-fire samples (Figure 1.9). Glossosomatids and Odonata (primarily *Oplonaeschna* sp.) increased in late post-fire samples, followed by *Ceratopsyche* sp., other Trichoptera (primarily *Hesperophylax* sp.), and *Isoperla* sp. (Table 1.2). *Simulium* sp. and non-elmids Coleopterans (*Agabus* sp.) were higher in pre-fire samples. Canonical variable-3 (not shown) separated early post-fire from late-post fire samples due to increases in *Baetis* densities.

Temporal trends of taxa-specific densities further explained differences in pre- and post-fire Capulin taxa compositions (Figure 1.10). Capulin showed more distinct colonization patterns than Frijoles. For instance, densities of taxa that were present immediately after the fire or in years with post-fire flashfloods were higher than pre-fire years (*Simulium* and *Agabus*) or fluctuated from year to year (Chironomidae and *Baetis*). Densities of several taxa returned to pre-fire densities in post-flood years (*Ceratopsyche* and Heptageniidae), and some exceeded pre-fire years (Glossosomatidae, *Isoperla*,

Odonata). A few taxa, including Elmidae, *Amphinemura*, did not return to pre-fire densities by the end of the study. Inter-annual patterns of taxa densities in Capulin were generally different from patterns observed in Frijoles. Exceptions include Diptera, Chironomidae, and *Ceratopsyche* sp., where yearly patterns, but not densities, were similar between canyons.

DISCUSSION

Chemical stream properties changed moderately immediately after the fire, but thereafter were only slightly elevated compared to pre-fire conditions in Capulin. Changes observed were largely due to increases in total dissolved solids, and were likely due to soil erosion into the stream during storm events. While erosion was not measured in this study, White (1996) found increased erosion for at least three years in canyons burned in the 1977 La Mesa fire. Other studies have found similar short- to moderate-term increases in cations, especially Ca^+ , K^+ , and Mg^+ , after a fire (see review in Gresswell 1999). Pulse increases in nitrogen and phosphorous were not observed in this study, but were observed for up to a week after other fires (Spencer and Hauer 1991; Brass et al. 1996). Point estimates of temperature in Capulin showed no change due to the Dome fire. However, changes in thermal stability (Royer and Minshall 1997) and temperature increases in smaller order streams (Minshall et al. 1997) have been observed in other studies.

Monthly and annual peak flows in Capulin increased by two orders of magnitude immediately after the Dome fire, and slowly dampened to reach pre-fire peak flows by 1999. A similar pattern was observed after the 1977 La Mesa Fire in Frijoles, suggesting that flood patterns were a consequence of fire. The magnitudes of the largest floods after both fires (at least $85 \text{ m}^3/\text{s}$) were equivalent to the 100-yr flood estimated for Pajarito streams (J. Veenhuis, USGS, unpublished data). Flashfloods are created when sediment and debris dams form from increased hillslope erosion during storm events, retain large volumes of water, and then burst. Thus, most post-fire floods occurred predictably during summer monsoon seasons when convectional storm events resulted in high erosion of burned soils. While peakflows were not associated with increased total rainfall in the Los Alamos area, it is unclear as to whether local rainfall events were unusually high in Capulin after the fire. Further, lack of daily stream flow and local rainfall data in Capulin prevented me from examining changes in flood frequency before and after the fire.

Dramatic hydrologic changes have been observed in other burned watersheds. For instance, Scott and Van Wyke (1990) found that a severe fire increased soil erodibility and repellency, and reduced infiltration, which resulted in hundred-fold increases in peak flow, quicker storm response ratios, and four-fold increases in sediment load in burned streams. Others have also found increases in annual runoff, storm response time, or frequency and magnitude of flood events associated with reduced evapotranspiration and interception from vegetation (Lavabre et al. 1993; Mackay and Band 1997). Minshall et al. (1997) found slightly increased annual discharge and earlier

spring snowmelt runoff peaks, but little change in baseflow or peak discharges after the Yellowstone fire. Increases in annual discharge did not correspond to increases in total annual precipitation, which was slightly lower in post-fire years compared to historical data. Troendle and Bevenger (1996) also found slight increases in annual water yield, but no difference in peakflow or storm response, in a study that compared a burned and unburned watershed. They attributed the lack of peakflow responses to a mild post-fire climate without extreme rainfall events. None of the studies discussed above found increased precipitation in burned watersheds as a result of wildfire.

