**­­­Fire transforms effects of terrestrial subsidies on aquatic ecosystem structure and function**

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**Significance Statement**

Wildfires can unleash vicious cycles by releasing CO2 into the atmosphere, creating hot and dry conditions that favor more frequent and intense wildfires, thereby accelerating further warming. Burning also liberates terrestrial plant detritus into rivers, lakes and the ocean, where it has the potential to alter the metabolic balance of ecosystems and exchange of CO2 with the atmosphere. We found that both the quantity of plant biomass and whether this biomass was burned or unburned altered CO2 release, aquatic production and respiration, and transfer of plant matter to animal consumers in experimental ponds. Wildfire may therefore induce feedbacks in ecosystem functions that cross the boundary between aquatic and terrestrial habitats.

**Abstract**

Fire can lead to transitions between forests and grassland ecosystems and trigger positive feedbacks to climate warming by releasing CO2 into the atmosphere. However, the effect of fire on the fate and impact of terrestrial organic matter in aquatic ecosystems is unclear. We performed a gradient design experiment adding 15 different amounts of burned or unburned plant detritus to freshwater pond mesocosms. The amount and burn status of terrestrial subsidies had non-linear impacts on dissolved organic carbon, ecosystem metabolism, greenhouse gas (GHG) concentrations, and trophic transfer efficiency that were shifted by burning. Fire altered the elemental and organic composition of detritus, with cascading implications on ecosystem function, magnifying the effect of detritus on aquatic ecosystem metabolism and reducing its effects on trophic transfer efficiency and GHG emissions. Our results indicate that the chemical transformation of plant matter by fire alters its fate and therefore the role of aquatic ecosystems in processing and storing carbon.

**Introduction**

Potential positive and negative feedback between ecosystems and the atmosphere present sources of uncertainty when forecasting future climate scenarios. Melting sea ice and permafrost, and the expansion of wildfire and biotic disturbances (e.g., forest insect outbreaks, invasive species), may liberate more carbon to the atmosphere and reduce land carbon sink capacities, unleashing vicious cycles and accelerating further warming [(1–4)](https://paperpile.com/c/d0xswa/5BAY+dWl3+a3ej+2P5l). Fires liberate terrestrial carbon and produce greenhouse gasses (CO2, CH4, N2O) and aerosols that shape the radiative balance of the atmosphere [(5)](https://paperpile.com/c/d0xswa/9vt5). Globally, CO2 emissions from wildfires contribute 1.8 Gt of C year-1 to the atmosphere (2000-2019) [(3)](https://paperpile.com/c/d0xswa/a3ej), equivalent to 5% of net carbon emissions in 2021 (34.9 GtCO2) [(6)](https://paperpile.com/c/d0xswa/Mrld). However, a combination of human behavior (i.e., ignition patterns) and land-use practices are expected to act in positive feedback with rising global temperatures and climate change [(3)](https://paperpile.com/c/d0xswa/a3ej) to increase the severity and frequency of wildfires [(7, 8)](https://paperpile.com/c/d0xswa/txis+FsNG).

Wildfires are important disturbances that structure biological communities and shape ecological properties of terrestrial [(9)](https://paperpile.com/c/d0xswa/nKIo) and inland aquatic ecosystems [(10)](https://paperpile.com/c/d0xswa/k37a) and the oceans [(11)](https://paperpile.com/c/d0xswa/SHR6). Wildfires generate pyrogenic materials (e.g., smoke, ash, woody debris) that destabilize soils and increase the flux of nutrients and organic materials into inland and coastal waters [(12, 13)](https://paperpile.com/c/d0xswa/uAWw+6wLR). The deposition of pyrogenic materials as detritus and aerosols can alter the biogeochemistry of waterways and fluvial networks [(14)](https://paperpile.com/c/d0xswa/2RSe) and contribute to marine phytoplankton blooms by increasing nutrient availability [(11)](https://paperpile.com/c/d0xswa/SHR6). The impact of fire disturbance on terrestrial systems depends on ecosystem type (i.e., wetland, grassland, riparian forest), fire severity, and time since disturbance [(15, 16)](https://paperpile.com/c/d0xswa/2GVM+Qa82). Fire affects nutrient export and retention by mobilizing nutrients (N and P) and producing partially combusted recalcitrant materials (pyrogenic or black carbon) [(10)](https://paperpile.com/c/d0xswa/k37a) that can have immediate and long term impacts on vegetation, soils, and watersheds [(17–19)](https://paperpile.com/c/d0xswa/NWBY+thLr+ho2b). Wildfires increase dissolved organic carbon (DOC), dissolved organic nitrogen (DON), fine-sediments, and particulate organic matter (POM) in streams [(20)](https://paperpile.com/c/d0xswa/gczA). The increase in erosion and detritus deposition in waterways can alter microbial metabolism and biogeochemical cycling [(16, 21)](https://paperpile.com/c/d0xswa/ExyI+Qa82), which can reduce water quality and drive low-O2 conditions with lethal consequences for aquatic organisms [(18, 22)](https://paperpile.com/c/d0xswa/thLr+dzDB). As such, fire represents a disturbance that precipitates rapid changes in ecosystem services and biodiversity both on land and in water.

