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Effects of wildfire on stream algal abundance, community structure, and nutrient limitation

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Abstract: We studied the effects of wildfires in southern California on stream algal communities and their responses to nutrient enrichment. The intensity of scouring floods, concentrations of nutrients during ensuing rains (4–13× increases depending on nutrient), and postflood sediment deposition were greater at sites in burned than in unburned basins (UN sites). Postfire storms reduced algal biomass >10× more at sites in burned than in unburned basins. After the fire and subsequent floods, algal biomass, particularly of *Cladophora*, was up to 5 (chlorophyll *a*) to 20 (macroalgal mass) times higher at sites in burned basins with burned riparian vegetation (BRB sites) than at sites in unburned basins (UN sites), but algal abundance at sites in burned basins with intact riparian vegetation (BRI sites) was as low as 10 to 30% of that recorded at UN sites. Two to 3 mo after the wet season, nutrient and algal levels were similar among sites in UN, BRI, and BRB basins. We used summer nutrient diffusing substrata (NDS) experiments where N, P, N+P, or neither were added and found that algal density, chl *a*, and chl *a*/algal unit increased by ~1.5 to 4.5× with N additions at sites in BRB and UN basins but did not change at sites in BRI basins. In contrast, algal biovolume increased 2 to 9× with N additions at all sites and with P addition at sites in BRI basins. General depressions in chl *a* by 40 to 50% with P addition were related to decreased chl *a*/algal unit. Diatoms increased with N and N+P additions at sites in UN and BRI basins and with P addition at sites in BRI basins but declined with P or N+P additions at sites in BRB basins, with cyanobacteria and green algae generally showing the opposite pattern. Algal responses to nutrient augmentation across sites were related to fire effects on riparian canopy cover, temperature, and ambient nutrient concentrations. Fire effects on algal communities and nutrient limitation appeared to be mediated through fire effects on flood disturbance and light regimes.

Key words: wildfire, stream algae, nutrients, canopy cover, nutrient diffusing substrata, Mediterranean climates

Fire is a pervasive and powerful agent that has profoundly influenced ecosystems throughout the world (Bowman et al. 2009, Pausas and Keeley 2009). The frequency and intensity of wildfires have increased and are predicted to further increase in many regions consequent to changing climate and human population expansion into wildland areas (Westerling et al. 2006, 2011, Syphard et al. 2007). Fires destroy upland and riparian vegetation, alter soils, and increase runoff and erosion, thereby affecting water quality, substrata composition, geomorphology, temperature, light levels, and allochthonous inputs in streams, with many repercussions for the stream biota (reviewed by Gresswell 1999, Verkaik et al. 2013). Fires are potent drivers of ecosystem change in Mediterranean climates because of seasonal droughts, large interannual variation in precipitation, accumulation of

fire-adapted plant biomass, and often steep terrain (Verkaik et al. 2013).

Two fires, in November 2008 and May 2009, burned steep foothill and mountain areas above Santa Barbara, California, USA (Cooper et al. 2015). We expected few immediate effects of these wildfires on stream ecosystems but that ensuing storms would increase runoff and erosion, engendering increased stream discharge, sediment transport and deposition, and nutrient concentrations (Coombs and Melack 2013). These particular wildfires had variable effects on riparian vegetation. At some stream reaches riparian vegetation was destroyed by wildfire, and at others riparian vegetation remained intact, allowing us to assess the effects of riparian burning on algal variables (Cooper et al. 2015). We also expected that if riparian vegetation

burned, leaf litter inputs and canopy cover would decrease and temperatures would increase (Verkaik et al. 2013, Cooper et al. 2015). We expected these changes in environmental conditions to have repercussions for the density, biomass, and composition of stream algal communities (Stevenson et al. 1996), so we focused on algal responses to wildfire during and after subsequent winter storms (Robinson et al. 1994, Earl and Blinn 2003).

We concentrated on algae because they are an important basal resource in stream food webs, support higher trophic levels, and have important effects on and are indicators of water quality (Stevenson et al. 1996, Klose et al. 2012). Algal biomass has shown the gamut of positive, negative, or no responses to fire (Minshall et al. 1995, 1997, 2001a, b, Earl and Blinn 2003, Bêche et al. 2005, Malison and Baxter 2010, Romme et al. 2011, Rugenski and Minshall 2014), presumably because of differences among systems in the time since fires; the frequency, intensity, and timing of fires and subsequent storms or runoff; and the complex network of abiotic and biotic factors influenced by fires that affects algal communities (Minshall et al. 2004, Verkaik et al. 2013). Wildfires affect nutrient concentrations and, where riparian vegetation burns, light and temperature levels. Therefore, we also examined how algal responses to nutrient enrichment varied across streams in unburned and burned basins with and without riparian vegetation loss to delineate some of the conditions that might elicit algal blooms and degrade water quality (Lange et al. 2011, Keck and Lepori 2012, Klose et al. 2012).

We used algal monitoring and nutrient diffusing substrata (NDS) experiments with and without nutrient amendments to examine fire effects on stream algal abundance, community structure, and nutrient limitation. We worked in streams draining basins that were unburned (UN), basins where upland vegetation burned but riparian vegetation remained intact (BRI), and basins where both upland and riparian vegetation burned (BRB). We predicted that algal biomass would be reduced more by scouring winter floods at sites in BRB and BRI basins than at sites in UN basins, but that algal biomass, especially large filamentous green algae and high-profile diatoms, would recover more quickly and reach higher levels at sites in BRB basins because of higher light, nutrient, and temperature levels than at sites in BRI and UN basins (Minshall et al. 1989, Passy 2007, Klose et al. 2012, Stenger-Kovacs et al. 2013). N appears to be the major nutrient limiting algal biomass in these and nearby streams in early summer (Goodridge and Melack 2012, Klose et al. 2012), so we hypothesized that algal responses to N additions would be greater at sites in BRB than in UN and BRI basins because of higher light levels at sites in BRB basins and greater at sites in UN than in BRI basins because ambient N concentrations would be lower and more limiting at sites in UN than in BRI basins (Taulbee et al. 2005, Hill and Fanta 2008, Kiffney 2008, Keck and Lepori 2012, Klose et al. 2012).

METHODS
Study sites

The Santa Ynez Mountains in Santa Barbara County, California, are a steep, coastal mountain chain with a Mediterranean climate, which is wet and cool from November through March and dry and warm from April through October. Average annual rainfall ranges from 100 cm/y in the mountains to 45 cm/y at sea level. Depending on the sampling time, we monitored 10 to 14 stream sites with discharge ranging from 0 to 0.005 m^3/s in summer and autumn to nearly 5 m^3/s during winter floods. Water temperatures ranged from 11 to 24°C between May and November and from 5 to 15°C between December and April. Drainage areas ranged from 3 to 13 km^2, elevations from 78 to 480 m asl, gradients from 4 to 13%, and baseflow stream widths from 2 to 5 m. Stream waters have a slightly alkaline pH (6.9–8.4), high conductivities (590–970 µS/cm), and low nutrient concentrations (ranges: NO_3^--N = 0.1–12.1 µM, $PO_4^{-3}-P$ = 0.2–1.2 µM). Stream substrata were dominated by gravel, cobble, boulders, and bedrock, but sand became prominent at sites affected by fire. Riparian vegetation was dominated by alder (*Alnus rhombifolia*), California laurel (*Umbellularia californica*), willow (*Salix* spp.), and California sycamore (*Platanus racemosa*), whereas upland areas were covered primarily by chaparral, with some coast live oak (*Quercus agrifolia*) woodland. Stream sites lay largely or entirely upstream of developed areas (drainage cover <4% urban, <6% agricultural).

Most chaparral in the mountains of Santa Barbara has burned in the last 50 to 60 y. Almost all fires were ignited by human activity, and fire frequency is increasing because of land use and climate changes (Barro and Conrad 1991, Syphard et al. 2007). The Tea Fire burned 7.85 km^2 above the cities of Santa Barbara and Montecito during 13–17 November 2008, and the Jesusita Fire burned 35.35 km^2 above the city of Santa Barbara from 5–18 May 2009. The Tea Fire burned small percentages (1 and 11%) of the drainage basins of 2 of our sites, but the subsequent Jesusita Fire burned greater percentages of the basins of both of these sites (19 and 74%) and the basins of 5 more study sites (fire extent = 49–81%), so our analyses concentrated on the effects of the Jesusita Fire on our study sites. The number of sampling sites in each basin burn category was 6 to 7 (UN), 2 (BRB), and 2 to 5 (BRI), depending on sampling date. No substantive rains (>5 cm) or floods occurred during the October 2008 to April 2009 wet season (2009 water year). Precipitation was near average, but runoff and stream discharge were higher during large storms in burned than unburned basins in the 2010 water year (Cooper et al. 2015).

