EFFECTS OF WILDFIRE AND POSTFIRE FLOODS ON STONEFLY DETRITIVORES OF THE PAJARITO PLATEAU, NEW MEXICO

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ABSTRACT.—Wildfires alter the quantity and quality of allochthonous detritus in streams by burning riparian vegetation and through flushing during postfire floods. As such, fire disturbance may negatively affect detritivorous insects that consume coarse organic matter. We assessed how 2 crown fires impacted stonefly detritivores in streams of the Pajarito Plateau, New Mexico. We documented stonefly populations before and after the fires and postfire floods, and compared recovery trajectories among unburned, lightly burned, and severely burned reaches. We also conducted experiments to assess burned detritus as a food resource for *Pteronarcella badia* Hagen. Specifically, we characterized microbial conditioning, nutrient content, and breakdown rates of burned and unburned deciduous leaves and pine needles. We compared colonization of *P. badia* in field-placed leaf packs and growth of *P. badia* in a microcosm experiment on burned and unburned treatments. Detritivorous stoneflies in Plateau streams survived wildfire, but were extirpated from burned reaches after severe postfire floods in both Capulin and Guaje canyon. In Guaje Canyon, *Amphinemura banksi* Baumann and Gaufin was more resilient to flood disturbance than *P. badia* and recolonized soon after floods abated, whereas recolonization of *A. banksi* was delayed in Capulin Canyon. Experiments revealed that detritus quality did not explain slow recovery; despite reduced microbial conditioning and decomposition rates, *P. badia* colonized and grew well on burned detritus. Instead, postfire floods removed shredder stoneflies and their detrital resources; and traits such as body size, voltinism, and dispersal likely interacted with the postfire landscape to shape recovery trajectories in burned streams.

RESUMEN.—Los incendios cambian la cantidad y calidad de la materia orgánica alóctona en los ríos mediante la quema de la vegetación ribereña; además, las inundaciones después de los incendios se llevan materia orgánica río abajo. Como tal, la perturbación por incendio puede afectar negativamente a los insectos detritívoros que consumen la materia orgánica gruesa. Evaluamos cómo 2 fuegos de copas afectaron a los plecópteros detritívoros en arroyos del Altiplano Pajarito, NM. Documentamos las poblaciones de plecópteros antes y después de los incendios e inundaciones y comparamos las trayectorias de recuperación entre áreas no quemadas, levemente quemadas y gravemente quemadas. También llevamos a cabo experimentos para evaluar los detritos quemado como fuente alimenticia para *Pteronarcella badia* Hagen. Específicamente, caracterizamos el acondicionamiento microbiano, el contenido de nutrientes y las tasas de descomposición de hojas caducifolias y hojas de pino quemadas y no quemadas. Comparamos la colonización de *P. badia* en paquetes de hojas colocadas en el campo, y su crecimiento en un experimento de microcosmos, en detrito quemado y no quemado. Los plecópteros detritívoros en los arroyos del Altiplano sobrevivieron a los incendios pero fueron extirpados de las áreas quemadas después de inundaciones severas que siguieron a incendios en los cañones Capulin y Guaje. En Guaje, *Amphinemura banksi* Baumann y Gaufin fue más resistente a la perturbación por inundación que *P. badia* y recolonizó poco después de que la inundación cedió, mientras que la recolonización de *A. banksi* tardó más en Capulin. Los experimentos revelaron que la calidad de los detritos no explican esta lenta recuperación; a pesar del menor acondicionamiento microbiano y las tasas de descomposición más bajas, *P. badia* colonizó y creció bien en detritos quemados. Es probable que las inundaciones después de los incendios se hayan llevado a los plecópteros y a los detritos que consumen, y que los rasgos tales como el tamaño del cuerpo, el voltinismo, y la dispersión hayan interactuado con el paisaje después del incendio para determinar las trayectorias de recuperación en arroyos quemados.

Allochthonous inputs of organic material are a primary source of energy in low-order woodland streams (Allan 1995). Riparian leaf litter and woody debris represent critical resources for invertebrate detritivores, who play an important role in both function and structure of lotic food webs. Functionally, detritivores are responsible for up to 25% of leaf litter degradation in streams (Petersen and Cummins 1974; see review in Allan 1995). Not surprisingly, experimental removal of detritivorous

invertebrates can result in lower decomposition rates of terrestrial organic matter (Wallace et al. 1982). Furthermore, shredder detritivores break down coarse organic material (CPOM) into finer materials, thereby increasing food availability to invertebrates who are collector filterers and gatherers (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

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populations (Rounick and Winterbourn 1983) and result in bottom-up effects on aquatic food webs (Wallace et al. 1997).