Wildfires alter the fate and impact of terrestrial organic matter which provides both inorganic nutrients that support primary producers and organic substrates (i.e., dissolved organic matter [DOM]) for growth of heterotrophic microbes in aquatic ecosystems [(23)](https://paperpile.com/c/d0xswa/ws0y), as well as humic organic compounds that absorb light and suppress photosynthesis [(24)](https://paperpile.com/c/d0xswa/i7jn). For instance, burning can alter both the elemental stoichiometry and chemical composition of organic matter (plant litter and soils) [(25, 26)](https://paperpile.com/c/d0xswa/BXHO+3mGo) through chemical transformations that impact its lability and susceptibility to microbial and photochemical transformations [(24, 27, 28)](https://paperpile.com/c/d0xswa/nQ0l+i7jn+Dw5o). These effects can propagate through forest food webs [(29)](https://paperpile.com/c/d0xswa/TB6y) and drive multi-year increases in nutrients and elemental concentrations in aquatic systems post-fire [(30)](https://paperpile.com/c/d0xswa/BOC3). Terrestrial subsidies can also support net heterotrophy resulting in lakes and rivers being net sources of CO2 to the atmosphere [(23)](https://paperpile.com/c/d0xswa/ws0y). Fluxes of allochthonous inputs after wildfires and floods may lead to enhanced browning, where silt and organic compounds affect light attenuation that reduce chlorophyll [(31)](https://paperpile.com/c/d0xswa/XdM4) and increase respiration, resulting in hypoxic or anoxic conditions [(18)](https://paperpile.com/c/d0xswa/thLr). These effects can further suppress microbial degradation and shift carbon cycling and turnover by increasing carbon storage in sediments [(32)](https://paperpile.com/c/d0xswa/p1z7). Furthermore, fire transforms the elemental composition of plant material, which may shape the processing and cycling of burned materials by microbes and the transfer of energy through food webs. As a result, burned and unburned detritus may have distinct impacts on the metabolic balance and functioning of aquatic ecosystems that determine the fate of terrestrial organic matter and the biological properties of aquatic food webs. As freshwater ecosystems absorb as much carbon in their sediments as the oceans, the effects of fire on aquatic ecosystem function may impact the global carbon cycle. However, the effects of fire on the fate and impact of terrestrial plant detritus in aquatic systems are largely unknown.

We performed a gradient-design mesocosm experiment to test the effects of terrestrial subsidies on experimental pond ecosystems and whether these effects were altered by burning. We ask how wildfire affects the fate and impact of terrestrial production in aquatic ecosystems and potential critical thresholds in the loading of external subsidies. Thirty 400L pond mesocosms received 15 different amounts of either burned or unburned plant detritus (sage and willow). We measured ecosystem metabolism by the amplitude of daily cycles in dissolved oxygen concentrations, and concentrations of dissolved greenhouse gasses (CO2 and CH4) at the water surface. Trophic transfer efficiency was tracked by labeling sage with 15N and measuring the incorporation of the heavy isotope into plankton biomass. We predicted that detrital loading would have unimodal effects on ecosystem metabolism, stimulating production and respiration at low levels due to fertilization but suppressing them at higher levels where oxygen and light were depleted. Because fire transforms the stoichiometry and organic chemistry of plant detritus, we predicted these non-linear functions to vary between the burned and unburned allochthonous sources, reducing ecosystem productivity and trophic transfer.

**Materials and Methods**

*Experimental design*

Thirty experimental mesocosms (400 L) were used to test the influence of plant biomass loading and burning effects on aquatic ecosystems. Fifteen mesocosms received unique amounts of either burned or unburned plant detritus, with two control tanks receiving no plant material. We used a regression design to test for non-linear response surfaces in the dependent variables. In this design, fifteen mesocosms contained gradually increasing quantities of either burned or unburned plant material ranging from 0 to 400 g of dried plant biomass, with stepwise increases in plant material ranging from 11 - 150% from one treatment level to the next. To account for water loss due to evaporation, water levels in the mesocosms were maintained by adding water from an adjacent 400 L reservoir tank on a weekly basis. Apart from mixing caused by periodic water additions, no attempts were made to stimulate flow, turnover, or to disturb detritus that settled at the bottom of tanks.

Each mesocosm was filled with municipal water (27 October 2021) and stocked with a concentrated mixture of live phytoplankton and zooplankton (< 63 μm mesh) collected from vertical tows at Lake Murray and Lake Miramar, San Diego, CA (28 October, 5 November 2021). A sample of this concentrated plankton material was filtered onto a pre-combusted (2 h, 550 °C) 0.7 μm GF/F filter and dried (60 °C) for isotope analysis (see below). We used plant biomass from two shrubs native to southern California and abundant in western North America: *Salvia leucophylla* (Greene) (hereafter, sage) and *Salix lasiolepis* (Benth.) (hereafter, willow). Twenty-three sage plants were purchased from a local nursery (9 June 2021) and grown in a 1:1 soil:vermiculite mixture in pots at the University of California San Diego Research Field Station (La Jolla, CA).

On 24 June 2021 sage plants were watered with a single pulse (100 ml) of 0.021 M 15NH4Cl in distilled water added to the base of the plants, elevating soil 15N abundance to an estimated 6.4 atom-percent. Sage plants were grown for 60 days until harvest on 9 September 2021. Willow plant material was collected on 6 October 2021 from the University of California Dawson Los Monos Reserve (Buena Vista, CA).