Overview of survey and experimental designs

We used 3 approaches to compare stream algal responses to wildfire and nutrient additions across different basin burn categories. We: 1) monitored riffle chlorophyll *a* (chl *a*)

concentrations and abiotic factors in early and late December 2009, just before and after the first rains of the wet season, and in March and June 2010; 2) surveyed algal abundance and community composition on hard substrata in the pools and riffles of study reaches in June 2010 (1 y after fires); and 3) conducted an NDS experiment examining the effects of nutrient additions on algal communities in July 2010. Algal responses to fire probably are mediated through the effects of fire on light, temperature, nutrients, and flooding disturbance. The monitoring work provided a context for evaluating algal responses to wildfire 1 y after fires (the survey), and the survey data additionally characterized the algal colonization pool for the NDS experiment. The NDS experiment was designed to assess the nature (N, P, N+P) and degree of nutrient limitation of algal density, biovolume, and chl a concentration and the effects of nutrient enrichment on algal community structure across sites in different basin burn categories.

Survey and monitoring program

Physical and chemical measurements

We measured water and sediment depth, stream width, % canopy cover (with a spherical densiometer), and water velocity at 60% depth (with a current meter) on each sampling date from December 2009–June 2010 in 5 riffles/site. In June we also measured these variables in each of 5 pools/site using the same methods, and we measured dissolved O_2 (DO) concentration (mg/L), conductivity (μS/cm), pH, and water temperature (°C) with a DO/conductivity and pH meter (YSI model 55; Yellow Springs Instruments, Yellow Springs, Ohio) at the upstream end of each reach.

We collected water samples for measurement of NO_3^--N, NO_2^--N, NH_4^+-N, and soluble reactive P (SRP, PO_4^{3-}-P) concentrations (μM) from the upstream end of each study reach on each sampling date. We filtered samples for dissolved inorganic nutrient analysis through 0.45-μm polycarbonate filters in the field and froze them until analysis. We measured dissolved nutrient concentrations spectrophotometrically on a Lachat Quikchem 8000 flow injection analyzer (Lachat Instruments, Milwaukee, Wisconsin) with standard methods (SRP: reaction with ammonium molybdate and ascorbic acid; NO_2^-/NO_3^-: reduction of NO_3^- to NO_2^-, diazotization of NO_2^- with sulfanilamide coupled with ethylenediamine dihydrochloride; NH_4^+: QuickChem Gas Diffusion Method 31-107-06-5-A).

Algal sampling

At each site on each sampling date from December 2009–June 2010, we sampled benthic algae (for chl a) from hard substrata (rocks, cobbles, boulders, bedrock) at each of 3 random locations in each of 5 riffles over a 100-m reach (n = 15 riffle samples/site on each date). We used a 2.6-cm-diameter, open-ended syringe with removable scouring pad attached to the bottom of the syringe plunger to remove algae from the substrata (described by Davies and

Gee 1993). We also sampled benthic algae (chl a and ash-free dry mass [AFDM]) from hard substrata at 3 random locations in each of 5 pools in June using the same methods (n = 15 pool samples/site). In the laboratory, we rinsed benthic periphyton on the scouring pads with deionized water and combined samples from each site to produce a hard substratum sample from each site on each date (pool and riffle samples were kept separate). We filtered subsamples through GF/C filters. We stored chl a filters frozen until analysis. We precombusted (500°C) and weighed filters for AFDM prior to filtration. We measured AFDM in subsamples after drying (60°C, 24 h), weighing, combusting (500°C, 2 h), and reweighing them. We extracted chl a from filters in 90% acetone (20°C, 24 h) and quantified chl a fluorometrically (Klose et al. 2012).

In June 2010, we subsampled each algal sample from each site for species identification and preserved subsamples in 10% sucrose-formalin. We identified algae in subsamples to the lowest possible taxonomic level (usually genus or species, references below) and enumerated units at 400× magnification under a compound microscope by means of standard methods (modified from Acker 2002). We calculated densities by enumerating all viable algal units from a known subsample volume with a Neubauer hemocytometer, then back calculated to areal densities given the proportion of the sample counted and the area sampled. For most taxa with distinguishable cells (all diatoms, cyanobacteria or green algae with large, easily discernible cells) we used cells as our counting unit, but for colonial and filamentous soft algae with small cells that were not easily discernible (e.g., Chroococcales, thin *Leptolyngbya*, *Oscillatoria*), we used a 10 × 10-μm area (colonies) or a 100-μm length (filaments) as our counting unit to ensure some comparability between distinguishable cells and colonies or filaments with very small cells. We estimated total algal biovolume by multiplying the counts of algal units by the average geometric dimensions of the unit for a given taxon (Hillebrand et al. 1999, Reavie et al. 2010). To account for size variability within algal species, we measured a minimum of 10 individuals from each species or, where <10 individuals were counted, we used literature data for biovolume calculations (Patrick and Reimer 1966, Krammer and Lange-Bertalot 1986, 1988, 1991a, b, Dillard 2008, Komárek and Hauer 2013).

In June 2010, we estimated algal % cover at each site by noting the algal type or bare substratum under each of 50 evenly spaced dots within a 28 × 28-cm quadrat on the clear Plexiglas® bottom surface of an underwater viewing bucket (Barbour et al. 1999). We categorized algal types as the genus of macroalga or as the thickness of mats dominated by diatoms (thin: <0.5 mm in height, medium: 0.5–2.0 mm, thick: >2.0 mm) (Klose et al. 2012). We estimated % cover by algal types for 2 hard and 2 soft substrata quadrats in each of 5 riffles and 5 pools at each site (10 quadrats for each of 4 subhabitats per site).

In June 2010, we also measured macroalgal dry mass in 2 Surber samples (bottom area of each = 0.09 m^2, mesh size = 250 μm) taken from each of 5 riffles and from hard substrata in each of 5 pools. We composited samples for each habitat type (pools vs riffles) at each site, separated substrata from organic matter via elutriation, and preserved samples in 70% ethanol. In the laboratory, we picked macroalgae retained by a 4-mm sieve, then air-dried and weighed this material to provide an estimate of macroalgal dry mass/m^2 for riffles and pools at each site.

NDS experiment

We conducted NDS experiments from 29 June–23 July 2010 (24 d). NDS units consisted of 30-mL plastic containers fitted at the top with 2.7-cm-diameter fritted glass disks and filled with 3% agar amended with 0.5 mol/L NaNO$_3$ (+N treatment), 0.5 mol/L KH$_2$PO$_4$ (+P treatment), or 0.5 mol/L NaNO$_3$ and 0.5 mol/L KH$_2$PO$_4$ (+N+P treatment). Associated controls (C) had no nutrient additions. These procedures created 4 experimental treatments with 5 replicate NDS units assigned to each treatment at each site (Tank et al. 2006, Johnson et al. 2009, Sanderson et al. 2009). We attached NDS containers to a Plexiglas® L-bar (5 cm on a side), secured the L-bar to rebar stakes driven into the stream bottom, and elevated the L-bar above the stream bottom so that NDS units were ~4 cm below the water surface (Klose et al. 2012). We deployed NDS arrays at 6 sites in UN, 2 in BRB, and 2 in BRI basins.

We collected NDS containers on 22–23 July and removed the glass disks and froze them prior to laboratory analysis. At each site, we collected and processed benthic algae from natural hard substrata in the same pools at the same depths at which the NDS units were deployed (see Algal sampling above). We measured current velocity, canopy cover, reach width, pool depth, temperature, and nutrient concentrations at each site at the end of the NDS experiment (see Physical and chemical measurements above) and counted the grazers on each NDS unit. We tested whether N and P continued to diffuse from NDS units at the end of the experiment by placing 1 NDS unit fitted with a new, clean glass disk from each treatment from each of 3 sites (1 from each basin burn category) in a jar containing 300 mL of double-deionized water that was agitated by aeration. After 48 h, water containing P-enriched NDS containers (+P and +N+P) had SRP concentrations that were ~700 to 1300× times higher and water containing N-enriched containers (+N, +N+P) had NO$_3$$^-$-N concentrations that were ~3500 to 24,000× higher than those in water containing control NDS units.

We analyzed 4 of the 5 disks from each NDS treatment at each site separately for chl a concentrations with the methods described above, except that we placed each thawed disk directly into 90% acetone for chl a extrac-

tion. We processed a 5th thawed disk from each treatment at each site to estimate the absolute and relative abundances of individual algal species. We removed algae from each disk with a nylon brush, suspended them in distilled water, and preserved them in 2% sucrose–formalin. We processed algal samples as outlined above.

Statistical analysis

We analyzed monitoring data (December 2009–June 2010) by 1-way analysis of variance (ANOVA) followed by Tukey's Honestly Significant Difference (HSD) tests to examine associations between physiochemical and algal variables and basin burn categories (UN, BRI, BRB). In all analyses we applied log(x) transformations to nutrient concentrations, current speed, conductivity, and algal density (June only), biovolume (June only), and biomass (chl a) data and arcsin√(x) transformations to data on proportional canopy cover and the proportions of different algal taxonomic groups.

For June algal samples from hard substrata, we used the relative abundances of algal taxa collected from pools and riffles (= habitats) at each site to calculate multivariate distances (Sørensen distance metric = Bray–Curtis or % dissimilarity index) between all pairs of sampling sites–habitats. We used nonmetric multidimensional scaling (NMDS) to display the similarity of algal community structure across sites–habitats and identified significant correlations (Pearson's r, $p < 0.05$) between NMDS axes and the relative abundances of algal taxa or transformed values for environmental variables. This analysis was complemented by the multiresponse permutation procedure (MRPP), which tested the null hypothesis of no difference in community structure among streams, habitats, and basin burn categories. We used Indicator Species Analysis (ISA) to identify algal species associated with basin burn categories. We used the Tichý and Chytrý (2006) φ coefficient to calculate the indicator value of each species for basin burn categories and randomization (Monte Carlo) tests to assess the statistical significance of maximum indicator values.