Invertebrate density and taxa richness were similar in Capulin and Frijoles before the 1996 Dome fire. However, severe reductions were observed in both measures after the first post-fire flood in 1996. Some recovery was observed in May and July of 1997, but post-fire flashfloods that occurred later in July severely reduced density and richness in October 1997. Similar decreases were not observed in Frijoles, and only slight seasonal reductions were observed in Frijoles in October 1997. Invertebrate densities recovered by May 1998, whereas taxa richness recovered a year later, once flashfloods had returned to pre-fire peakflows. Both taxa density and richness in Capulin increased over Frijoles levels in October 1999 and 2000. In general, taxa richness and density responses both demonstrated low resistance to fire disturbance, whereas densities showed much high resilience than taxa richness.

Studies of other wildfires show varied impacts on density and taxa richness. Rinne (1996) found severe reductions in macroinvertebrate densities and diversity in

first-order, southwestern streams due to increased sediment-laden floods, or "slurry flows", for several years post-fire. In contrast, density and taxa richness changed little after the 1988 Yellowstone fire in both low and high order streams (Minshall et al. 1997). In general, insect density is more resilient to wildfire disturbance compared to taxa richness and diversity, and both measures often show recovery after several years post-fire (see review in Gresswell 1999). Moderate to fast recovery has also been observed for a range of other large-scale or chronic disturbances (e.g. channel alterations, pollution, and timber practices), even in communities with low resistance (see review in Niemi et al. 1990).

Changes in invertebrate community composition in Capulin also paralleled fire-induced changes in peakflow. However, community composition did not recover by May 2001 and was thus less resilient than insect density or taxa richness. While pre-fire community composition was similar in 1994 and 1995, assemblage structure changed substantially in the year of the fire and the most severe flood. Communities continued to move further away from pre-fire composition in 1997 and 1998 when flashfloods were still present but much reduced. During these post-fire years with flashfloods, Capulin shifted to a community dominated by early colonizing, disturbance-tolerant taxa such as *Simulium* sp., Chironomidae, and *Baetis* sp. Common pre-fire taxa such as amphinemurid stoneflies and elmids were more sensitive to flooding and were thus eliminated. Several taxa that were rare or absent before the fire, such as *Agabus* sp. and several dipterans, appeared in Capulin in 1997 - 1998 and then disappeared in later years. Community composition changed trajectory by 1999, the first year without a major

flashflood, resulting in a new suite of "recovered" invertebrate taxa in 2000 and 2001, including *Oplonaeschna* sp., *Glossossoma* sp., and *Ceratopsyche* sp. These taxa recovered to higher densities than pre-fire densities, which along with lack of recovery of pre-fire taxa (elmids and *Amphinemura* sp.), contributed to differences in composition between 1994-1995 and 2000-2001 communities.

Minshall et al. (1997) also noted shifts in invertebrate community composition in 20 streams of various size and burn percentage for up to five years after the 1988 Yellowstone Fire. Similar to our study, densities of baetid mayflies and Chironomidae increased in early post-fire years, while heptageniid mayflies densities decreased. In contrast, amphinemurid stonefly (*Zapada* sp.) densities were less impacted. Community composition changes occurred to varying degrees across different stream orders, and were attributed to reduced food quality, taxa life-history traits, and increases in woody debris. In a more detailed analysis of taxa-specific responses in Cache Creek after the Yellowstone fire, Mihuc et al. (1996) found that elmids, heptageniid and *Ephemerella* sp. mayflies, glossosomatid caddisflies, and *Isoperla* sp. stoneflies were still reduced four years after the Yellowstone fire (Mihuc et al. 1996). These taxa were also reduced in Capulin for up to three to four years after the Dome fire.

Whether predictable successional patterns exist in stream insect communities, or whether disturbance continually resets the successional trajectory to result in non-equilibrium communities, remains to be determined (Minshall and Petersen 1985; Townsend 1989; Reice 1994; Fisher 1990; Paine et al. 1998). Patterns of recolonization

after massive floods or dam failures, landslides, fires, pesticides, etc. were reviewed (Niemi et al. 1990; Yount and Niemi 1990). These papers report evidence for general patterns of reassembly, where early colonists such as dipterans (Chironomidae and *Simulium* sp.), and some Ephemeroptera (*Baetis* sp.) dominated immediately after a disturbance. Many Plecoptera, Trichoptera and Coleoptera taxa were absent or reduced in post-disturbance communities for several years (also see examples in Cushing and Gaines 1989). WE found similar patterns in assembly of taxonomic Orders, where *Simulium* blackflies and other dipterans, baetid mayflies, and Chironomidae midges were early colonists, and common pre-fire stoneflies and beetle taxa were late colonists.