Sage and willow leaves and stems (< 2 cm diameter) were kept separate and air dried in a greenhouse for 24 h, followed by 24 h in a drying oven (45 °C). Once dried, plant biomass was cut into small pieces (< 10 cm) and divided into groups that either remained unburned or were exposed to fire. To simulate the non-uniform effects of wildfire on plant biomass, we exposed burned plant material to varying degrees of burning at low and high burn severity, determined through visual assessment of burning. Plant material (leaves and stems) was loaded into 75 L aluminum containers and flamed with a handheld butane torch. To control the extent of burning, flames were extinguished with aluminum lids. The low and high severity burned plant materials were pooled according to plant species. In total ~2 kg of burned and unburned material was harvested for both sage and willow.

We analyzed plant isotopic ratios and elemental composition to evaluate the effects of fire on the starting plant materials added to mesocosms and the contribution of isotope tracer (i.e., 15N) to aquatic food webs. Leaves (~ 5 mg) from each species (sage and willow) and treatments (burned and unburned) were separately ground and packed in tin capsules for C and N isotope analysis (see below). Percent concentrations of nitrogen (N), sulfur (S), phosphorus (P), potassium (K), and zinc (Zn) were measured separately for leaves and woody stems of both burned and unburned sage and willow plant biomass at A&L Western Laboratories (Modesto, CA). A dried sample of plant materials for each species was also stored for stable isotope analysis (*see below*).

Burned and unburned plant materials for each species were weighed and packed into leaf litter bags (25 × 15 cm nylon bags of 250 μm mesh size) to prevent leaf detritus transfer among tanks and increase negative buoyancy, while also allowing for invertebrate grazing and water flow. Each experimental mesocosm contained an equal mass of sage and willow for their respective fire-treatment (burned or unburned material), such that the lowest and highest plant biomass treatments (5 g and 400 g dry biomass added) received 2.5 or 200 g of both willow and sage, respectively. On 5 November 2021, litter bags containing either burned or unburned sage and willow were placed into respective mesocosms; two tanks were left as controls where plankton were stocked but no plant materials were added.

*Sampling design and response metrics*

Mesocoms were sampled five times during the experimental period: once at the start of the experiment before plant materials were added (3 November 2021, Time-0), and four times after the addition of plants on 5 November 2021: Time-1 (15 November 2021), Time-2 (6 December 2021), Time-3 (3 January 2022), and Time-4 (2 February 2022) – respectively, 10, 31, 59, 89 days after the start of the experiment.

Environmental parameters (temperature, dissolved oxygen, pH, conductivity) were measured throughout the study using a YSI Pro-Plus handheld multiparameter water sensor (YSI Inc., Yellow Spring, OH) calibrated against certified standards. During each discrete sampling period, measurements of dissolved oxygen concentration were made three times (dawn-dusk-dawn) to calculate net primary productivity (NPP) and respiration (R).

Isotope values were assessed in plankton (> 63 μm) and particulate organic material (POM; < 63 μm) at two time points (Days 10 and 31) by collecting water samples with integrated water samplers. Water samples were filtered through a 63 μm mesh separating the plankton and POM, and each fraction was filtered onto a pre-combusted (2 h, 550 °C) 0.7 μm GF/F filter. Filters were wrapped in pre-combusted aluminum foil, frozen (-20 °C), and freeze-dried. Once dried, the loaded biomass was scraped from the surface of the GF/F filter using a razor blade into a mortar and either cut with scissors or ground with a pestle before being packed into tin capsules for analysis. Approximately 10% of samples were run in duplicate. In addition to plankton and POM, dried leaves from (1) burned and unburned sage and willow and (2) the > 63 μm concentrated plankton (~1.5 g) from Lake Murray were ground and sampled for isotope analyses (*n* = 4-7 each). Measurement of nitrogen stable isotope values (δ15N), carbon and nitrogen content, and atom percent (at-% 15N) were made using an elemental analyzer-isotope ratio mass spectrometer (EA-IRMS) at the University of California Davis Stable Isotope Facility. Isotope values for non-enriched, natural abundance samples are reported in delta values (δ) using per mil (‰) notation relative to atmospheric N2 standards (air). Enriched samples are reported in absolute abundance of 15N (i.e., at-% 15N). Reproducibility of isotope abundance measurements was always within ± 0.2 ‰.

δ15N values of 15N-labeled sage (nitrogen source 1 [δ15N of 296 ‰], a proxy for allochthonous nutrients) and the stock zooplankton mixture at natural abundance (nitrogen source 2 [δ15N of 11 ‰], a proxy for autochthonous nutrients) were used in a two member mixing model to determine the trophic transfer efficiency of nitrogen through aquatic food webs [(33)](https://paperpile.com/c/d0xswa/7fMD). We used the mixing model to calculate the % sage-derived 15N (hereafter, sage-15N) as a proxy for terrestrial contributions to plankton nutrition. δ15N values of non-labeled willow (δ15N of 13 ‰) overlap with those of the plankton mixture; therefore, mixing models calculated the contribution of 15N entering plankton from sage alone and did not account for added terrestrial subsidies from willow. Therefore, values here are not meant to estimate full flow of plant-derived N into higher trophic levels.

Water samples for DOC and total dissolved nitrogen (TDN) were collected at five timepoints using an integrated water sampler placed randomly across each tank; total dissolved phosphorus (TDP) was measured at one time point (Day-31). DOC and TDN water samples were filtered (pre-combusted 0.7 μm GF/F filters), stored in pre-combusted borosilicate amber vials, and acidified (37% HCl) to a pH of 3. Mesocosm DOC and TDN were measured in the WIRLab at San Diego State University using a high temperature combustion method (Shimadzu TOC-L Total Organic Carbon and Total Nitrogen Analyzer) calibrated with potassium hydrogen phthalate standards (1 - 50 mg C/L, 1 - 10 mg N/L). Approximately 10% of samples were run in duplicate, with standard deviations of repeat-measurements falling within 10% of mean values. TDP was measured at the University of Hawai‘i Hilo Analytical Laboratory on a Lachat QuikChem 8500 series 2 Flow-Injection Analyzer using USGS I-4650-03 for external digestion and US-EPA method 365.3 for phosphorus analysis (detection limit of 3.1 μg/L P).