To test whether different algal variables responded to nutrient additions in the NDS experiment, we used pairwise comparisons of values of an algal variable for a nutrient amendment treatment (+N, +P, +N+P) with values for its associated unenriched control for sites in each basin burn category (2-tailed paired t-tests). We used ANOVAs to test whether grazer densities differed among nutrient treatments and basin burn categories. We calculated log response ratios (LRRs) for algal responses to nutrient amendments at each site (e.g., LRR = ln[chl a concentration in nutrient amendment treatment/chl a concentration in control treatment], calculated separately for +N, +P, and +N+P treatments). We tested whether LRR values differed significantly from 0 (mean >2 SE from 0, confirmed by t-tests where replication was sufficient), were associated with ba-

sin burn categories (ANOVAs followed by Tukey's HSD tests), and were related to environmental variables (regression analyses) (Sanderson et al. 2009, Klose et al. 2012). In initial regression models, we used LRR values as the dependent variables and temperature, transformed canopy cover, and transformed ambient NO_3^--N and SRP concentrations as independent variables. We eliminated nonsignificant ($p > 0.1$) independent variables through stepwise-backward elimination to produce the most parsimonious final regression model (as judged by Akaike Information Criteria). We noted marginally significant ($p < 0.10$) algal responses to burn categories or environmental factors because of the low power of some statistical tests (e.g., $n = 2$ for BRI and BRB basins in the NDS experiment).

We used NMDS, MRPP, and ISA analyses on the relative abundances of algal taxa to examine differences in algal community structure between natural hard substrata in pools and control NDS units and among the NDS units assigned to different nutrient treatments across sites in different basin burn categories. We performed all univariate statistical analyses with JMP (version 7.0 for Windows; SAS Institute, Cary, North Carolina), and all multivariate analyses with PC-ORD software (version 5; MjM Software, Gleneden Beach, Oregon).

RESULTS
Physical and chemical changes after fire

Fine sediment depths and nutrient concentrations were greater at sites in BRB and BRI than in UN basins after the first rains of the wet season. NH_4^+-N concentrations showed the greatest difference between burn categories after the first rains (Fig. 1A). NO_3^--N concentrations were greater at sites in BRB and BRI than in UN basins through the wet season (Fig. 1B), and SRP concentrations were greater at sites in BRI than in UN basins through June (Fig. 1C) (Tukey's HSD test, $p < 0.05$). Canopy cover was less (Fig. 1D) and temperature and conductivity higher at sites in BRB than in BRI and UN basins, and sediment depth was greater (Fig. 1E) and stream depth lower at sites in BRB and BRI than in UN basins (Tukey's HSD tests, $p < 0.10$ to < 0.01; Table 1). By late July, average pool depth and reach width were lower in BRB and BRI than in UN basins for sites used in the NDS experiment (ANOVAs, $p < 0.05$), whereas current velocities tended to be greater at sites in BRI basins, and canopy cover less and temperature greater at sites in BRB basins, than at other sites (ANOVAs, current velocity: $p < 0.08$, canopy cover: $p < 0.0005$, water temperature: $p < 0.08$; Table 2). Nutrient concentrations did not differ significantly among sites in different burn categories by late July (ANOVA, $p > 0.10$; Fig. 1A–C). Mean NO_3^--N concentrations tended to be higher at sites in BRI and BRB than in UN basins, but mean NH_4^+-N and SRP concentrations were similar among sites in different burn categories (Table 2).

Algal responses after fire

Riffle algal biomass (as chl a) was reduced to a greater proportionate degree at sites in BRI and BRB than in UN basins by scouring floods after the fires. However, after floods had subsided, algal biomass, primarily filamentous forms like *Cladophora*, recovered more quickly and reached higher levels at sites in BRB (high light, high nutrients) than in BRI (low light, high nutrients) and UN (low light, low nutrients) basins (Fig. 2A, B). Riffle algal biomass had converged to similar levels among sites in different burn categories by June, but pool algal biomass was greater at sites in UN and BRB than in BRI basins (Fig. 2C). Pool algal biomass at sites in BRB and UN basins decreased sharply and was similar to biomass at sites in BRI basins by late July (Fig. 2C). In June, macroalgal biomass was higher in pools at sites in BRB than in BRI or UN basins and higher in riffles at sites in BRB than in BRI basins (Fig. 2D). Chl a concentration was significantly higher on control NDS units than on natural hard substrata in the same pools at the same depths at the end of the NDS experiment (paired t-test, $t_{1,9} = 7.0$, $p < 0.0001$; Fig. 2C).

We identified 103 algal taxa, including 69 diatoms, 16 cyanobacteria, 16 green algae, and 2 red algae (Appendix S1). In June 2010, algal density, biovolume, and species richness on hard substrata in both pools and riffles were significantly greater at sites in BRB than in BRI basins and, in pools, were higher at sites in UN than in BRI basins (Fig. 2E). Diatom density and biovolume and green algal biovolume in pools and riffles, and the density and biovolume of cyanobacteria in riffles, were marginally or significantly lower at sites in BRI than in BRB and UN basins (ANOVAs followed by Tukey's HSD tests). In June, algal biovolumes were dominated (>75% of biovolume) by *Cladophora* in 14 samples, but *Cladophora* was absent from 6 samples, including 5 from shaded sites in UN basins. *Cladophora* made up only 0 to 10% of algal densities across sites (average = 2.1% of densities), despite dominating biovolume and cover at sites in BRB basins (Fig. 2F). In pools, thick diatom films occupied more space at sites in UN than in BRI and BRB basins ($F_{2,7} = 9.1$, $p < 0.01$), and thin diatom films occupied more space at sites in BRI than in UN and BRB basins ($F_{2,7} = 4.3$, $p < 0.05$). In riffles, *Stigeoclonium* occupied more space at sites in BRB than in BRI and UN basins ($F_{2,7} = 21.3$, $p < 0.001$).

Two NMDS axes accounted for 88% of the variation in the multivariate data set (2-dimensional stress = 12.0; orthogonality of axes = 100%; final instability = 0.00000; Fig. 3). Axis 1 accounted for 59% of the multivariate variation and primarily separated sites in BRI and BRB basins from sites in UN basins, whereas axis 2 accounted for 29% of the multivariate variation and separated sites in BRI basins from sites in BRB basins. Correlations between NMDS axis scores and algal taxa and abiotic factors indicated that sites in UN basins were positively associated with molar dissolved inorganic N (DIN)/SRP ratios and the relative abundances
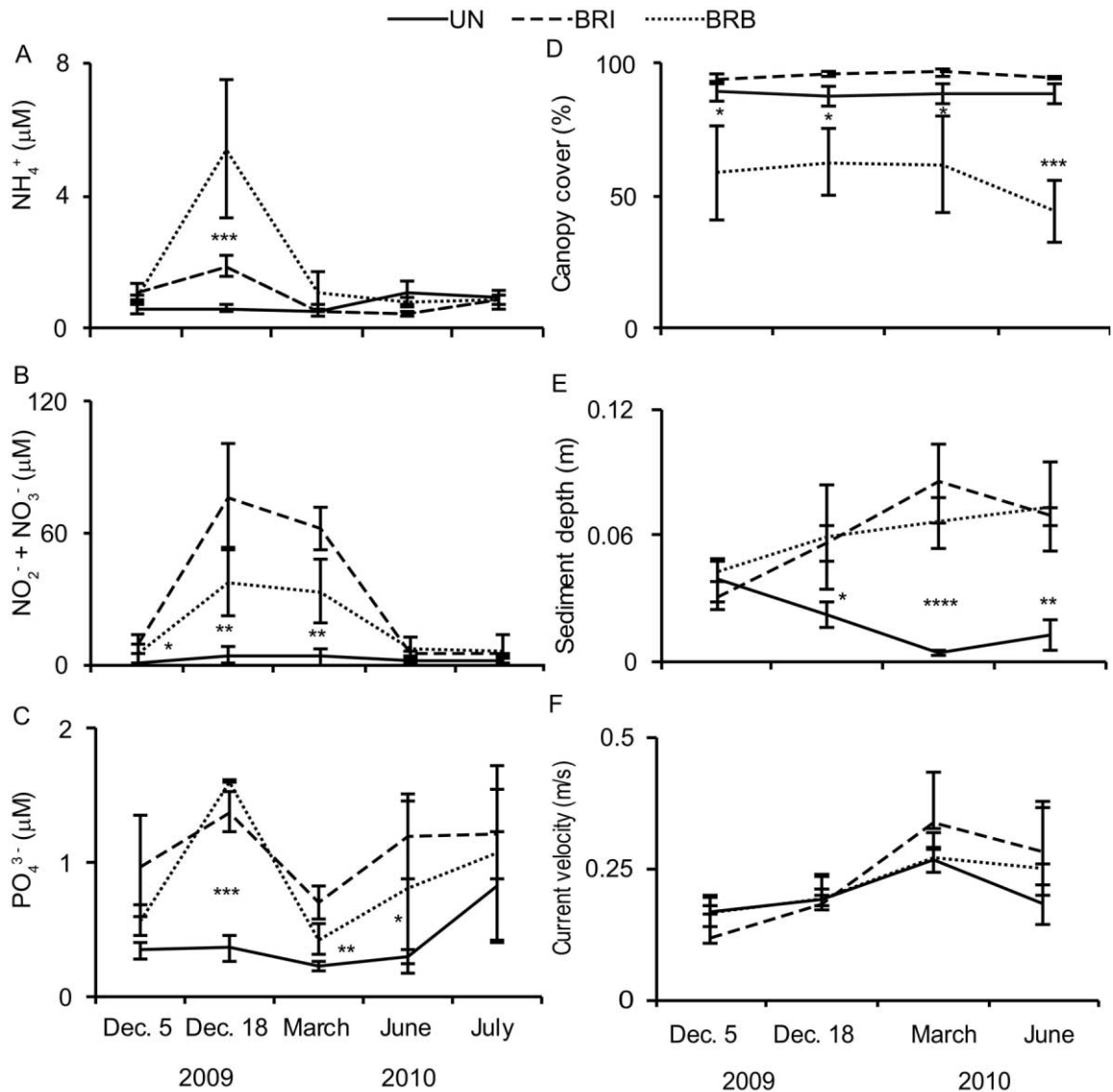
Figure 1. Mean (± 1 SE) NH_4^+ (A), $NO_2^- + NO_3^-$ (B), PO_4^{3-} (C) concentrations, and canopy cover (D), sediment depth (E), and current velocity (F) in streams draining unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). Asterisks denote the results of analyses of variance testing effects of burn category (UN: $n = 6$–7 sites, BRI: $n = 3$–5 sites, BRB: $n = 2$ sites) on response variables for each date. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, **** = $p < 0.0001$.