Community shifts after a wildfire and other large-scale or chronic disturbances have often been interpreted in light of taxa-specific life-history traits, including functional feeding strategies, voltinism and egg diapause, drift capability, and adult dispersal (Wallace 1990). While life-history traits are no doubt significant in determining whether invertebrate taxa can persist in disturbed aquatic systems, anecdotal explorations and one-trait-at-a-time associations between traits and environmental conditions misses important interactions of these traits. Certain "suites" of traits may allow some taxa to pass environmental "filters" associated with disturbance (Poff 1997). For instance, in this study, a collector-gatherer taxa that is bi-voltine and a strong swimmer (*Baetis* sp.) was far more tolerant to post-fire flood regimes than a collector-gatherer that is a semi-voltine and a clinger (elmid beetles). Similarly, semi-voltine diving beetles (*Agabus* sp.) colonized before uni-voltine dragonflies, despite the fact that both taxa are predators and strong adult fliers. A comprehensive model that links suites of life-history traits with

disturbance conditions to predict recolonization dynamics is strongly needed. Several simpler trait-based analyses have recently been presented (Poff and Allan 1995; Doledec et al. 1996; Legendre et al. 1997; Poff 1997; Billheimer et al. 2001; MacRury, unpublished data, Chapter 4).

CONCLUSION

This study was unique in that before and after comparisons could be made for both a burned and an unburned system. Our results strengthen previous findings that wildfire can have major impacts on physical and chemical stream characteristics of streams and benthic invertebrate communities (Gresswell 1999). The 1996 Dome fire in Bandelier National Monument resulted in dramatic changes in stream hydrology and more severe impacts and slower recovery of aquatic invertebrates compared to other western wildfire studies. However, similar to other wildfire and catastrophic disturbance studies, invertebrate density was the most resilient response, taxa richness showed intermediate resilience, and community composition showed low resilience. All three responses were ramped, rather than press, because they tracked post-fire chemical hydrologic recovery over the course of the study. This study demonstrates that monitoring programs that 1) only emphasize traditional endpoints such as insect density, biomass, and taxa richness; 2) do not measure physical and chemical impacts and recovery; and 3) do not have pre-disturbance data, may under-estimate the recovery time after disturbance. Finally, this research highlights the need for a better linkage between

life-history traits and environmental conditions so that recolonization patterns after disturbance can be better understood.

LITERAURE CITED

- American Public Health Association (APHA). 1989. Standard Methods for the Examination of Water and Wastewater. 17th Edition. Washington, DC.
- Billheimer D., P. Guttorp, and W. F. Fagan. 2001. Statistical interpretation of species composition. *Journal of the American Statistical Association* 96: 1205 - 1214.
- Boulton, A. J., C. G. Peterson, N. B. Grimm, and S. G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology* 73: 2192-2207.
- Brass, J. A., V. G. Ambrosia, P. J. Riggan, and P. D. Sebesta. 1996. Consequences of fire on aquatic nitrate and phosphate dynamics in Yellowstone National Park. Pps.53 - 57 in J. Greenlee, editor. *The Ecological Implications of Fire in Greater Yellowstone: Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem*. International Association of Wildland Fire, Fairfield, Washington, USA.
- Cannon, S. H. and S. L. Reneau. Evaluation of conditions necessary for the generation of fire-related debris flows, Capulin canyon, New Mexico. Submitted to *GSA Bulletin*.
- Cushing, C. E. and W. L. Gaines. 1989. Thoughts on recolonization of endorheic cold desert spring-streams. *J. N. Am. Benthol. Soc.* 8: 277-287.
- Death, R. G. and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* 76: 1446-1460.
- Doledec S., D. Chessel, C. F.J. Ter Braak, and S. Champely. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics* 3: 143 - 166.
- Fisher S. G. 1990. Recovery processes in lotic ecosystems: Limits of successional theory. *Environmental Management* 14: 725-736.
- Gray, L. J. and S. G. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *Am. Mid. Nat.* 106:249-257.
- Gresswell, R. E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 128(2): 193-214

- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *J. N. Am. Benthol. Soc.* 19(4): 573 – 592.
- La Point, T. W., M. Parker, C. A. Brewer, and M. Crossey. 1983. Impact of fire on recreation stream water quality and spawning habitat. Final Report to the USFS (Cooperative Agreement 28-C2-222), Laramie, Wyoming, USA.
- Lavabre, J., D. S. Torres, and F. Cernesson. 1993. Changes in the hydrological response of a small Mediterranean basin a year after a wildfire. *Journal of Hydrology* 142: 273-299.
- Legendre, P. R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78: 547 - 562.
- Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *J. Fish. Aquat. Sci.* 49: 617-628.
- Mackay, D. S., and L. E. Band. 1997. Forest ecosystem processes at the watershed scale: dynamic coupling of hydrology and canopy growth. *Hydrological Processes* 11: 1197-1217.
- McIntyre, M. J. and G. W. Minshall. 1996. Changes in transport and retention of coarse particulate organic matter in streams subjected to fire. Pps. 59 - 75 in J. Greenlee, editor. *The Ecological Implications of Fire in Greater Yellowstone: Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem*. International Association of Wildland Fire, Fairfield, Washington, USA.
- Mihuc, T. B., G. W. Minshall, and C. T. Robinson. 1996. Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. Pps. 83 - 94 in J. Greenlee, editor. *The Ecological Implications of Fire in Greater Yellowstone: Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem*. International Association of Wildland Fire, Fairfield, Washington, USA.
- Minshall, G. W. and R. C. Petersen Jr. 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. *Archiv fuer Hydrobiologie* 104: 49 - 76.
- Minshall, G. W., C. T. Robinson, and D. E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. *Can. J. Fish. Aquat. Sci.* 54: 2509-2525.
- Niemi, G. J., P. DeVore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J. D. Yount, and R. J. Naiman. 1990. Overview of case studies on recovery of aquatic systems from disturbances. *Environmental Management* 14: 571 - 587.

- Novak, M. A. and R. G. White. 1989. Impact of a fire and flood on the trout population of Beaver Creek, upper Missouri basin, Montana. Pages 120-129 in F. Richardson and R. H. Hamre, eds. Wild Trout IV: proceedings of the symposium. U. S. Government Printing Office, Washington D. C.
- Paine, R. T. and M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535 - 545.
- Pippin, W. F. and B. D. Pippin. 1980. Aquatic invertebrates of Rito de los Frijoles, Bandelier National Monument, New Mexico. National Park Service. Report number NPS-PX 7029-7-0958. Bandelier National Monument, New Mexico.
- Pippin, W. F. and B. D. Pippin. 1981. Aquatic invertebrates from Capulin Creek, Bandelier National Monument, New Mexico. National Park Service. Report number NPS-PX 7029-0-0296. Bandelier National Monument, New Mexico.
- Poff, N. L. and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1805 - 1818.
- Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology* 76: 606-627.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am Benthol. Soc.* 16: 391-409.
- Purtymun, G. M. and H. Adams. 1980. Geohydrology of Bandelier National Monument, New Mexico. Los Alamos National Laboratory. Report number LA-8461-MS. Los Alamos National Laboratory, Los Alamos, New Mexico.
- Quinn, J. M. and C. W. Hickey. 1990. Magnitude of effects of substratum particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research* 24: 411 - 427.
- Reice, S. R., R. C. Wissmar, and R. J. Naiman. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic systems. *Environmental Management* 14: 647 - 659.
- Reice, S. R. 1994. Nonequilibrium determinants of biological community structure. *American Scientist* 82: 424-435.
- Reneau, S. L., S. H. Cannon, and J. E. Veenhuis. Rapid incision in response to post-fire floods: Implications for channel evolution and terrace development. Submitted to *Journal of Geology*.