*Greenhouse gas concentrations*

Samples for carbon dioxide (CO2) and methane (CH4) greenhouse gasses were collected from each tank on Days-0, 10, 31 and 59 of the experiment using the headspace method [(34, 35)](https://paperpile.com/c/d0xswa/3ywL+rnOg). Background concentrations of CO2 and CH4 in ambient air were collected at each sampling day by collecting 12 mL of air in evacuated Exetainers (Labco Limited). Day-0 ambient air CH4 concentrations were determined to be outliers and were discarded, being replaced with ambient CH4 concentrations for Day-10. Tank water temperatures were recorded and for each tank, 35 mL of surface water (0.1 m depth) was collected in a sterile 60 mL syringe. An additional 25 mL of ambient air was collected into the same syringe. The syringe containing water and air was shaken for 2 minutes to reach equilibration and air was then injected into evacuated Exetainers for CO2 and CH4 quantification. Samples were stored upside down at room temperature and sent for analysis within three weeks to the University of California Davis Stable Isotope Facility.

Analysis of atmospheric CO2 was performed using a Thermo Scientific GasBench II coupled to a Thermo Finnigan Delta Plus XL isotope-ratio mass spectrometer. Analysis of atmospheric CH4 was performed on a Thermo Scientific GasBench II + PreCon trace gas concentration system coupled to a Thermo Scientific Delta V Plus isotope-ratio mass spectrometer. Molar concentrations of CO2 and CH4 in water were calculated based on headspace concentrations of CO2 [(36)](https://paperpile.com/c/d0xswa/oTpc) and CH4 [(37)](https://paperpile.com/c/d0xswa/4ZDt) and gas solubilities using the appropriate temperature and atmospheric pressure corrected Henry’s constant and accounting for the amount of CO2 or CH4 added by ambient air [(38)](https://paperpile.com/c/d0xswa/J658). Unlike CH4, CO2 undergoes dynamic chemical equilibrium with multiple carbonate species and in the absence of measurements of total alkalinity or dissolved inorganic carbon, quantification of CO2 concentration using the headspace method can lead to poor resolution in undersaturated samples at low pCO2 [(39)](https://paperpile.com/c/d0xswa/BEXe). Therefore, CO2 concentration measurements herein should be considered a relative measure, with the goal of comparing differences among treatments in response to plant biomass loading and burning.

*Statistical analysis*

The effects of treatment (burned and unburned) and plant biomass loading on the response variables were analyzed using generalized additive models (GAMs) in the *mgcv* package in R [(40)](https://paperpile.com/c/d0xswa/82S7). Each time point was analyzed individually to account for the dynamic changes in response metrics over the course of the experiment since full models (i.e., the inclusion of all time points) introduced extreme concurvity. Within each time point, we applied GAMs in a model selection framework that compared three models: the ‘simplest’ model including only a single global smoother fit to all data; a model with a global smoother and a parametric ‘Treatment’ term, allowing different intercepts for burned and unburned treatments; and a more complex model with a factor-smooth term which provided different smoothers for each treatment in addition to a parametric term for treatment-specific intercepts. This approach allowed us to evaluate the relationship between response variables and plant biomass gradient with the hypotheses that these relationships were non-linear and either offset according to treatments and/or exhibited distinct treatment-specific structure [(41)](https://paperpile.com/c/d0xswa/ZohR). Candidate models were compared using Akaike Information Criterion (AIC), and models with the lowest AIC value selected. GAMs were inspected for model concurvity using the ‘concrvity’ function in the package *gratia* [(42)](https://paperpile.com/c/d0xswa/bII0). Model fits were assessed using ‘gam.check,’ with analysis of variance (ANOVA) tables generated using ‘anova.gam’ in the *mgcv* package to provide Wald tests of significance for parametric and smooth terms. In models testing 15N-enrichment and the % contribution of sage-15N to plankton, size fraction (i.e., <63 μm POM and >63 μm zooplankton) was also included as a parametric term for model selection. In all cases, differences between burned and unburned treatments were illustrated by plotting the “difference smooth” using ‘plot\_difference’ in *tidymv* [(43)](https://paperpile.com/c/d0xswa/6uws), which calculates the differences between smooths of two conditions and determines regions of significance as areas where *s*(treatment 1) - *s*(treatment 2) is greater than zero and does not include treatment-smooth confidence intervals.

A series of linear models and non-parametric tests were used to evaluate differences in δ15N values and C:N ratios across starting materials (willow, sage, plankton; leaves vs. stems) and effects of burning treatments on starting plant materials. Using pooled values for burned and unburned leaves, Mann-Whitney *U*-tests evaluated differences in δ15N and C:N between the plant materials (15N-labeled sage versus non-labeled willow leaves) and non-labeled materials (willow versus the plankton stock). Burning effects on δ15N and C:N in sage leaves and willow leaves were evaluated in separate one-way linear models. A two-way linear model was used to test treatment (burned, unburned) and plant material type (leaves, stem) effects on sage and willow biomass (nitrogen (%N), potassium (%K), phosphorus (%P), sulfur (%S), zinc (Zn ppm)), with ANOVA tables generated using Type III sum of squares in the *car* package [(44)](https://paperpile.com/c/d0xswa/CkCx).