Disturbances that alter terrestrial-aquatic ecotones, such as agricultural practices (Delong and Brusven 1993, Townsend et al. 1997a), logging (Webster et al. 1990, Bilby and Bisson 1992), and fire (Britton 1990, McIntyre and Minshall 1996, Minshall et al. 1997), often dramatically alter terrestrial subsidies of leaf litter into streams. Wildfires also reduce in-stream retention of detritus through post-fire flooding, removal of debris dams, and changes in woody debris inputs (Bilby 1981, Minshall et al. 1997, Robinson et al. 2005). Loss of riparian subsidies after wildfire and poor retention of burned leaf litter have been correlated with functional shifts in benthic invertebrate communities from specialist detritivores, such as shredders, to communities dominated by generalist herbivore-detritivores (Mihuc et al. 1996, Minshall et al. 2001, Vieira et al. 2004). For example, Vieira et al. (2004) found that the shredder stonefly *Amphinemura banksi* Baumann and Gauvin (Nemouridae) was strongly affected by wildfire and associated postfire flooding and, despite being common in prefire communities, did not recover even after 6 years. These studies suggest that wildfire may have long-term impacts on shredder stonefly species in burned watersheds.

Along with reducing detritus quantity, fire can also reduce the quality of detritus by increasing charcoal content (Minshall et al. 1997) and initiating moderate- to long-term changes in riparian vegetation species (Britton 1990). For example, Mihuc and Minshall (1995) assessed the nutritional value of experimentally burned riparian vegetation as a food source for benthic macroinvertebrates and found that most taxa, including the generalist detritivore stonefly *Zapada columbiana* Claassen (Nemouridae) could not grow on severely (100%) burned detritus. However, *Z. columbiana* grew on coarse detritus that had been "naturally" (35%) burned in a fire. It also grew on periphyton. This dietary flexibility likely facilitated rapid recovery of *Z. columbiana* in streams burned in the Yellowstone wildfires (Mihuc et al. 1996, Minshall et al. 1997, Mihuc and Minshall 2005). Detritivores that specialize their feeding behaviors, such as shredders that require or prefer coarse detritus, may be more adversely

affected by changes in detritus quality and quantity after a wildfire.

We had the unique opportunity to employ a before-after approach to assess how detritivorous stoneflies (Pteronarcyidae, Capniidae, and Nemouridae) of the Pajarito Plateau (hereafter "plateau") near Los Alamos, New Mexico, responded to wildfire disturbance. Over the last 3 decades, large-scale (>50 km²) crown fires have burned several canyon-bound drainages of the plateau, while other drainages remained relatively unaffected. Burned canyons experienced extensive removal of riparian vegetation and multiple 100-year floods in the year of the fires, followed by a progressive dampening of flood magnitudes as hillslope and riparian vegetation recovered (Veenhuis 2002, Gallaher and Koch 2004). Aquatic insect communities were dramatically altered by postfire flooding, with notable declines of specialist feeding groups such as grazers and shredders (Vieira et al. 2004). Our research investigated effects of the 1996 Dome Fire and the 2000 Cerro Grande Fire on detritivorous stoneflies in plateau canyons. To gauge recovery, we compared stonefly responses after the fires and flooding to prefire populations in lightly burned and unburned stream reaches.

In addition to our field study, we experimentally investigated how changes in detritus quality after the fire may have influenced postfire responses of the shredder stonefly *Pteronarcella badia* Hagen (Pteronarcyidae). This species is common in most plateau streams and is amenable to handling in the laboratory because of its large body size. First, we conducted an in situ field experiment to compare microbial activity and nutritional content of burned and unburned detritus representing 2 common riparian resources in plateau streams: narrowleaf cottonwood leaves (*Populus angustifolia* James; hereafter referred to as "leaves") and ponderosa pine needles (*Pinus ponderosa* Douglas ex Lawson and C. Lawson; hereafter referred to as "needles"). We also compared colonization of *P. badia* on these 4 leaf litter treatments. Secondly, we conducted microcosm experiments to compare growth of *P. badia* on burned and unburned leaves and needles. We hypothesized that microbial activity and nutrient content, and thus growth and colonization of *P. badia*, would be highest on unburned leaves and lower on burned detritus treatments.

Fig. 1. Map showing recent crown fires and burn severity in canyons of the Pajarito Plateau, near Los Alamos, New Mexico, including the study streams Capulin Creek, Guaje Creek, and Frijoles Creek (Rito de los Frijoles). Black circles indicate the study reaches.

METHODS

Survey of Detritivore Stonefly Populations

We surveyed the stonefly populations in Pajarito Plateau streams of Bandelier National Monument and Santa Fe National Forest, near Los Alamos, New Mexico (Fig. 1). The plateau slopes toward the Rio Grande in a series of canyons and mesas. First-order streams drain these canyons and are similar in watershed area (approximately 50 km²), flow permanence (e.g., spring-fed upper reaches, perennial mid-canyon segments, and ephemeral tributaries), gradient (changing from 3% to 7% with altitude), and baseflow (0.05 m³ · s⁻¹). Riparian vegetation includes narrowleaf cottonwood and

ponderosa pine, as well as western boxelder (*Acer negundo* Linnaeus) and alder (*Alnus oblongifolia* Torrey). Plateau streams differ in wildfire history, where they were burned prior to 1980 (e.g., Frijoles Canyon), in the 1996 Dome Fire (e.g., Capulin Canyon), or in the 2000 Cerro Grande Fire (e.g., Guaje Canyon).