- Resh, V. H., A. V. Brown, A. P. Covich, M.E. Gurtz, H. W. Li, G. W.. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* 7: 433-455.
- Rieman, B. and J. Clayton. 1997. Wildfire and native fish: issues in forest health of sensitive species. *Fisheries* 22: 6-15.
- Rinne, J. N. 1996. Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the Southwest United States. *North American Journal of Fisheries Management* 16: 653-658.
- Royer, T. V. and G. W. Minshall. 1997. Temperature patterns in small streams following wildfire. *Arch. Hydrobiol.* 140: 237-242.
- Scott, D. F. and D. B. Van Wyk. 1990. The effects of wildfire on soil wettability and hydrological behaviour of an afforested catchment. *Journal of Hydrology* 121: 239-256.
- Sheldon, A. L. 1984. Colonization dynamics of aquatic insects. In V. H. Resh and D.M. Rosenberg, eds. *The Ecology of Aquatic Insects*. Praeger, NY, USA.
- Spencer, C. N and F. R. Hauer. 1991. Phosphorous and nitrogen dynamics in streams during a wildfire. *J. N. Am. Benthol. Soc.* 10: 24-30.
- Stevens, L. WE. 1996. Benthic macroinvertebrates as indicators of water quality: comparison of full and subsample techniques. M. Sc. Thesis, Colorado State University, Fort Collins, CO.
- Stewart-Oaten, A., W. M. Murdoch, and K. R. Parker. 1986. Environmental impact assessment: "pseudoreplication" in time? *Ecology* 67: 929-940.
- Touchan, R., C. D. Allen, and T. W. Swetnam. 1996. Fire history and climate patterns in Ponderosa pine and mixed-conifer forests of the Jemez Mountains, northern New Mexico. Pages 33-46 in C. D. Allen, ed. *Fire effects in southwestern forests: proceedings of the second La Mesa Fire symposium, 1994 March 29-31, Los Alamos, NM*. Gen. Tech. Report RM-GTR-286. U. S. Dept. of Agriculture, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *J. N. Am. Benthol. Soc.* 8: 36-50.
- Townsend, C. R., M. R. Scarsbrook, and S. Doleddec. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *J. N. Am. Benthol. Soc.* 16: 531-544.

- Troendle, C. A. and G. S. Bevenger. 1996. Effect of fire on streamflow and sediment transport, Shoshone National Forest, Wyoming. Pps. 43- 52 in J. Greenlee, editor. The Ecological Implications of Fire in Greater Yellowstone: Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem. International Association of Wildland Fire, Fairfield, Washington, USA.
- U. S. Environmental Protection Agency (US EPA). 1983. Methods for Chemical Analysis of Water and Wastewater. EPA 600/4-79-020. Environmental Monitoring Support Laboratory, Cincinnati, OH.
- Van Wagner, C. E. 1983. Fire behavior in northern conifer forests and shrublands. In R. W. Wein and D. A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystems. John Wiley and Sons, New York, New York, USA. Pps: 65-80.
- Veenhuis, J. 2001. Effects of wildfire on the hydrology of Capulin and Rito de los Frijoles canyons, Bandelier National Monument, New Mexico. Water-resources investigation report 01-XXXX: DRAFT.
- Wallace, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environ. Manag. 14: 605-620.
- White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pgs. 3 - 9 in S. T. A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, USA.
- White, W.D. 1996. Geomorphic response of six headwater basins fifteen years after the La Mesa fire, Bandelier National Monument. Pps. 95 - 113 in USFS General Technical Report RM-GTR-286: 95, New Mexico, USA.
- Yount, J. D. and G. J. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance: a narrative review of case studies. Environmental Management 14: 547 - 569.

Table 1.1. Taxa scores along the first two canonical variables from canonical discriminant analysis conducted with Frijoles (unburned) and Capulin (burned) canyons. Key taxa are in bold.