**Results**

*Elemental analyses*

We observed differences in elemental concentrations in plant material among species, tissue types, and burning treatments, with the largest differences found between species and plant parts (*SI Appendix*, Table S1 and S2). For sage, burning reduced leaf %N but increased stem %N, and increased %K in both leaf and stem samples (*SI Appendix*,Fig. S1). Willow showed greater and more consistent shifts in elemental composition, with burning increasing %N, %P, and %K in both leaf and stem samples and increasing %S and Zn ppm in leaves alone (*SI Appendix*, Fig. S1).

*Dissolved organic carbon*

Prior to the addition of plant material DOC concentrations were low, averaging ~ 3 mg/L across all mesocosms. Ten days following the addition of plant material, DOC increased to ~ 60 mg/L in highest treatments (Fig. 1). Plant biomass loading had significant non-linear effects on DOC concentrations throughout the experiment, and DOC concentrations showed distinct patterns between burned and unburned treatments. This relationship was strongest early in the experiment when DOC concentration was highest (Days 10 and 31) but was reduced in subsequent samplings as DOC declined (Fig. 1). The rise in DOC with detrital loading also differed among burned and unburned treatments at the first three time points (Days 10, 31, 59) (*SI Appendix*, Fig. S2), as indicated by best-fit model AIC (*SI Appendix*, Table S3) and differences between factor smoothers (*SI Appendix*, Table S4). DOC was lower in the burned than unburned treatment in mid-range plant additions (~100 - 300 g) at Day-10 and Day-31 (~200 - 300 g); however, DOC was highest in the burned 400 g treatment at Day-31 and remained elevated in burned tanks (~250 - 400 g) through Day-59 (Fig. 1 and *SI Appendix*, Fig. S2). By the last sampling period (Day-89), DOC still showed a positive relationship with plant biomass loading, although this effect was small (total DOC range 4 - 12 mg/L) and equivalent between burning treatments (Fig. 1 and *SI Appendix*, Fig. S2).

*Total dissolved nitrogen and phosphorus*

The addition of plant material had significant non-linear effects on TDN that persisted through Day-89 (*SI Appendix*, Fig. S3). This shape of the non-linear relationship was similar between burned and unburned treatments at Day-10. Subsequently, burned and unburned treatments diverged and maintained statistical differences through Day-89. TDN tended to be lower in burned tanks at Day-31 (*p*=0.053) but was notably higher in high-range (> 200 g) burned treatments at Day-59 and mid-range treatments (~ 100-250 g) at Day-89 (*SI Appendix*, Fig. S4 and Table S3 and S4). Phosphorus (as TDP) in treatment water was only measured once during the experiment (Day-31). Similar to DOC at Day-10, TDP increased in both treatments with plant biomass loading and was higher in burned vs. unburned tanks especially at high-biomass loading tanks (*SI Appendix*, Fig. S5 and Tables S3 and S4).

*Net primary productivity and respiration*

Dissolved oxygen (DO as % O2) measurements showed consistent patterns among paired dawn measurements (separated by 24 h) in each time point (*SI Appendix*, Fig. S6). Percent O2 showed considerable change over time and treatments (*SI Appendix*, Fig. S7, model fits in Tables S5 and S6). Relative to unburned tanks, % O2 was consistently higher in mid-range burned treatments and lower in burned treatments receiving the highest plant material (400 g) (*SI Appendix*, Fig. S6).

NPP (as Δ % O2 from dawn to dusk) showed a significant non-linear relationship with plant biomass across all four time points. NPP was greater in burned relative to unburned tanks through Day-59 (Fig. 2A and *SI Appendix*, Table S7 and S8). At Day-10, NPP exhibited an exponential decline with highest values in low-plant biomass treatments that also tended to be higher in burned tanks with low-plant biomass (Fig. 2A and *SI Appendix* Fig. S8A). By Day 31, NPP had stabilized across the plant-biomass gradient but a negative relationship between NPP and biomass loading remained (Figs. 2A and *SI Appendix*, Fig. S8A), and NPP was higher in burned tanks (*p*=0.007). This pattern continued through Day-59, with an increasing unimodal relationship where highest NPP was observed in mid-range tanks (100-200g) and burned tanks (*p=*0.012) (*SI Appendix*, Table S8). By Day-89, NPP in unburned tanks was flat across the plant biomass gradient (*p*=0.327) (Fig. 2A), while NPP in burned tanks continued to show a unimodal relationship with plant biomass (*p*=0.020). NPP at Day-89 was significantly lower in burned tanks receiving >250 g plant material compared to unburned tanks (Fig. 2A and *SI Appendix*, Fig. S8A).

Respiration (R, Δ % O2 from dusk to dawn) mirrored NPP and was greatest (most negative) in low-biomass treatments throughout the experiment. We observed significant non-linear associations between R and plant biomass at Day-10 that did not differ between treatments (*p*=0.229) (Fig. 2B); however, by Day-31 R was offset by treatment-level intercepts, with an overall significant effect of treatment driving greater rates of respiration (more negative) in burned tanks (*p*=0.019) (*SI Appendix*, Table S7 and S8). Treatment-specific non-linear effects of plant addition on R were found for both burned and unburned treatments at Day-59 (*p*<0.001) and burned tanks alone at Day-89 (*p*=0.004). Significant differences between treatment R were in mid-range burned tanks (~100-225 g) at Day-59 where R was greatest, and in high-range treatments (300-400 g) at Day-89 where rates of R were reduced (least negative change in O2) (Fig. 2B, and *SI Appendix*, Fig. S8B).