Plateau streams are snowmelt-driven in mid-spring and typically show flashy responses to monsoon precipitation in summer (Beeson et al. 2001). Monsoonal flood magnitudes increase significantly following wildfires in burned drainages. After the Dome and Cerro Grande fires, annual peak flows increased from a pre-fire average of less than 1 m³ · s⁻¹ to 100-year floods with magnitude greater than 80 m³ · s⁻¹

in the first postfire year (Veenhuis 2002, Gallaher and Koch 2004). Severe flooding and debris flows in burned canyons dramatically altered stream geomorphology (see Fig. 2), sediment transport, and bed substrate and stability (Cannon and Reneau 2000, Cannon et al. 2001, Vieira et al. 2004). Postfire flood magnitudes progressively dampen each year from 100-year flooding to $10\text{--}20\text{ m}^3 \cdot \text{s}^{-1}$ in the next year after a fire, to $2\text{--}5\text{ m}^3 \cdot \text{s}^{-1}$ in the second and third postfire years (e.g., Fig. 2h), and ultimately back to prefire levels by 5 years after a fire. Hydrological recovery depends on the location and intensity of monsoonal storms and also on the reestablishment of riparian and hillslope vegetation, especially at severely burned sites (see Fig. 2c).

Previous taxonomic surveys in streams of the Plateau and adjacent Jemez Mountains show that resident stonefly species are typical of the Rocky Mountains and the Southwest (Jacobi and Baumann 1983, Jacobi et al. 2005, Vieira et al. 2009). Plateau stoneflies considered to be detritivores, as determined from the North American Aquatic Invertebrate Database (Vieira et al. 2006), include *A. banksi*, *P. badia*, several species of *Capnia* (Capniidae), *Paraleuctra occidentalis* (Banks) (Leuctridae), and the nemourids *Malenka coloradensis* (Banks), *Zapada cinctipes* (Banks), and *Zapada haysi* Ricker. The 2 common species of the region, *A. banksi* and *P. badia*, differ significantly in species traits known to influence resilience to hydrologic disturbances, including body size, voltinism, larval drift, and adult dispersal (Townsend et al. 1997b, Vieira et al. 2004). *Amphinemura banksi* is a small, univoltine species with moderate drift propensity of nymphs and weak adult dispersal abilities. By contrast, *P. badia* is a large-bodied stonefly with a semivoltine life cycle, minimal nymph drift, and moderate (but still relatively local) aerial dispersal of adults (Vieira et al. 2006).

We collected benthic invertebrates in Capulin, Guaje, and Frijoles canyons as described in Vieira et al. (2004). Simply stated, we collected invertebrates with a $750\text{-}\mu\text{m}$ mesh Surber sampler (0.093 m^2 area) from randomly selected riffles ($n = 6\text{--}9$) in each study reach and identified organisms to the genus or species level. Individuals were enumerated and densities (individuals per 0.093 m^2) of *A. banksi*, *P. badia*, and total stonefly detritivores were calculated for each sample event. Sample sites chosen to

document the impacts of the Dome Fire included severely burned reaches in Capulin (no riparian vegetation) and unburned reaches of Frijoles. Sample events included the spring (April–May), summer (July–August), and fall (September–October) before the Dome Fire (1994–1995); 2 weeks after the first postfire 100-year flood (July 1996); and in spring, summer, and fall of postfire recovery years (1997–2002). To document impacts of the Cerro Grande Fire, 2 elevations were sampled in Guaje Canyon. Lower reaches were severely burned (Fig. 2c), and upper reaches were only lightly burned (Fig. 2d). Samples were collected before the Cerro Grande Fire in spring 1998 and in spring, summer, and fall 1999; immediately after the fire but before flooding (June 2000); 3 weeks after the first postfire 100-year flood (September 2000); and in spring and fall of postfire recovery years (2001–2002).

Burned Detritus Experiments

Narrowleaf cottonwood leaves and ponderosa pine needles were gathered prior to abscission and dried at 56°C for 24 hours. These needles and leaves were then burned in a muffle furnace at 450°C to simulate a fire. We modified the 100% burn treatment as described by Mihuc and Minshall (1995) such that burned materials were brittle with a charcoal residue but were still available as CPOM to shredders. More severe burn methods were undesirable because leaves and needles disintegrated into ash. Each of 4 detritus treatments, burned and unburned leaves and needles, were weighed into 8-g dry-weight samples. Artificial leaf packs were constructed by placing leaves or needles in 2.27-kg citrus bags (Cady Bag County, Pearson, GA) with $5 \times 5\text{-mm}$ mesh openings. Leaf packs were transported in plastic bags to prevent leaf or needle loss prior to the study.