of the cyanobacterium *Leptolyngbya* spp. and the diatoms *Navicula tripunctata*, *Epithemia adnata*, and *Navicula* spp. Sites in BRB and BRI basins were associated with high relative abundances of the diatoms *Cocconeis pediculus* and *Synedra ulna* and the chlorophyte *Cladophora* sp. The high axis 2 scores calculated for sites in BRI basins were associated with high canopy cover, high SRP concentrations, and high relative abundances of the diatoms *Cocconeis placentula*, *Achnanthidium minutissimum*, and *Planothidium lanceolatum*, whereas the low axis 2 scores for sites in BRB basins were associated with high NH_4^+-N levels and high relative abundances of the diatom *Rhoicosphenia curvata* (Fig. 3). Algal community structure differed among streams (MRPP, stream effect: $A = 0.48$, $t = -8.4$, $p < 0.000001$) and

burn categories ($A = 0.12$, $t = -5.1$, $p < 0.001$) but not between pools and riffles within streams (pool vs riffle: $A = -0.03$, $t = 2.2$, $p \approx 1.0$). *Leptolyngbya* spp. and *E. adnata* were associated with sites in UN basins, *C. placentula* and *A. minutissimum* were associated with sites in BRI basins, and *S. ulna* was associated with sites in BRB basins (ISA Monte Carlo test, $p < 0.05$).

NDS experiment: nutrient amendment effects on algal and grazer abundance

We observed significant differences in algal responses to nutrient amendments across basin burn categories. Algal density (Fig. 4A), biovolume (Fig. 4B), chl *a* concentra-

Table 1. Stream names, codes, coordinates, and mean values for selected physical and chemical features for study sites in Santa Barbara County, California, measured from 16–22 June 2010. Basin burn categories were: UN = unburned, BRI = burned with riparian canopy intact, BRB = burned with riparian canopy burned. z = maximum depth, T = temperature, DO = dissolved O_2, Cond = conductivity. Significant effects of basin burn category on variables are denoted next to variable names. * = $p < 0.05$, [M] = $p < 0.10$. Sites marked NDS were used in the nutrient diffusing substrata experiment.

Stream name	Code	Fire category	Latitude (°N)	Longitude (°W)	Elevation (m)	Pool width (m)	Pool z* (m)	T* (°C)	DO (mg/L)	Cond[M] (µS/cm)	pH
Arroyo Hondo[NDS]	AH	UN	34.489907	−120.143013	78	4.5	0.81	15.6	10.0	765	8.3
El Capitan[NDS]	EL	UN	34.482938	−120.017504	119	4.1	0.41	13.9	10.0	536	8.1
Refugio[NDS]	RE	UN	34.506218	−120.064933	118	3.2	0.44	17.2	10.8	701	8.5
Romero[NDS]	RO	UN	34.458571	−119.591069	358	2.4	0.51	14.5	9.6	651	8.3
San Jose[NDS]	SJ	UN	34.492925	−119.803048	278	7.3	0.97	13.9	9.7	780	8.5
San Onofre	SO	UN	34.481451	−120.188898	96	1.9	0.45	15.6	8.5	904	8.0
San Ysidro[NDS]	SY	UN	34.452924	−119.621784	182	3.8	0.62	15.8	9.8	629	8.4
Cold Springs	CS	BRI	34.456563	−119.653326	192	1.8	0.19	15.1	9.8	596	8.5
Mission (Rocky Nook)	MRN	BRI	34.443747	−119.709493	108	2.3	0.34	18.7	10.8	927	8.6
Rattlesnake (Lower)[NDS]	RL	BRI	34.464474	−119.687972	369	1.8	0.34	16.0	9.4	636	8.4
Rattlesnake (Upper)[NDS]	RU	BRI	34.470763	−119.688856	480	1.8	0.24	14.7	9.8	526	8.4
San Roque	SR	BRI	34.465553	−119.731284	227	3.6	0.48	18.1	9.4	784	8.2
Mission (BG)[NDS]	MI	BRB	34.460483	−119.71012	238	1.7	0.28	18.3	10.6	953	8.2
San Antonio[NDS]	SA	BRB	34.467248	−119.77312	133	3.2	0.30	19.0	10.5	975	8.5

tion (Fig. 4C), and chl *a*/algal unit (Fig. 4D) increased with N addition but chl *a* and chl *a*/unit decreased with P addition at sites in UN and BRB basins. With N addition LRRs for biovolume, chl *a*, and chl *a*/unit were greater at sites in BRB than in BRI basins and, in the case of biovolume, in UN basins. In contrast, algal density and chl *a* were not significantly affected by nutrient additions at sites in BRI basins, except that algal density increased with N+P addition. At sites in BRI basins, algal size (biovolume/algal

Table 2. Mean (± SE) values of physicochemical variables at sites in unburned (UN), burned with riparian canopy intact (BRI), and burned with riparian canopy burned (BRB) basins at the end of the nutrient diffusing substrata experiment, 22–23 July 2010. Means with the same superscript are not marginally or significantly different ($p > 0.10$, Tukey's Honestly Significant Difference test). SRP = soluble reactive P.

Variable	UN	BRI	BRB
Pool depth (m)	0.28 ± 0.04[A]	0.12 ± 0.01[B]	0.14 ± 0.04[B]
Reach width (m)	4.2 ± 0.7[A]	1.8 ± 0.03[B]	2.4 ± 0.8[B]
Current velocity (m/s)	0.05 ± 0.01[B]	0.12 ± 0.04[A]	0.03 ± 0[B]
% canopy cover	92 ± 4[A]	97 ± 1[A]	44 ± 3[B]
Temperature (°C)	16.9 ± 0.4[B]	16.1 ± 0.3[B]	20.1 ± 2.6[A]
NH_4^+-N (µM)	0.93 ± 0.23	0.86 ± 0.28	0.90 ± 0.12
NO_3^--N (µM)	2.3 ± 1.0	5.0 ± 0.2	6.9 ± 6.7
SRP (µM)	0.83 ± 0.41	1.21 ± 0.34	1.07 ± 0.65

unit) increased with N or P added alone (Fig. 4E) and algal biovolume increased with any nutrient addition, tending to increase more at sites in BRI than in UN or BRB basins when P was added (Fig. 4B). Like at sites in UN and BRB basins, chl *a*/algal unit declined with P addition at sites in BRI basins (Fig. 4D), and chl *a*/biovolume decreased with the addition of N or P at sites in both BRI and BRB basins (Fig. 4F).

Across all sites, LRRs for algal biovolume, chl *a*, and chl *a*/algal unit when N (either alone or with P) was added were negatively related to % canopy cover, whereas algal density LRRs for N and N+P additions were negatively related to ambient NO_3^--N concentration (Table 3). Chl *a* and chl *a*/unit LRRs for P addition were positively related to ambient NO_3^--N concentration, whereas biovolume LRRs for N+P addition and chl *a*/unit LRRs for P addition were negatively related and algal density LRRs for N addition were positively related to ambient SRP concentration. Temperature was significantly related to LRRs for biovolume, chl *a*/biovolume, and algal size only where N+P was added.