*Trophic transfer efficiency and plankton 15N-labeling*

We assessed trophic transfer efficiency using the integration of sage-15N into zooplankton biomass as a proxy for the input of plant nutrition to consumers. Analysis of plant materials before being added to mesocosms showed isotope labeling (i.e., 15N) increased the δ15N isotope values of both burned-and-unburned sage (*p*<0.001), and burning treatment did not affect leaf δ15N values for sage (*p*=0.423) or willow (*p*=0.485) (see *SI Appendix, Supplemental Results* and Fig. S9 and Table S9). Isotope mixing models showed a significant effect of plant addition and burning on the trophic transfer efficiency (% sage-15N) in plankton at Day-10 and Day-31 (*p*<0.001) (*SI Appendix*, Tables S10 and S11), with overall efficiency and lower % sage-15N in burned relative to unburned treatments (Fig. 3); no difference between plankton size fractions (< 63 μm, > 63 μm) was observed at either time point (*p*≥0.196) (*SI Appendix*, Table S11). At Days-10 and 31, both treatments showed a non-linear relationship between % sage in plankton and plant biomass loading (*p*<0.001) (*SI Appendix*, Table S11), where plankton % sage-15N increased with plant biomass following a saturating relationship. However, an asymptote for % sage-15N in the burned treatment occurred at lower plant addition levels in the burned treatment at Day-10 (~300 g of plant biomass). At Day-31 % sage-15N substantially declined in 400 g burned treatment (Fig. 3). Overall, burning decreased trophic transfer efficiency and the incorporation of sage-15N into plankton in treatments receiving 50-400 g of material at Day-10 and ~ 75-125 g and >300 g at Day 31 (*SI Appendix*, Fig. S10). These results show a greater integration of plant-derived nitrogen into the biomass of plankton consumers in unburned treatments and a pronounced drop off in trophic efficiency and greater autochthonous nutrition in burned treatments as plant loading increased (Fig. 3).

Greenhouse gasses

Prior to the addition of plant materials (Day-0), CO2 concentrations in tanks ranged from 20 - 40 μM (Fig. 4A). After the addition of plant material, CO2 concentrations had increased to > 300 μM CO2 in the highest biomass tanks by Day-10. Significant relationships between CO2 concentrations and plant material were found for both burned and unburned treatments at all time points (*p*<0.001). CO2 concentrations were consistently higher in the unburned relative to burned tanks in treatments receiving 100 - 325 g plant material at Days-10, 31, and 59 (*SI Appendix*, Fig. S13 and Table S12 and S13). However, CO2 concentrations were highest in the burned treatments receiving 400 g plant material at Days-31 and 59 (Fig. 4A).

In contrast to CO2, the concentrations of CH4 increased through time but were less impacted by treatments or plant biomass (Fig. 4B). Treatment effects were most apparent at Day-10, where CH4 concentrations showed a non-linear relationship for unburned tanks only (*p*=0.001) and were higher in unburned tanks relative to burned tanks receiving >250 g of plant-biomass (Fig. 4B and *SI Appendix*, Fig. S13). No relationship between CH4 concentrations and plant-biomass or treatment was seen at Day-31 (*p*=0.659), although burned tanks tended to have higher CH4 concentrations in burned tanks at Day-59 (*SI Appendix*, Fig. S13 and Table S13).

**Discussion**

Our results indicate that the fate and impact of terrestrial organic subsidies in aquatic ecosystems show non-linear dependencies on loading of terrestrial detritus that are functionally altered by fire. The degradation of plant material in aquatic systems liberates nutrients and increases organic carbon [(45)](https://paperpile.com/c/d0xswa/UwVt) which can stimulate production under low plant-loading by supplying limiting nutrients [(24)](https://paperpile.com/c/d0xswa/i7jn). However, high plant loadings lead to light attenuation and can suppress aquatic primary production and respiration due to light absorption and oxygen depletion [(24)](https://paperpile.com/c/d0xswa/i7jn) and reduce ecosystem stability by perturbing rates of nutrient turnover [(46)](https://paperpile.com/c/d0xswa/YasZ). Our results show that, in addition to its impacts on terrestrial ecosystems, fire also alters the metabolism, trophic efficiency and greenhouse gas production of aquatic systems by changing the chemistry of detritus. Burning enhanced the impact of detrital loading on ecosystem production and respiration and dampened its effects on GHG concentrations and trophic transfer to plankton consumers. More frequent and intense wildfire may therefore alter the capacity of aquatic systems to store, transform and exchange carbon with the atmosphere.