Ninety-six leaf packs (24 per treatment) were placed at 2320 m elevation in the Cache La Poudre River, Fort Collins, Colorado, on 22 October 1999 (4.6°C , $10.6\text{ mg DO} \cdot \text{L}^{-1}$, 7.3 pH, and 50 mS conductivity; DO = dissolved oxygen). A maximum of 10 leaf packs, including at least 2 from each detritus treatment, were randomly allocated to each of 10 wooden racks (1.5 m long) and tethered with 36-cm cable ties. Racks were placed in 2 rows ($n = 5$ each) in the center of a wide riffle (15 m), perpendicular to the current and at a depth of 0.5 m.

Fig. 2. Photos depicting the impacts of intense crown fires and postfire floods on streams of the Pajarito Plateau, near Los Alamos, New Mexico. Photos show (A) lower Guaje Canyon before the 2000 Cerro Grande Fire; (B) Frijoles Canyon (burned in 1977); (C) lower Guaje after the fire; (D) upper Guaje postfire, with a spot fire on the right bank; (E) Capulin Canyon following the first 100-year flood after the 1996 Dome Fire (flood scars evident); (F) lower Guaje after the first 100-year flood; and (G) upper Guaje after moderate postfire flooding (widened, shifting gravel); and (H) a $3 \text{ m}^3 \cdot \text{s}^{-1}$ flood in Capulin (1998).

Discharge was stable and at low-flow conditions (approximately $0.7 \text{ m}^3 \cdot \text{s}^{-1}$) throughout the study period. Leaf packs were collected after 27 days ($n = 12$) and 50 days ($n = 12$). On each date, leaf packs were sampled in a stratified random fashion, where at least one of each treatment was sampled from each rack. Leaf packs (including invertebrates) were collected with a 250- μm mesh dipnet, placed in large plastic bags filled with stream water, and transported in coolers to the laboratory.

All invertebrates from each leaf pack were preserved in 80% ethanol and *P. badia* individuals were enumerated. After all invertebrates were removed, leaf packs collected after 27 and 50 days were rinsed with water, dried at 56°C for 24 hours, and weighed to the nearest 0.1 mg to obtain final dry mass. For 50-day samples, 1 g of dried leaves or needles was randomly selected from 5 leaf packs from each treatment and pooled for nutritional analysis. A CHN-1000 carbon hydrogen nitrogen analyzer (LECO, St. Joseph, MI) was used to measure percent carbon and percent nitrogen (an indication of protein content). Total lipid (% solvent extract) was determined from the sample with chloroform-methanol extraction.

We measured changes in dissolved oxygen across detritus treatments, in which microbial respiration was used as a surrogate for microbial colonization and conditioning. Water for the experiment was obtained from Horsetooth Reservoir, Fort Collins, Colorado, and was filtered (0.45 μm) to remove organics and other microbes. Three leaves or needles from each of the 4 treatments (unburned leaves, burned leaves, unburned needles, and burned needles) were randomly selected from 50-day leaf packs and were randomly allocated to each of twelve 50-mL beakers ($n = 3$ per treatment). Four additional beakers, 2 with unburned leaves and 2 with burned needles, were used as range finders to terminate the study before 100% oxygen loss occurred. Two beakers without detritus were included as a positive control to account for residual microbial activity in the reservoir water. At time zero, dissolved oxygen ($\text{mg} \cdot \text{L}^{-1}$) was measured in each beaker. 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 hours, DO was measured again and wet weights (g) of leaves or needles in each beaker were

recorded. This experiment was immediately repeated in a second trial.

Pteronarcella badia Growth Experiment

Live *P. badia* (length: $\bar{x} = 7.46 \text{ mm}$, $\text{SD} = 0.89$, mid-instar stage) were collected in October 1999 from the Cache La Poudre River, below where the leaf packs were deployed. Organisms were transferred to stream microcosms at Colorado State University, Fort Collins, Colorado, and allowed to acclimate for 24 hours without food. Microcosms were oval ($76 \times 46 \times 14 \text{ cm}$) flow-through fiberglass tanks with a water volume of 13 L and a current of $30 \text{ cm} \cdot \text{s}^{-1}$ generated by a paddle wheel. Unfiltered water was supplied from Horsetooth Reservoir (11.7°C , $7.7 \text{ mg DO} \cdot \text{L}^{-1}$, 7.7 pH and $60 \mu\text{S}$ conductivity), and microcosms were housed in a greenhouse to provide a natural light regime. Treatment cages were constructed with Tupperware® containers ($15.5 \times 11 \times 11 \text{ cm}$). We drilled 6-cm-diameter holes into each side of the cages and covered the holes with 250- μm mesh to allow water flow without losing detritus. Four cages were placed in each of the 10 microcosm chambers.

Detritus treatments were randomly allocated among the 4 cages in each of 10 stream microcosms ($n = 10$ cages per detritus treatment). Leaves and needles in the cages were overlain with a piece of plastic mesh ($6 \times 6 \text{ cm}$, 1-mm² opening) and a small cobble was placed on top to anchor the mesh and to provide cover for *P. badia*. Flow-through holes in the cages were kept clean of debris and algae. Individual *P. badia* were immobilized with carbonated water, placed on a wet sponge, and measured for length with digital calipers. Then 3 individuals were randomly assigned to each of the 40 cages. Test organisms fed *ad libitum* on the treatments for 12 days, after which they were measured again using the same methodology for live insects. Individuals were then sacrificed, and both body length and head capsule widths were measured to validate live measurement techniques. Mean length of live individuals per cage was used to compare growth before and after the feeding experiment.