TAXA SPECIES	CAN1	CAN2
<i>Baetis tricaudatus</i>	-0.04	0.00
<i>Ephemerella</i> sp.	-0.17	0.42
Heptageniidae (<i>Nixe</i> sp., <i>Cynigmula</i> sp., and <i>Epeorus</i> sp.)	0.29	0.44
<i>Paraleptophlebia</i> sp.	0.16	0.13
Other Ephemeroptera (<i>Drunella</i> sp., <i>Ameletus</i> sp., <i>Tricorythodes</i> sp.)	-0.25	0.12
<i>Amphinemura</i> sp.	0.46	0.38
<i>Isoperla</i> sp.	-0.25	0.34
<i>Pteronarcella</i> sp.	0.46	-0.14
Other Plecoptera (<i>Capnia</i> sp., <i>Triznaka</i> sp., <i>Sweltza</i> sp., <i>Hesperoperla</i> sp.)	0.33	-0.02
<i>Brachycentrus</i> sp.	0.50	-0.11
<i>Ceratopsyche</i> sp.	-0.13	0.46
<i>Lepidostoma</i> sp.	0.21	0.33
Other Trichoptera (<i>Hesperophylax</i> sp., <i>Ochotrichia</i> sp., <i>Ocetis</i> sp., <i>Polycentropus</i> sp., <i>Rhyacophila</i> sp.)	0.10	0.07
Glossosomatidae (<i>Agapetus</i> sp. and <i>Glossosoma</i> sp.)	-0.58	0.63
Chironomidae (Tanytarsinae, Tanypodinae, Orthocladinae, Chironominae)	-0.16	-0.03
<i>Dicranota</i> sp.	0.20	0.01
Other Tipulidae (<i>Antocha</i> sp., <i>Hexatoma</i> sp., <i>Pedicia</i> sp., <i>Tipula</i> sp.)	0.08	0.07
<i>Maruina</i> sp.	-0.17	-0.07
<i>Simulium</i> sp.	-0.29	-0.41
Other Diptera (<i>Calopharus</i> sp., <i>Chelifera</i> sp., <i>Dixa</i> sp., <i>Hemerodromia</i> sp., <i>Limnophorus</i> sp., <i>Oreogeton</i> sp., <i>Palpomyia</i> sp., <i>Pericoma</i> sp.)	-0.39	-0.10
Elmidae (<i>Optioservus</i> sp., <i>Zaitzevia</i> sp.)	0.93	0.29
Odonata (<i>Oplanaeschna</i> sp., <i>Argia</i> sp.)	-0.49	0.63
Coleoptera and other (<i>Agabus</i> sp., <i>Helichus</i> sp., Hemiptera, Petrophilidae)	-0.16	0.03

Table 1.2. Taxa scores along the first three canonical variables from canonical discriminant analysis conducted with Capulin (burned) canyons only. Key taxa are in bold.

TAXA SPECIES	CAN1	CAN2
<i>Baetis tricaudatus</i>	0.06	0.03
<i>Ephemerella</i> sp.	-0.04	0.59
Heptageniidae (<i>Nixe</i> sp., <i>Cynigmula</i> sp., and <i>Epeorus</i> sp.)	-0.58	0.30
<i>Paraleptophlebia</i> sp.	0.04	0.48
Other Ephemeroptera (<i>Drunella</i> sp., <i>Ameletus</i> sp., <i>Tricorythodes</i> sp.)	0.30	0.47
<i>Amphinemura</i> sp.	-0.80	0.10
<i>Isoperla</i> sp.	0.06	0.61
Other Plecoptera (<i>Capnia</i> sp., <i>Triznaka</i> sp., <i>Sweltza</i> sp., <i>Hesperoperla</i> sp.)	-0.14	0.09
<i>Ceratopsyche</i> sp.	-0.15	0.66
<i>Lepidostoma</i> sp.	-0.55	0.09
Other Trichoptera (<i>Hesperophylax</i> sp., <i>Ochotrichia</i> sp., <i>Ocetis</i> sp., <i>Polycentropus</i> sp., <i>Rhyacophila</i> sp.)	0.19	0.63
Glossosomatidae (<i>Agapetus</i> sp. and <i>Glossosoma</i> sp.)	0.06	<u>0.92</u>
Chironomidae (Tanytarsinae, Tanypodinae, Orthocladinae, Chironominae)	0.32	0.25
<i>Dicranota</i> sp.	0.01	0.21
Other Tipulidae (<i>Antocha</i> sp., <i>Hexatoma</i> sp., <i>Pedicia</i> sp., <i>Tipula</i> sp.)	0.15	0.53
<i>Maruina</i> sp.	0.19	0.16
<i>Simulium</i> sp.	<u>0.41</u>	<u>-0.49</u>
Other Diptera (<i>Calopharus</i> sp., <i>Chelifera</i> sp., <i>Dixa</i> sp., <i>Hemerodromia</i> sp., <i>Limnophorus</i> sp., <i>Oreogeton</i> sp., <i>Palypomia</i> sp., <i>Pericoma</i> sp.)	0.33	0.00
Elmidae (<i>Optioservus</i> sp., <i>Zaitzevia</i> sp.)	<u>-0.97</u>	0.11
Odonata (<i>Oplonaeschna</i> sp., <i>Argia</i> sp.)	-0.11	0.72
Coleoptera and other (<i>Agabus</i> sp., <i>Helichus</i> sp., Hemiptera, Petrophilidae)	0.03	-0.15

LIST OF FIGURES

Figure 1.1. Location of Bandelier National Monument (bolded region) and Sante Fe National Forest, near Los Alamos, NM. Solid lines represent land ownership boundaries, and broken lines indicate streams that drain from the Pajarito Plateau into the Rio Grande River.