We found that increased loading of terrestrial material and DOC to drives unimodal effects on ecosystem metabolism as tanks transitioned from nutrient- to light-limitation [(24, 46)](https://paperpile.com/c/d0xswa/YasZ+i7jn). Burning magnifies these patterns, with greater rates of system production and respiration at intermediate loading (Fig. 2). At high plant-loading (> 250g) burned tanks showed chronic destabilization with lower NPP, R, and DO over ~ 90 days (Fig. 2, S6). Burning chemically transforms plant biomass [(29)](https://paperpile.com/c/d0xswa/TB6y) in ways that alter the feedbacks that link aquatic ecosystems to the metabolism, storage, and processing of terrestrial productivity. Wildfire impacts to aquatic ecosystems can persist for decades [(17)](https://paperpile.com/c/d0xswa/NWBY) but are especially dynamic in the first 5 years post-fire [(47)](https://paperpile.com/c/d0xswa/KE9C). Indeed, over the short period of our experiment (~ 90 d) we observed substantial temporal variability in water quality and productivity, suggesting a critical transition between terrestrial loading/DOC concentrations and the stimulatory effect of limiting nutrients on aquatic productivity [(48)](https://paperpile.com/c/d0xswa/IzJ7). These results suggest that positive impacts of fire on liberating dissolved organic and inorganic nutrients (e.g., N, P, DOC) [(49)](https://paperpile.com/c/d0xswa/kUMg) and stimulating water column production at low and intermediate loadings gives way to tipping points where aquatic ecosystems are driven to dystrophic states under conditions of high biomass introduction. Fire also reduced both GHG concentration and the transfer of detritus (plant-derived nitrogen) to higher trophic levels (Figs. 3, 4). Therefore, accounting for feedback between wildfire and aquatic productivity and CO2 concentration from freshwater ecosystems may be critical to a complete accounting of the role of fire in the global carbon cycle [(50–52)](https://paperpile.com/c/d0xswa/kaD6+7DOX+1KIs).

We found that the impacts of fire and terrestrial subsidies on aquatic ecosystems vary greatly over time and in response to the amount of plant material introduced. For instance, terrestrial loading led to rapid, non-linear increases in DOC and CO2 concentrations at Day 10 that reduced aquatic NPP and R to near zero as biomass loading increased. The non-linear relationship between plant biomass loading and DOC concentration indicates that organic carbon tended to be respired and released as CO2 at intermediate concentrations, but to accumulate in the water column at the highest loading levels. Bacteria actively respire terrestrial-DOC (t-DOC) in lakes, and bacterial contributions to productivity and respiration increase with DOC loading [(46)](https://paperpile.com/c/d0xswa/YasZ). However, little of this respired t-DOC (i.e., bacterial pathway) is transferred to higher trophic levels compared to terrestrial particulate organic carbon (POC) [(53)](https://paperpile.com/c/d0xswa/ZN93). Elevated microbial respiration under increased plant-loading contributed to hypoxia, which reduced the efficiency of biological degradation of organic material at the highest loading levels. A companion study (Spiegel et al., in review) found microbes were responsible for more decomposition than photodegradation in our experiment, and that the highest rates of DOC decomposition occurred at intermediate concentrations. The saturating relationship between detrital loading and CO2 ppm also indicates that organic carbon was mineralized at slower rates at the highest concentrations where DOC accumulated and DOC respiration was lower in burned treatments (Fig. 4), possibly due to fire-effects on DOC composition and reduced lability due to increased aromaticity. Over time, a unimodal pattern relating terrestrial inputs with ecosystem metabolism emerged, and by Day-31 declines in DOC and CO2 concentrations were matched with greater rates of NPP and R with distinct non-linear relationships across the plant-biomass gradient between the burned and unburned treatments. These patterns show that rising inputs of terrestrial detritus into aquatic systems – a global phenomenon known as “browning” [(45)](https://paperpile.com/c/d0xswa/UwVt) – produce non-linear feedbacks where both respiration and oxygenic primary production are stimulated by terrestrially-derived nutrients and organic compounds at low and intermediate levels, but suppressed by a combination of hypoxia, light limitation, and greater aromaticity at the highest levels [(46)](https://paperpile.com/c/d0xswa/YasZ).

Burning altered the shapes of the non-linear functions between terrestrial loading and carbon dynamics and their evolution over time. Tanks receiving burned plant material had significantly higher NPP than those with unburned material (Days-10, 31, 59) and R (Days-31, 59) and this effect was most pronounced at intermediate loading treatments. The greater stimulation of ecosystem metabolism – primarily NPP – in burned treatments may be a result of increased concentrations of limiting nutrients (%N, %P, %K, %S, %Zn) (*SI Appendix*, Fig. S1) or greater consumption of terrestrial-DOM by heterotrophic bacteria in burned tanks releasing inorganic substances that favor autochthonous nutrient pathways [(46, 54)](https://paperpile.com/c/d0xswa/sDiW+YasZ). However, at high plant-loading, dissolved phosphorus accumulated and this effect was accentuated by burning (Fig. S5), indicating a reduction of energy transfer across trophic levels [(46)](https://paperpile.com/c/d0xswa/YasZ) – possibly due to a combination of fire-induced changes in DOC chemistry (increased aromaticity) (Spiegel et al, in review; [49)](https://paperpile.com/c/d0xswa/kUMg), plant polyphenols affecting enzyme activity [(55)](https://paperpile.com/c/d0xswa/825r), and nutrient cycling between autotrophic and heterotrophic microorganisms [(56)](https://paperpile.com/c/d0xswa/MhHp). Greenhouse gasses also showed distinct responses to fire later in the experiment, with burned tanks exhibiting both lower (mid-range plant-loading) and higher (high-range plant-loading) CO2 than unburned tanks at Days-31 and 59. CH4 concentrations increased with time across all tanks and were higher in the burned treatment at the end of the experiment. The lower CO2 concentrations in the burned treatments at intermediate loading likely reflect the effects of elevated CO2 uptake due to higher NPP than in the unburned tanks. Taken together, these results show that the chemical transformation of terrestrial plant biomass by fire can lead to changes in the functioning of aquatic ecosystems that depend on both the loading of allochthonous materials and time since disturbance.