Grazer densities on NDS units were highly variable and similar among NDS treatments across sites (means ± SE: control = 2061 ± 1014, +N = 2096 ± 787, +P = 1712 ± 943, +N+P = 1886 ± 626 individuals/m²). Within NDS treatments, grazer density did not differ among burn categories. However, log(grazer density) was positively related to log(chl *a* concentration) across NDS treatments and sites ($r = 0.42$, $p < 0.01$, $n = 40$).
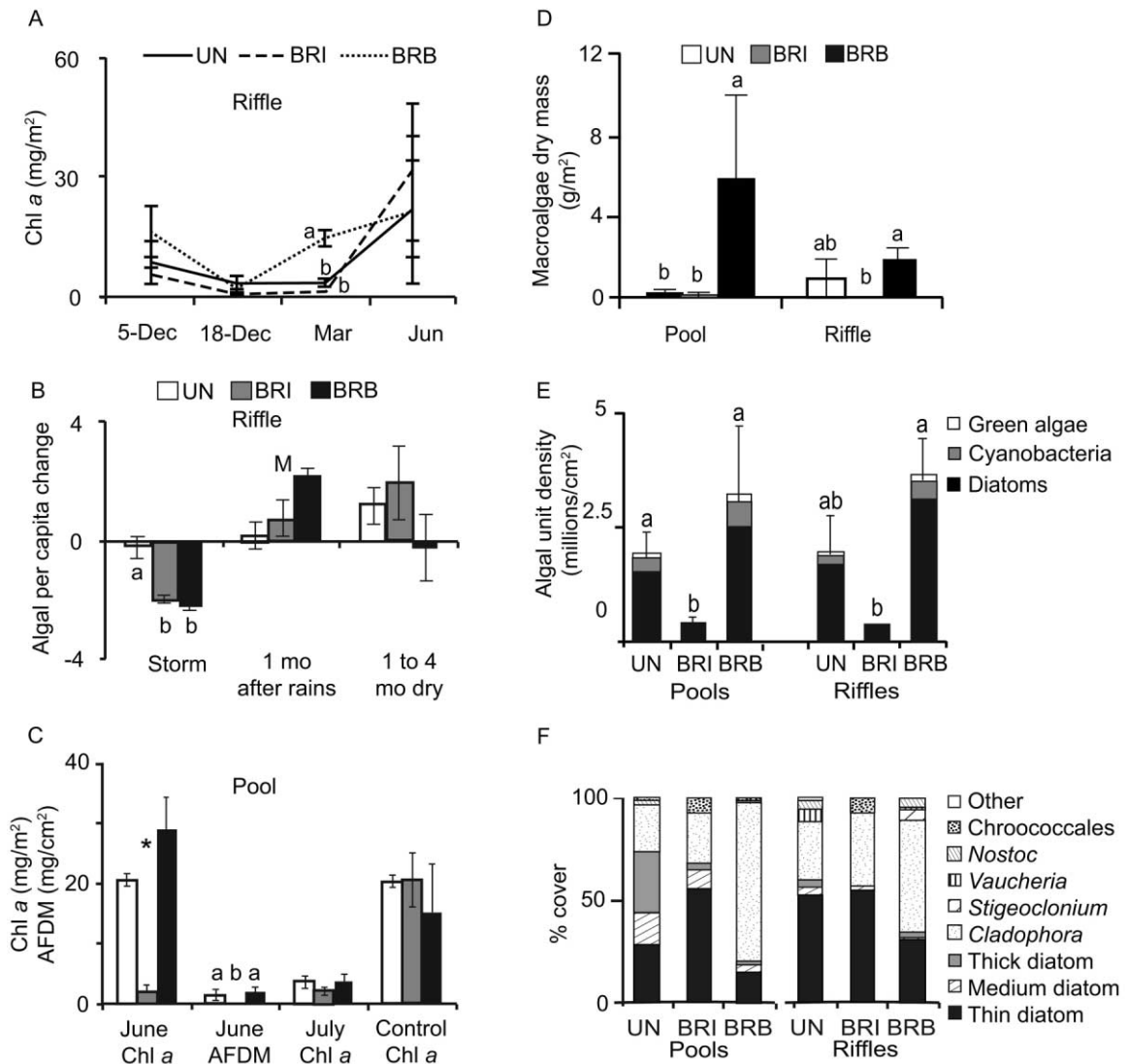
Figure 2. Mean (±1 SE) riffle chlorophyll *a* (chl *a*) concentrations (A) and per capita changes in riffle chl *a* concentrations from one time to the next (= ln[chl *a* at time 1/chl *a* at time 0]) (B), pool chl *a* concentrations in June and July 2010, pool ash-free dry mass (AFDM) concentrations in June, and chl *a* concentrations on control (unenriched) nutrient diffusing substrata units in July (C), and macroalgal dry mass (based on Surber samples) (D), algal density (E), and % cover by diatom mats and macroalgae (F) in pools and riffles in June 2010 at streams draining unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). Other designations as in Fig. 1, with the addition that ^{M} = *p* < 0.10. Bars with the same letter are not significantly different (Tukey's Honestly Significant Difference, *p* > 0.05).

NDS experiment: nutrient amendment effects on algal community structure

We collected 87 algal taxa from NDS units, including 57 diatoms, 14 green algae, 15 cyanobacteria, and 1 red alga. The 20 most abundant taxa across all NDS units consisted of 16 (primarily unicellular) diatoms and 4 cyanobacteria (Chroococcales spp. [*Gloeocapsa* and *Aphanothece* species], *Gloeocapsa punctata*, *Leptolyngbya* spp., and *Cylindrospermum* sp.). Mean total taxon richness on NDS units was lower at sites in BRI (9.5 ± 1.2) than in BRB (20.0 ± 0.5) and UN basins (20.6 ± 2.2) (mean richness/300 cells, $F_{2,7}$ = 4.5, *p* < 0.06), but the relative re-

sponses (LRRs) of taxon richness to N, P, and N+P additions did not differ among burn categories. Among general taxonomic groups, diatom biovolume increased with N and N+P additions at sites in UN and BRI basins and with P addition at sites in BRI basins, but declined with P and N+P additions at sites in BRB basins (Fig. 5A). In contrast, cyanobacteria biovolume generally increased with nutrient additions at sites in BRB basins but declined with nutrient additions at sites in BRI basins (Fig. 5B). Green algae were absent from NDS units at sites in BRI basins and showed a marginally higher increases in biovolume at sites in BRB than in UN basins when N alone
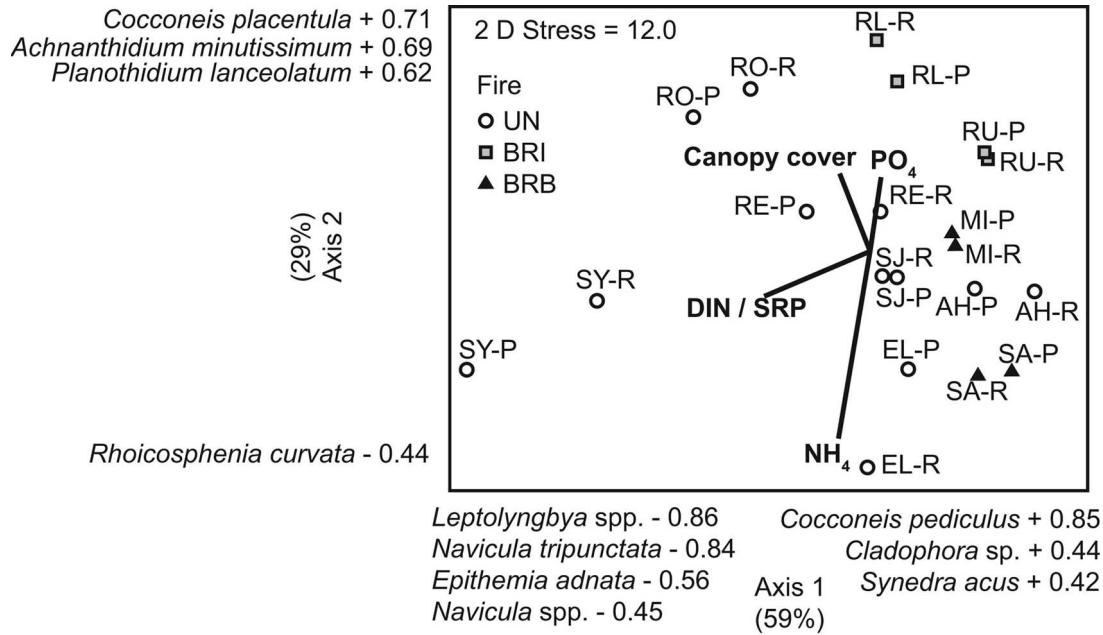
Figure 3. Ordination plot of nonmetric multidimensional scaling analysis (NMDS) of the relative abundances of algal species in pools (P) and riffles (R) at sites (see Table 1 for stream codes) in unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). The % variation in the multivariate data set attributable to each NMDS axis is shown next to each axis label. The correlation coefficients (Pearson's r) of common taxa (occurring in ≥½ of samples) significantly related ($p < 0.05$) to each axis are shown in the margins. Vectors show the direction and strength of environmental factors significantly correlated with the 2 axes. 2 D = 2-dimensional, DIN/SRP = dissolved inorganic N/soluble reactive P molar ratio.

was added (Fig. 5C). Diatom biovolume LRRs for N and N+P additions were negatively related to temperature and ambient SRP concentration (Appendix S2). Cyanobacteria density and biovolume responses to N and N+P additions were consistently negatively related to % canopy cover, and green algal density and biovolume responses to the additions of all nutrients were positively related to temperature (Appendix S2).