Statistical Analysis

Recovery of total density of stonefly detritivores in plateau streams and a comparison of how *A. banksi* and *P. badia* responded to fire and postfire floods were investigated

graphically and with descriptive statistics. To assess colonization across leaf pack treatments, we compared the number of *P. badia* per gram of detritus in each leaf pack at the time of collection (27 days and 50 days). Leaf pack breakdown rates (k) after 27 days and 50 days were calculated as the percent loss of dry mass per day relative to the initial dry mass at time zero. Microbial respiration was calculated as the percent loss in DO ($\text{mg} \cdot \text{L}^{-1}$ per g detritus) after 18 hours, after being adjusted for DO changes in water-only beakers, compared to DO at time zero. *Pteronarcella badia* growth was calculated as the percent change in mean length per treatment cage relative to the mean initial length of the same cage.

We employed ANOVA and Tukey's HSD test to assess differences among the 4 treatments in leaf pack breakdown rate, *P. badia* colonization, microbial respiration, and *P. badia* growth. In initial ANOVA models, we included block effects due to microcosm, sample time (27 days vs. 50 days), trial (DO), position of wooden racks in the stream, and all 2-way interactions. However, if blocks and covariates were highly insignificant ($P > 0.5$), they were removed for a simplified collapsed model of burn treatment, detritus type, and burn $\times$ detritus type interactions. Tukey's tests corresponded to the collapsed models. Assumptions of normality, heterogeneity, and independence of errors were checked with diagnostic tests available in SAS statistical software (SAS Institute, Inc. 1996), and transformations were performed when indicated.

RESULTS

Stonefly Population Surveys

The dominant stonefly detritivores in Capulin Canyon prior to the Dome Fire included Nemouridae (primarily *A. banksi* and *Z. cinctipes*) and species of the winter stonefly genus *Capnia*. Nemourids were common across all 3 canyons prior to fire and flood disturbance. *Pteronarcella badia* was common in Frijoles Canyon and in Guaje Canyon prior to the Cerro Grande Fire. Interestingly, *P. badia* was absent from Capulin, even prior to the fire, despite the fact that this stonefly is present in most canyons of the plateau. This absence is difficult to explain, because nearby canyons with *P. badia* populations are similar to Capulin in both aquatic and riparian habitat features. Capniidae nymphs were col-

lected throughout the study in low numbers in all 3 canyons, probably due to the coarse mesh size used for sampling. Therefore, temporal trends for this family were included in the analysis for total stonefly detritivore densities but were not specifically analyzed.

The total number of stonefly detritivores in the 3 canyons varied considerably across both years and seasons where higher densities were observed in summer and fall sampling events (Fig. 3). Mean densities (standard deviation) were similar in the 2 prefire years for most of the study reaches (Frijoles, 20.3 [34.5]; Capulin, 21.1 [17.9]; lower Guaje, 21.7 [17.9]; and upper Guaje, 11.9 [6.5]). No shredder stoneflies were collected in Capulin canyon 2 weeks after the first postfire (100-year) flood in July 1996, and they remained absent at study sites until fall 1997. Thereafter and throughout the study period, densities remained lower than mean prefire levels, and also lower than densities in unburned Frijoles Canyon. In Guaje Canyon, we were able to compare direct effects of wildfire on detritivorous stonefly densities to the impacts of the first 100-year flood event after the fire. Densities increased almost 4-fold immediately following the fire in June 2000 (Fig. 3). We observed that all invertebrates, including shredder stoneflies, were congregated in the leaf litter. Detritus may have served as a refuge from the ash covering the stream bottom.

While the fire itself did not significantly impact detritivorous stoneflies in Guaje Canyon, densities were reduced to zero at both lower and upper reaches 3 weeks after the first postfire flood in September 2000 (Fig. 3). Stream reaches at both elevations were flooded, despite differences in fire effects on riparian vegetation, because severely burned upper hillslopes of the watershed created intense runoff through ephemeral tributaries and overland flow (Beeson et al. 2001). However, lower-elevation sites experienced cumulative hydrologic effects from upstream, which resulted in more-severe flood magnitudes. Organisms were likely flushed downstream during this 100-year flood event. Lower Guaje reaches, where stream morphology and bed substrate were more significantly altered by flooding (e.g., deep incision, shifting gravel bed; Fig. 2), showed minimal recolonization of shredder stoneflies until 2002. By contrast, densities recovered a year earlier in the upper Guaje reaches (Fig. 3), where the

Fig. 3. Natural log of mean density (individuals per 0.093 m²; error bars represent standard error; $n = 6-9$) for total stonefly detritivores in Pajarito Plateau streams (near Los Alamos, NM) before and after (A) the 1996 Dome Fire and (B) the 2000 Cerro Grande Fire. Marks on the x-axis correspond to winter, spring, summer, and fall of each year. Arrows indicate the date of fires in Capulin and Guaje canyons, while blocks indicate summers with severe 100-year floods (thick block), moderate 10-year floods, and minor 2-5-year floods (thin block). Frijoles Canyon did not experience unusual flooding during the study period from 1994 to 2002.

bed substrate stabilized more rapidly after the first postfire flood season (N. Vieira, personal observation).