Figure 1.2. Map of study streams and their location relative to recent wildfires in Bandelier National Monument and Sante Fe National Forest, near Los Alamos, NM. Solid lines represent land ownership boundaries, and broken lines indicate streams that drain from the Pajarito Plateau into the Rio Grande River. Locations of study reaches in Capulin and Frijoles are indicated with solid squares.

Figure 1.3. Means and 95% confidence intervals of total dissolved ions (n=3 per sample date) before and after the 1996 Dome fire in a burned canyon (Capulin) and a reference canyon (Frijoles), Bandelier National Monument, Los Alamos, NM. Arrows indicate dates of known flashflood events.

Figure 1.4. Concentrations of major cations (calcium, sodium, magnesium) and anions (sulfate) in a burned canyon (Capulin) and a reference canyon (Frijoles), Bandelier National Monument, Los Alamos, NM.

Figure 1.5. Annual peakflows (m^3/s) in Frijoles (burned in the 1977 La Mesa fire) and Capulin (burned in the 1996 Dome fire) streams, in Bandelier National Monument and Sante Fe National Forest, near Los Alamos, NM.

Figure 1.6. Means and 95% confidence intervals of insect densities recorded before and after the 1996 Dome fire in a burned canyon (Capulin) and a reference canyon (Frijoles), Bandelier National Monument, Los Alamos, NM. Results of two-sample t-tests, on log-transformed values, are also reported with the following conventions: NS: $p > 0.2$; * : $p < 0.003$; and ** : $p < 0.0009$. All values between 0.003 and 0.2 are also reported.

Figure 1.7. Means and 95% confidence intervals of insect taxa richness recorded before and after the 1996 Dome fire in a burned canyon (Capulin) and a reference canyon (Frijoles), Bandelier National Monument, Los Alamos, NM. Results of two-sample t-tests, on log-transformed values, are also reported with the following conventions: NS: $p > 0.2$; * : $p < 0.003$; and ** : $p < 0.0009$. All values between 0.003 and 0.2 are also reported.

Figure 1.8. Mean canonical discriminant analysis values for invertebrate composition in Capulin (burned) and Frijoles (unburned) canyons and the important taxa that discriminated the following groups: pre-fire (1994-1995), early post-fire (1996 - 1997), intermediate post-fire (1998-1999), and late post-fire (2000 and 2001) for each canyon (n = 54, 27, 54, and 36, respectively, for both canyons).

Figure 1.9. Mean canonical discriminant analysis values for invertebrate composition in Capulin (burned) canyon and important taxa that discriminated the following groups: 1994 (n=27), 1995 (n=27), 1996 (n=9), 1997 (n=18), 1998(n=27), 1999 (n=27), 2000 (n=27), and 2001(n=9).

Figure 1.10. Annual mean densities (and 95% confidence intervals) of taxa that discriminated yearly communities of Capulin canyon in canonical discriminant analysis (sample sizes reported in text). Solid line = Capulin and dotted line = Frijoles.

LIST of APPENDICES

Appendix 1_1. Means of physical and chemical parameters for each sample date in a burned (Capulin) and unburned (Frijoles) canyon. N = 3 for parameters at each sample date, and "." = measure not taken at that date. Variability was generally low ($CV < 0.2$) and was thus not reported.

Appendix 1.2a. Mean densities and 95% confidence intervals for Capulin (burned) invertebrate taxa that were dominant in both Capulin and/or Frijoles (all taxa that were $>1\%$ of total abundances for each canyon). All values were rounded to the nearest whole number, and fractions were rounded up to a value of 1, to show presence of lower-abundance taxa.

Appendix 1.2b. Mean densities and 95% confidence intervals for Frijoles (unburned) invertebrate taxa that were dominant in both Capulin and/or Frijoles (all taxa that were $>1\%$ of total abundances for each canyon). All values were rounded to the nearest whole number, and fractions were rounded up to a value of 1, to show presence of lower-abundance taxa.

Appendix 1.3. Regression of monthly peakflows recorded in Frijoles (burned in the 1977 La Mesa fire) and Capulin (burned in the 1996 Dome fire) canyons against total monthly rainfall recorded at the nearest permanent rainfall recorder