The 2-dimensional NMDS solution accounted for 76% of the variation in the multivariate data set (stress = 17.6, orthogonality of axes = 100%, final instability = 0.00000). Axis 2 separated sites in BRB basins, which were characterized by high light and temperature levels and high relative abundances of *Achnanthidium* and *Nitzschia* spp., from sites in BRI basins, which were characterized by high NO_3^--N concentrations, low light and temperature, and

Table 3. Results of regression analyses examining relationships between environmental variables and algal responses (log response ratios) to nutrient enrichment (+N, +P, +N+P). Initial models included arcsin$\sqrt{(x)}$-transformed proportion canopy cover, temperature, and log(x)-transformed ambient concentrations of NO_3^- and PO_4^{3-}. Only significant or marginally significant models are shown. AIC = Akaike's Information Criterion, Chl a = chlorophyll a. * = $p < 0.05$, ** = $p < 0.01$, ^{M} = $p < 0.10$.

Nutrient	Response	Intercept	Canopy	Temperature	NO_3^-	PO_4^{3-}	R^2	$F_{1,8}$	AIC
+N	Density	0.2			−0.6*	+1.0*	0.43	4.4^M	18.3
+N+P	Density	0.8**			−0.2^M		0.40	3.9^M	9.2
+N	Biovolume	3.4**	−2.1*				0.51	10.4*	23.9
+N+P	Biovolume	9.5**	−1.7**	−0.4**		−0.7*	0.75	10.2**	21.9
+N	Chl a	2.8**	−1.5*				0.34	5.6*	24.0
+P	Chl a	−0.9***	0.5^M		0.2^M		0.53	5.5*	9.0
+N+P	Chl a	2.9*	−1.8*				0.37	6.3*	26.7
+N	Chl a/unit	1.2*	−0.7^M				0.30	4.9^M	8.5
+P	Chl a/unit	−0.1			0.4*	−0.8*	0.37	3.6^M	12.6
+N+P	Chl a/unit	2.0**	−1.5**				0.52	10.8**	16.9
+N+P	Chl a/biovolume	−5.1*		0.3*			0.40	7.1*	29.4
+N+P	Algal size	3.8*		−0.2*			0.44	7.9*	21.7

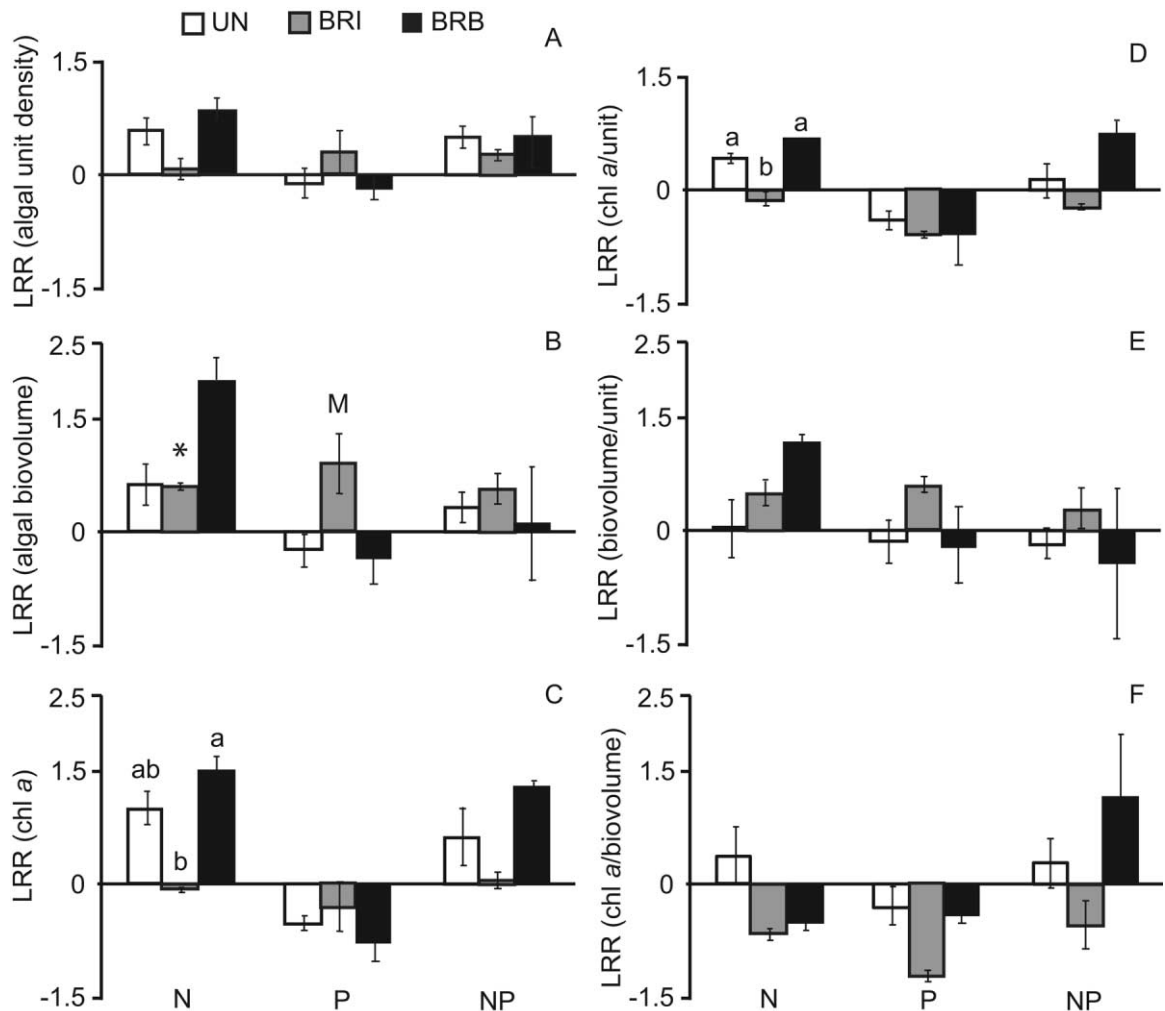Figure 4. Mean (±1 SE) log response ratios (LRRs) for total algal density (A), total algal biovolume (B), chlorophyll *a* (chl *a*) concentration (C), chl *a*/algal unit (D), algal size (biovolume/unit) (E), and chl *a*/biovolume (F) responses to additions of N, P, and N+P for streams in unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). Mean LRR values (individual bars) that are >2 SEs different from 0 indicate significant increases or decreases in response to enrichment (confirmed by *t*-tests where feasible; not indicated on the figure for visual clarity). Effects of basin burn category on LRR values were tested with analysis of variance (ANOVA). Cases in which the ANOVA indicated significant or marginally significant effects but Tukey's Honestly Significant Difference (HSD) tests did not identify differences among means are indicated by a symbol above the group of bars (* = $p < 0.05$, ᴹ = $p < 0.10$). Cases in which Tukey's HSD tests did detect differences among means are indicated by letters above individual bars. Bars with the same letter are not significantly different ($p > 0.05$).

high relative abundances of *P. lanceolatum* and *C. placentula*. Sites in UN basins had more variable environmental conditions and fell between sites in BRI and BRB basins on the plot (Fig. 6). *Amphora pediculus*, *R. curvata*, and *E. adnata* were associated with NDS units at UN sites, *Navicula* spp., *P. lanceolatum*, and *C. placentula* were associated with sites in BRI basins, and *A. minutissimum* and Chroococcales spp. were associated with sites in BRB basins (ISA Monte Carlo test, all $p < 0.05$). El Capitan Creek had the lowest % canopy cover among sites in UN basins, and its algal assemblages resembled those at sites in BRB basins.

Algal community structure on NDS units differed considerably among streams, and algal communities from the 4 NDS treatments from each stream occupied a similar region of ordination space and were separated from those in nearby streams (MRPP stream effect, $A = 0.36$, $t = -13.5$, $p < 0.001$; Fig. 6). Algal communities on NDS units also differed among burn categories (burn categories: $A = 0.12$, $t = -10.5$, $p < 0.001$), but nutrient treatments ($A = -0.03$, $t = 1.9$, $p \approx 1.0$) generally had little effect on algal community structure compared with other sources of community variation. On the other hand, ordination vectors from control to nutrient-amended NDS units tended to point in
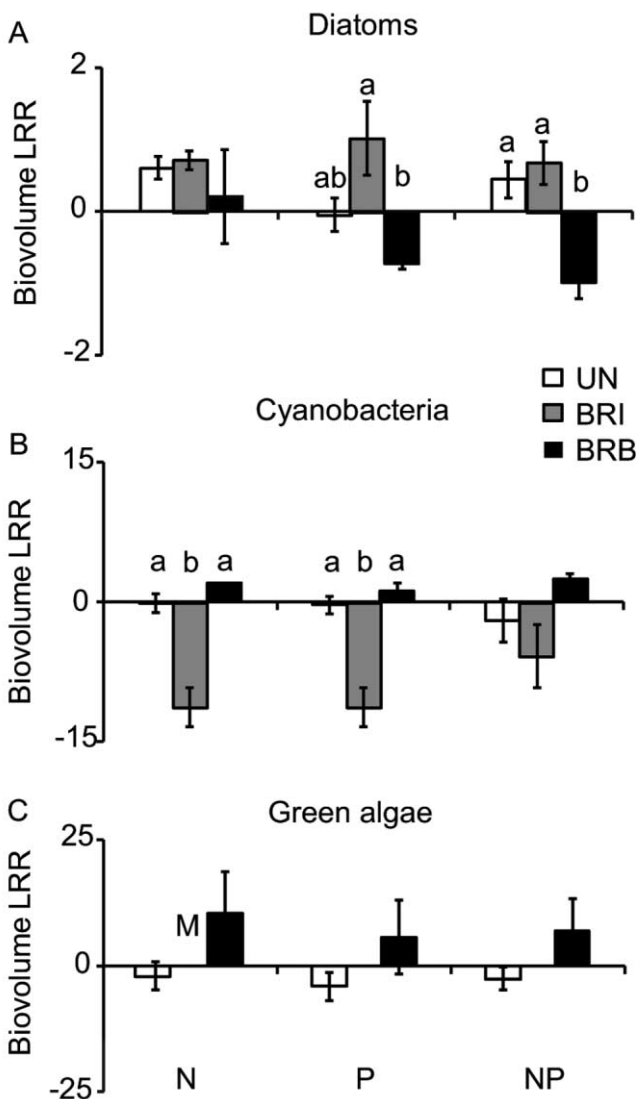
A Diatoms