Both *A. banksi* and *P. badia* were common in Guaje Canyon, a situation that allowed us to compare recovery trajectories of these 2 species. Recovery of shredder stoneflies in lower Guaje Canyon was largely driven by recolonization success of *A. banksi* (Fig. 4). Populations of *P. badia* in lower Guaje did not return to prefire densities during the study. By contrast, *A. banksi* recovered to prefire densities by May 2002, only 2 years postfire. Similar interspecies differences were observed in upper Guaje, where *A. banksi* recolonized to prefire densities earlier in spring 2001 (Fig. 4). *Pteronarcella badia* recolonized upper sites by summer 2001 but at lower densities than prefire den-

sities. By 2002, *P. badia* densities were similar to prefire levels in the upper Guaje reach.

Burned Detritus Experiments

Cottonwood leaf packs lost a higher percentage of their original mass compared to pine needle leaf packs after both 27 days and 50 days of conditioning (Table 1). Unburned cottonwood leaves showed the highest loss of 48.8% ($k = 0.01$ per day), while burned pine showed the lowest loss of 24.4% ($k = 0.005$ per day). For all treatments, the majority of detrital loss occurred in the first few weeks and was likely due to leaching and mechanical breakdown. Total percent loss was similar between 27-day and 50-day samples within treatment types, and there were no significant block effects due to location in the stream ($df_{\text{model}} = 95$, $P_{\text{model}} = 0.7988$). A

Fig. 4. Natural log of mean density (individuals per 0.093 m²; error bars represent standard error; $n = 6-9$) for 2 shredder stonefly species, *Amphinemura banksi* and *Pteronarcella badia*, in Pajarito Plateau streams (near Los Alamos, NM) before and after the 2000 Cerro Grande Fire. Graphs show the impacts in (A) lower Guaje Canyon and (B) upper Guaje Canyon. Arrows indicate the fire. See Fig. 3 for postfire flooding events.

TABLE 1. Mean percent loss of dry leaf pack biomass consisting of burned and unburned ponderosa pine needles and deciduous cottonwood leaves. Leafpacks were conditioned for 27 days or 50 days in the Cache la Poudre River, Colorado. Initial dry mass of each leaf pack was 8 g ($n = 12$).

Detritus type	Days	Burned		Unburned	
		Mean % loss	SD	Mean % loss	SD
Cottonwood leaves	27	38.57	5.62	47.60	1.89
	50	34.37	2.73	48.83	2.91
Ponderosa pine needles	27	24.39	8.66	24.58	8.56
	50	25.38	14.68	25.03	3.18

collapsed 2-way ANOVA model, with 27-day and 50-day samples combined, revealed that burn treatment, detritus type, and the burn $\times$ detritus type interaction contributed to differences in decomposition ($df_{\text{model}} = 95$; all $P < 0.0001$). Total percent loss was highest for unburned leaves, followed by burned leaves, and then burned and unburned needles (Fig. 5). In contrast to differences in leaf pack breakdown rates, *P. badia* colonization was similar

across the 4 treatments (Fig. 5). There was no significant difference in colonization between 27-day and 50-day treatments, or between detritus types or burn treatments (ANOVA: log-transformed data, $df_{\text{model}} = 95$, $P_{\text{model}} = 0.6911$).

Although burned leaves and needles were notably different in texture and color than unburned organic material, nutritional analysis indicated a similar chemical makeup between

Fig. 5. Mean (and 95% confidence intervals) of (A) total percent loss of dry mass of, and (B) number of *Pteronarcella badia* colonizing on, artificially constructed leaf packs containing burned and unburned ponderosa pine needles and cottonwood leaves ($n = 24$). Mean (and 95% confidence intervals) for (C) oxygen use (% change from time zero of $\text{mg O}_2 \cdot \text{L}^{-1}$ per g) of microbes ($n = 6$ –10) and (D) growth (% increase in length mm) of *P. badia* on each detritus treatment ($n = 10$) are also presented. Letters represent results of Tukey's multiple comparisons tests; different letters represent statistical differences ($\alpha = 0.05$).

TABLE 2. Nutritional analysis of burned and unburned ponderosa pine needles and cottonwood leaves conditioned for 50 days in the Cache la Poudre River, Colorado. Percent solvent extract represents both nutritive and nonnutritive 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

burned and unburned treatments within each detritus type (Table 2). However, there were general differences between needles and leaves. Burned and unburned needles were higher in lipids and carbon but lower in nitrogen content compared to leaves. Leaves and needles also differ in lignin and tannins; however, these parameters were not measured.