B Cyanobacteria

C Green algae

Figure 5. Mean (±1 SE) log response ratios (LRRs) for the total biovolumes of diatoms (A), cyanobacteria (B), and green algae (Chlorophyta) (C) to additions of N, P, and N+P in the nutrient diffusing substrata experiment for streams in unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). Bars with the same letter are not significantly different (Tukey's Honestly Significant Difference, $p > 0.05$); [M] indicates the analysis of variance was marginally significant ($p < 0.10$), but Tukey's Honestly Significant Difference (HSD) tests did not identify differences among means.

the same direction along axis 1, significantly differing from random expectation (Fisher's exact test, $p = 0.03$), indicating that nutrient amendment increased the relative abundance of Chroococcales spp. and decreased the relative abundances of *Leptolyngbya* spp., *Navicula* spp., and *Nitzschia gracilis* (Fig. 6). The ordination vectors pointing from control to enriched (+N, +P, and +N+P) units along axis 1 were significantly longer for sites in BRB than in UN basins (Tukey's HSD, $p < 0.05$; mean axis 1 vector lengths:

BRB = 0.90 > UN = 0.16 with BRI = 0.74 not different from the other 2 categories), indicating that the switch from *Leptolyngbya* and *Navicula* to Chroococcales communities with nutrient enrichment was stronger at sites in BRB than in UN basins (Fig. 6).

DISCUSSION

Responses of stream algal communities to wildfire

Our results indicate that the structure and abundance of stream algal communities are affected by wildfire, mediated through fire effects on physicochemical conditions resulting from the destruction of upland and, in some cases, riparian vegetation. In general, flood discharge, suspended sediment concentrations during floods, sediment depths, and wet-season nutrient concentrations were greater at sites in BRI and BRB than in UN basins in response to fire effects on basinwide runoff, erosional, and nutrient uptake and mobilization processes. In contrast, light and temperature were higher at sites in BRB than in BRI and UN basins because local riparian vegetation had burned and opened the canopy at sites in BRB basins (Coombs and Melack 2013, Cooper et al. 2015, our study). Our results show that algal biomass (as chl *a*) was reduced by sediment-laden, high flows during postfire floods in burned basins, but that algal biomass, dominated by filamentous green algae, rebounded to high levels after floods in streams with high levels of nutrients and light (i.e., streams in BRB basins), and persisted at low levels of small, adnate diatoms where light remained limited (streams in BRI basins). However, some of these effects were brief. Algal biomass converged among sites in different burn categories by June in riffles and by July in pools, 2 to 3 mo after the last rains of the wet season, perhaps because NO_3^--N concentrations decreased at sites in BRI and BRB basins. On the other hand, differences in algal community composition among burn categories, particularly BRB vs BRI basins, were still observable on natural hard substrata in pools and riffles by late June and on NDS units in pools at the end of July.

Minshall et al. (1989) hypothesized that algal abundance would increase after fires because of increases in light and nutrient levels, but most authors (Robinson et al. 1994, Minshall et al. 1995, 1997, 2001b, 2004, Earl and Blinn 2003, Bêche et al. 2005, Arkle and Pilliod 2010, Malison and Baxter 2010, Romme et al. 2011) have recorded either no or negative algal biomass responses to fire. These results led Minshall et al. (2004) to conclude that postfire scouring floods and turbid stream waters offset the influences of increased nutrient and surface light levels on algal abundance. On the other hand, results of some studies indicate that blooms of colonial and filamentous algae (e.g., *Cladophora*) can occur after fires (Minshall et al. 2004, Oliver et al. 2012, Verkaik et al. 2013, Cooper et al. 2015), and Rugenski and Minshall (2014) reported that algal biomass (as chl *a*) increased after fires during a drought with
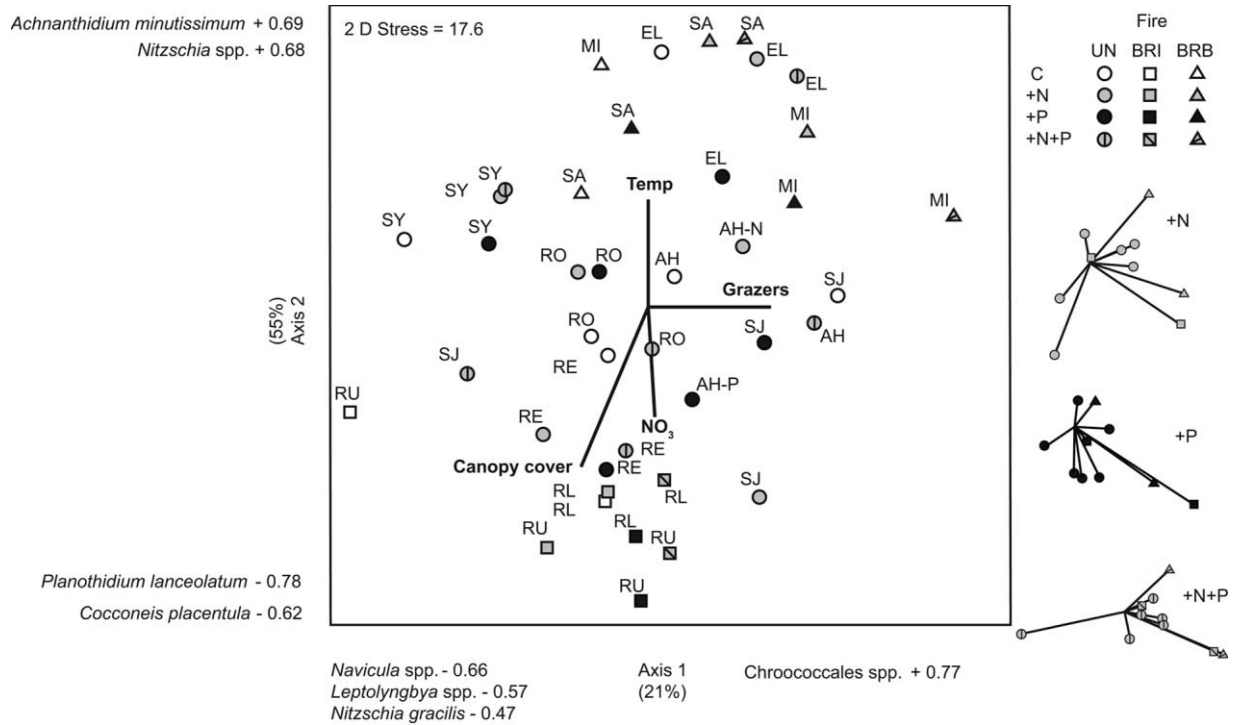
Figure 6. Ordination plot of nonmetric multidimensional scaling (NMDS) analysis of the relative abundances of algal species on nutrient diffusing substrata (NDS) units assigned to nutrient treatments (C = control, +N, +P, +N+P) at sites (see Table 1 for stream codes) in unburned (UN) basins and burned basins where riparian vegetation remained intact (BRI) or burned (BRB). Other designations as in Fig. 3. Diagrams to the right of the ordination plot show site NMDS axis score vectors from control to nutrient enriched NDS units, with +N, +P, and +N+P vectors shown from top to bottom and end symbols denoting basin burn category. Vector origins are centered on 0.

no scouring floods. Thus, our results and these studies collectively suggest that algal abundance can be drastically reduced by scouring floods after fires, but that these effects will be variable because of differences in runoff and sediment loads associated with the extent and severities of fire, the slope, aspect, and soil depths of basins, the gradients and orders of streams, and the intensity, magnitude, timing, frequency, and duration of postfire storms or runoff events (Minshall et al. 1995, Gresswell 1999, Verkaik et al. 2013, Rugenski and Minshall 2014).

Algal recovery after postfire floods, in turn, will depend on in-stream suspended sediment and dissolved nutrient levels, which are influenced by the fire, basin, and meteorological variables listed above and by light and temperature levels, which are influenced by the severity and extent of fires in riparian zones. Congruent with other studies (Kiffney et al. 2004, Kiffney 2008, Lange et al. 2011, Stancheva et al. 2012), our results suggest that adequate light levels are needed to allow algal biomass, particularly filamentous green algal biomass, to respond to elevated nutrient concentrations, but that high algal levels can be maintained only if both light and nutrient levels remain high. One common result from past studies is that small, adnate diatom taxa dominate in streams after fire, presumably because they colonize quickly after scouring flood disturbance or

ash and sediment deposition (Robinson et al. 1994, Earl and Blinn 2003). In our study, low profile, unicellular, small diatoms (*Achnanthidium, Cocconeis, Planothidium*) composed a greater proportion of the algal community at BRI sites, which were typified by high disturbance and nutrient levels but low light levels, than at BRB and UN sites. We suggest that algal communities in shaded BRI streams recovered slowly after scouring floods because of light limitation and were dominated by early colonizing species, whereas species that thrive under high resource (light, nutrient) conditions (green algae, high-profile diatoms) became more abundant at BRB sites (Passy 2007, Lange et al. 2011, Stenger-Kovacs et al. 2013, Verkaik et al. 2013). Cyanobacteria also recovered more quickly after scouring disturbance where light levels were high (sites in BRB basins > sites in BRI basins; see Whitton 2012).

Values of driving variables (sediment, nutrients, light, temperature) and their consequent effects on algal communities will depend on the time since fires and floods and recovery of associated terrestrial vegetation (Rugenski and Minshall 2014, Cooper et al. 2015). Algal communities are dynamic and responsive to the severity of and time since disturbances and to changes in resource conditions. Therefore, frequent sampling will be needed to reveal the trajectory of algal responses to fire, and peaks in

algal biomass will coincide with periods when light and nutrient levels are high and sufficient time has elapsed since disturbance to allow algal colonization and growth (Biggs and Close 1989).

Effects of nutrient amendment effects on algal communities

The results of our NDS experiment indicated that algal abundance and community responses to nutrient additions were affected by wildfire mediated through fire effects on stream physicochemical conditions. However, the results were complex and depended on the nutrient added, the algal abundance metric (density, biovolume, chl *a*) and algal group considered, and basin burn categories, which differed in nutrient, light, and temperature conditions. To our knowledge, no previous investigators have examined algal responses to nutrient additions in the context of fire effects on stream systems, so we compared our results to those from studies of the direct effects of stream light and ambient nutrient conditions, 2 key factors affected by fire, on algal responses to nutrient amendments.

Algal density and chl *a* concentration responded positively to N-only additions but only at sites in BRB and UN basins. This result suggests that algal responses to inputs of limiting nutrients were muted where disturbance legacies were high and light levels were low (i.e., at BRI sites). This interpretation was corroborated by significant negative relationships between the responses of algal biovolume and chl *a* concentration to N addition and canopy cover, which agree with the results of other studies showing that algal responses to nutrient amendments increase with increasing light levels (Taulbee et al. 2005, Hill and Fanta 2008, Kiffney 2008). In addition, algal density responses to N addition were negatively related to ambient NO_3^--N concentrations, a result congruent with a recent meta-analysis and empirical studies that showed negative relationships between algal responses to inputs of limiting nutrients and ambient concentrations of limiting nutrients (Sanderson et al. 2009, Keck and Lepori 2012, Klose et al. 2012). These results suggest the primacy of light levels, and diminishment of nutrient limitation as ambient concentrations of limiting nutrients increase, in controlling algal colonization and growth responses to nutrient additions (Kiffney 2008, Keck and Lepori 2012). Low light and high nutrient levels at BRI sites would be expected to suppress algal responses to nutrient additions, but algal biovolume increased with addition of all nutrients at sites in BRI basins, perhaps because algal size increased with N and P additions at sites in BRI basins. Our results suggested that, in some cases, algal responses to one nutrient increased with increasing ambient concentrations of the other nutrient (e.g., algal density LRR with N addition increased with ambient SRP concentrations, as in a study by Sanderson et al. 2009).

Algal density did not change appreciably with P addition at all sites, and algal biovolume either increased (BRI) or did not significantly change (BRB, UN) with P addition. However, chl *a* tended to decline with P addition across sites, apparently because of decreases in chl *a* per algal unit or biovolume. These results agree with those of other studies showing depression of chl *a* with P addition (e.g., Sanderson et al. 2009, Klose et al. 2012) and appear to be explained by changes in chlorophyll content per algal unit because algal density and biovolume did not change or increase with P inputs. These results further suggest that chlorophyll depression with P amendments may be caused by changes in algal physiology or species composition, such as observed shifts from communities with greater relative abundances of *Navicula* spp., *N. gracilis*, and *Leptolyngbya* to communities with a greater representation of Chroococcales spp. as nutrient inputs increased. Grazing pressure had little influence on the results, because grazer densities on NDS units did not vary systematically across nutrient treatments or burn categories.

These results suggest that fire effects on riparian vegetation and, hence, light and temperature levels, are paramount in determining algal responses to nutrient addition. However, algal abundance responses to nutrient amendments also were probably affected by the indirect effects of fire on the composition of the algal colonization pool for NDS units. The dominant algae colonizing and growing on NDS units were small diatoms, such as *A. minutissimum* and *Nitzschia* spp. at warm, open sites in BRB basins; *P. lanceolatum*, *C. placentula*, and *Navicula* spp. at cool, shaded sites in BRI basins; and *A. pediculus*, *R. curvata*, and *E. adnata* and the cyanobacteria *Leptolyngbya* and Chroococcales spp. at sites in UN basins. However, cyanobacteria and green algae were rare and absent, respectively, on NDS units at sites in BRI basins but were relatively abundant or present, respectively, on NDS units at sites in BRB and UN basins, generally reflecting the initial algal assemblages on natural substrata at sites in different burn categories. Unlike initial natural assemblages, *Cladophora* was virtually absent and associated probable epiphytes were rare on NDS units. NDS algal communities were dominated by a few small, fast-colonizing taxa, whose species composition differed between sites in BRI and BRB basins (Figs 6, S1, Appendix S3).

The algal pools available to colonize NDS units were determined, to some degree, by the effects of fire on algal communities, as mediated through fire effects on flood disturbance, light, nutrient, and temperature conditions, but algal groups responded to nutrient additions in different ways in different basin burn categories. Diatom abundance increased with N and N+P additions at sites in UN basins and with the addition of all nutrients at sites in BRI basins, but decreased with P and N+P additions at sites in BRB basins, whereas cyanobacteria and green algae (absent at sites in BRI basins) showed the opposite pattern

and decreased or disappeared with the addition of nutrients at sites in BRI basins and increased with N and N+P additions at sites in BRB basins. These results suggest inhibitory effects of filamentous algae on benthic diatoms under high light conditions (van der Grinten et al. 2005). Differences in cyanobacterial species composition on NDS units at sites in BRI vs BRB basins probably also conditioned algal biomass responses to nutrient additions, because Chroococcales spp., which consistently increased with nutrient additions across sites where it was present, were abundant on NDS units only at sites in BRB basins and were absent from NDS units at sites in BRI basins, whereas *Leptolyngbya*, which decreased with nutrient additions across sites, was collected commonly from NDS units at sites in BRB and UN basins and from control units at sites in BRI basins. Rejmánková and Komárková (2005) reported that Chroococcales cyanobacteria and Chlorophyta showed strong, positive responses to nutrient additions, but that slow-growing *Leptolyngbya* spp. showed no response. However, Loza et al. (2014) showed positive responses of a *Leptolyngbya* species to N addition. In general, then, unicellular diatoms showed the greatest proportionate responses to nutrient amendments in cool, shaded streams, whereas cyanobacteria showed increasing responses to N amendments as light levels increased, and green algae showed increasing responses to N amendments as temperature increased (van der Grinten et al. 2005, Stancheva et al. 2012, Snelder et al. 2014). These results suggest that fire influences algal community structure via its effects on light, temperature, and flooding disturbance, and these effects alter the responses of total algal abundance or biomass to nutrient enrichment.

Conclusions

Our results indicate the primacy of disturbance and canopy cover in determining the responses of stream algal density, biovolume, biomass (as chl *a*), community structure, and nutrient limitation to wildfires. Scouring floods after fires removed most algae from stream substrata, but subsequent recovery depended on canopy cover and was rapid where riparian vegetation was burned and slow where riparian vegetation remained intact. Algal species composition also was affected. High-profile diatoms, cyanobacteria, and green algae were more prominent in streams where the riparian canopy was opened by fires, and small, low-profile diatoms dominated streams in burned basins where the riparian canopy remained intact. Wildfire also altered the colonization pool and the subsequent responses of colonizing taxa to nutrient additions in NDS experiments. Our study indicates that fires, by changing disturbance, light, temperature, and nutrient regimes, influence algal communities and algal nutrient limitation with repercussions for stream food webs (Kiffney 2008, Wootton 2012, Cooper et al. 2015). From a management perspective, special consideration should be accorded to protecting riparian vegetation, eschewing removal of live trees or snags before, during, and after fires to reduce stream temperatures, suppress filamentous algal blooms, and enhance allochthonous inputs (Reeves et al. 2006, Stone et al. 2010, Sweeney and Newbold 2014, Cooper et al. 2015).

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