Microbial respiration differed substantially among treatments. In both respiration trials, 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 2 treatments). Microbial respiration was highest on unburned leaves, followed by burned leaves, and lowest on unburned and burned needles (Fig. 5). There was no significant difference between trials (log-transformed data, $\text{df}_{\text{model}} = 31$, $P_{\text{model}} = 0.3584$) in the global model. Therefore, we ran a collapsed ANOVA model with both trials combined. Burn treatments and detritus types were different ($P < 0.0001$ for both

factors; $df_{\text{model}} = 31$), but there was no significant interaction ($df_{\text{model}} = 31$, $P = 0.5813$).

Pteronarcella badia Growth Experiment

In the microcosm growth experiment, only 9 of the 120 *P. badia* died from unknown causes, and these individuals were excluded from analysis. *Pteronarcella badia* grew an average of 1.4 mm in length (approximately 20% of their initial length) over 12 days on all treatments (Fig. 5). Relative growth rates were similar across detritus type and burn treatments, and there were no significant block effects due to microcosm (ANOVA: $df_{\text{model}} = 39$, $P_{\text{model}} = 0.9211$).

DISCUSSION

Stonefly detritivore populations in Pajarito Plateau streams were markedly reduced in burned canyons after intense crown wildfires, but these reductions corresponded to severe postfire flooding rather than to the direct effects of fire. Both *A. banksi* and *P. badia* populations showed no resistance to 100-year floods after the Dome and Cerro Grande fires and showed low resilience to moderate flooding in the year following the fires. *P. badia* was notably less resilient than *A. banksi* and had not fully recovered in severely burned reaches of Guaje Canyon 2 years after the Cerro Grande Fire. While previous studies showed that *A. banksi* required more than 6 years to recover in Capulin Canyon after the Dome Fire (Vieira et al. 2004), this species showed much higher resilience in Guaje Canyon, especially in lightly burned upper reaches. Other studies have shown that the nemourid *Zapada columbiana* (Mihuc and Minshall 1995, Minshall et al. 1997), and shredders in general (Minshall et al. 2001), were fairly resilient to fire-related disturbances following the Yellowstone fires. Another stonefly shredder, *Yoraperla* sp. (Peltoperlidae), recolonized quickly through drift in Washington streams that remained hydrologically stable after a wildfire (Mellon et al. 2008). Our study suggests that *P. badia* populations may be particularly sensitive to postfire flood disturbances.

Both our field surveys and our growth experiments indicated that reduced food quality associated with burned riparian vegetation does not explain the strong negative response of *P. badia* to the Cerro Grande Fire. Stonefly shredders colonized ash-covered detritus at high densities immediately after the fire, even in severely

burned reaches. In addition, *P. badia* both colonized and grew on burned coniferous and deciduous detritus in our experiments. Growth on burned detritus treatments was likely due to the fact that burning did not significantly alter protein content in the leaves or lipids in the needles, both of which are indicators of nutrition for stream detritivores (Short et al. 1980, Cargill et al. 1985). Lower microbial colonization on burned detritus, especially on burned needles, did not negatively impact *P. badia* growth. Apparently, there were enough microorganisms conditioning the burned detritus to render it a palatable and nutritious food source.

In contrast to our study, Mihuc and Minshall (1995) found that 10 of 11 insect taxa could not grow on 100% burned detritus, and they cited low lipid and protein content and reduced microbial densities as potential explanations. Compared to our study, Mihuc and Minshall (1995) also found greater reductions in microbial colonization and alteration of nutritional content as a result of more-intense burning. Our experimental burn treatment was more similar to their 35% natural burn. They found slightly higher bacterial colonization on this naturally burned material, and as such, 3 generalist detritivores grew on this treatment, including the nemourid stonefly *Z. columbiana*. In addition to growing on partially burned materials, *Z. columbiana* also fed and grew on periphyton, demonstrating that this species has a flexible detritivore-herbivore feeding strategy and is not a specialist on CPOM. Dietary flexibility was corroborated by the fact that this species showed isotope signatures for both periphyton and detritus in the field (Mihuc and Minshall 2005) and this flexibility may explain the high resilience of *Z. columbiana* populations after wildfire (Minshall et al. 1997). Herbivory is common in other North American nemourids (Vieira et al. 2006) and may have facilitated *A. banksi* colonization success after postfire floods abated in burned plateau canyons.

While postfire flooding clearly impacted detritivorous stonefly densities, we could not separate organism loss via flooding from the indirect effects of reduced detrital retention, which can also influence shredder populations (Muotka and Laasonen 2002, Lepori et al. 2005). Most aquatic organisms in Guaje and Capulin canyons, including detritivorous stoneflies, were extirpated after moderate to severe postfire flooding (Vieira et al. 2004). We also observed repeated flushing of detritus as a

result of these floods, with minimal additions of new leaf litter until riparian vegetation reestablished. Others have observed reduced or variable retention of CPOM due to hydrologic instability after wildfires (e.g., McIntyre and Minshall 1996, Robinson et al. 2005, Arkle et al. 2010). Our findings are consistent with those of Arkle et al. (2010), who found that post-fire hydrology interacts with riparian cover, detrital resources, and sediment loads in a complex fashion to influence benthic invertebrate recovery. For example, recovery trajectories to prefire levels differed widely across study reaches. Shredder stonefly densities recovered earliest in upper Guaje Canyon, where the riparian zone was minimally damaged in the fire. By contrast, densities of stonefly detritivores, and also of total invertebrate shredders (Vieira et al. 2004), had not fully recovered in Capulin Canyon 6 years postfire, even though mature woody riparian species had reestablished.

Recovery trajectories not only differed across study sites, but also between stonefly species. *Pteronarcella badia* populations demonstrated less resilience than *A. banksi* populations after the Cerro Grande Fire. Even after flood magnitudes dampened, *P. badia* had still not recovered in either lightly or severely burned reaches of Guaje Canyon by the end of the study. By contrast, *A. banksi* populations recovered to prefire densities in upper Guaje reaches one year after the fire and in the severely burned lower reaches by spring 2002. Species traits related to hydrologic disturbance may explain these differences in recovery trajectories (Rader 1997, Richards et al. 1997, Townsend et al. 1997b). First, *P. badia* is semivoltine and thus may require a higher degree of hydrological and streambed stability to complete their life cycle. For example, Feminella (1996) demonstrated that another pteronarcid, *Pteronarcys* sp., was restricted to streams with a high level of flow permanence and stability, whereas univoltine *Amphinemura* sp. and Capniidae were ubiquitous even in intermittent streams in Alabama. Second, *P. badia* nymphs are larger bodied and probably more easily entrained by floods compared to *A. banksi*, which can seek refugia in microhabitats. Finally, *P. badia* may have weaker dispersal mechanisms. For example, nymphs of this species are less prone to drift compared to the smaller-bodied nemourids and capniids. *Pteronarcella badia* is a strong flyer and could have colonized via aerial dis-

persal in Guaje Canyon. However, both *P. badia* and *A. banksi* adults tend to remain local (within 1 km) after emergence (Vieira et al. 2006).

Our research on 2 fires of the Pajarito Plateau confirms that ecological responses in burned watersheds of the western United States vary dramatically across individual fires, taxonomic groups, burned streams, and even across reaches within a burned stream (e.g., Minshall et al. 1997, Gresswell 1999, Malison and Baxter 2010). We found notable differences in how detritivorous stonefly species responded to wildfires versus postfire flooding, and also in how these stoneflies recovered between burned canyons of the plateau. Differences can be evaluated in context of the mosaic of fire disturbance and the landscape that characterizes the plateau. For example, the forested headwaters of Guaje Canyon were relatively unburned in the Cerro Grande Fire, whereas the Dome Fire burned Capulin Canyon up to the intermittent spring seeps where the perennial reach begins. The presence of pristine, perennial headwaters in Guaje Canyon provided a nearby source of invertebrate colonists, especially for *A. banksi*, which has stronger drift behaviors than *P. badia*. Unburned headwaters in Guaje Canyon also likely provided CPOM to burned reaches below. While recolonization from upstream springs has been noted in other montane desert streams following floods (Molles 1985), invertebrate communities in the seeps of upper Capulin Canyon are fairly depauperate (Vieira et al. 2004). Therefore, postfire colonization of stoneflies in burned reaches of Capulin Canyon likely occurred via aerial adult dispersal. The canyons-mesa topography of the plateau, the rarity of perennial tributaries, and the intermittency between the perennial stream segments and the Rio Grande River pose strong colonization barriers to dispersal. The reliance on aerial versus drift dispersal, especially given these barriers, may explain why *A. banksi* recovery was significantly delayed in Capulin Canyon compared to Guaje Canyon.

Our study suggests that headwaters of the Pajarito Plateau system should be considered for fire management in unburned watersheds and prioritized for rehabilitation efforts in burned watersheds. Such efforts will reduce postfire flooding magnitudes, maintain refugia for aquatic organisms, provide a colonist pool for degraded reaches, and preserve riparian resources and the detrital subsidies they provide to lotic food

webs downstream and in the headwaters. Lake et al. (2007) argue that headwaters normally must be functional in order to support restoration actions in degraded reaches downstream, especially in those headwaters prone to hydrologic disturbance, because downstream reaches are inherently impacted by stream stability above. Riparian fuel reduction management through prescribed burns, thinning, or other management actions may provide a solution to protect riparian vegetation and streams in headwater areas. This relatively new practice has obvious potential benefits in protecting critical habitats, but how much these benefits are realized is largely untested and thus unknown (Stone et al. 2010). For example, only a handful of studies exist to indicate that prescribed burns have minimal impacts to stream communities compared to wildfires (e.g., Beche et al. 2005, Arkle and Pilliod 2010). Until riparian fuel management and headwater protection strategies gain traction and can be optimized for regional landscapes and riparian types (Pettit and Naiman 2007), streams will remain at the mercy of severe fires and postfire flooding in western watersheds.

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