Increasing plant detritus increased DOC and other humic compounds that limited primary production and resulted in greater reliance of heterotrophic zooplankton on terrestrial resources. Zooplankton can utilize terrestrial organic carbon (t-OC), although the benefits of t-OC for zooplankton nutrition and growth is debated [(57–59)](https://paperpile.com/c/d0xswa/m0kh+Fq87+Rpoq). Relative to autochthonous nutrition, t-OC is low in nutritional quality due to high C:P and low unsaturated fatty acids [(57)](https://paperpile.com/c/d0xswa/m0kh). In natural lakes, increasing t-OC and allochthony can reduce zooplankton production [(59)](https://paperpile.com/c/d0xswa/Rpoq). Greater consumption of recalcitrant carbon and an inefficient microbial loop [(60)](https://paperpile.com/c/d0xswa/XHov) may explain lower zooplankton production and rates of nutrient transfer across trophic levels where t-POC is high. The percent sage-15N in two zooplankton size fractions increased with plant-loading and was reduced in burned treatments; thus burning reduced trophic transfer efficiency of plant N to higher trophic levels (Fig. 3). While mixing model values represent the relative contribution of sage as a terrestrial resource to plankton, they do not represent full accounting of terrestrial inputs due to the added contribution of willow (at natural isotope abundance). Plant-derived N incorporation in zooplankton depended on the interaction between the plant-loading and burning treatments. The saturating kinetics of this relationship show the assimilation of plant derived nitrogen to zooplankton increased proportionally as NPP decreased, supplying nutrients up to the highest loading levels where trophic transfer was markedly reduced. This effect was most notable in the burned treatments where zooplankton contained less sage-15N than in the unburned treatment.

Lower DOC (Fig. 1) and higher NPP (Fig. 2) in burned tanks also coincided with a greater proportion of autochthonous nutrition and less plant-derived nutrition (using % sage-15N as a proxy) in zooplankton compared to unburned treatments. A companion study (Spiegel et al. in review) found that burned sage decomposed twice as fast as burned willow after ~90 d, but the decomposition of burned and unburned sage was largely equivalent across the plant-loading gradient. Therefore, the lower % sage-15N in burned treatments and the marked decline in % sage-15N with high plant-loading (particularly for burned treatments) are likely not driven by difference in rates of 15N release from burned/unburned sage, but instead changes in dissolved compounds, their lability, and composition (e.g., aromaticity) [(17, 49)](https://paperpile.com/c/d0xswa/kUMg+NWBY). Overall, this pattern indicates that the effects of fire on biogeochemistry, microbial communities, and ecosystem metabolism are intimately related, and fire affects the trophic transfer of detrital nutrients to top consumers through alternate energy pathways.

Our study suggests that a complete accounting of the impact of wildfire on the global carbon cycle must include feedbacks to the functioning of aquatic ecosystems. Inland waters transform and store carbon in their sediments at rates comparable to the global oceans [(61)](https://paperpile.com/c/d0xswa/Q86K). Many lakes are net sources of carbon to the atmosphere due to respiration of organic material of terrestrial origin [(62)](https://paperpile.com/c/d0xswa/tHcO). Growing inputs of plant detritus into lakes and rivers lead to browning [(45)](https://paperpile.com/c/d0xswa/UwVt), and increased frequency and severity of wildfires [(8)](https://paperpile.com/c/d0xswa/FsNG) are two symptoms of recent global climate change and human activities. Our results indicate that these two forces may interact in ways that affect the capacity of aquatic systems to store, process and emit carbon. Accurate forecasts of ongoing climate change require integrative models that incorporate feedbacks within and between aquatic and terrestrial ecosystems and consideration of how changing ignition patterns and wildfires will modify the global carbon cycle.

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**Conflict of Interest Statement**

The authors declare no conflicts of interest.

**Data accessibility**

All data and scripts are available at Github (http://www.github.com/cbwall/Pyromania) and are archived at Zenodo (xxx – will update following peer review).

*Abbreviations*: DO (dissolved oxygen), DOC (dissolved organic carbon), NPP (net primary photosynthesis), R (respiration), TDN (total dissolved nitrogen, TDP (total dissolved phosphorus), N (nitrogen), P (phosphorus), K (potassium), S (sulfur), Zn (zinc)

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**Main Text Figures**

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**Fig. 1**. Dissolved organic carbon (DOC) concentration across time in treatments receiving burned and unburned plant material at the start of the experiment and four sampling periods after plant material added. Lines represent best-fit generalized additive models (GAMs) with treatment-level 95% confidence intervals. Black lines with gray confidence intervals indicate global smoothers across all data points; solid (*burned*) and dotted (*unburned*) colored lines indicate factor-smooths that vary between treatments.

Chart

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**Fig. 2**. (**A**) Net ecosystem productivity (NPP) and (**B**) respiration (R) in treatments receiving burned and unburned plant material across four sampling periods. Lines represent best-fit generalized additive models (GAMs) with treatment-level 95% confidence intervals. Black lines with gray confidence intervals indicate global smoothers across all data points; solid (*burned*) and dotted (*unburned*) black lines together represent treatment-level intercepts with global smoothers; colored lines indicate factor-smooths that vary between treatments.



**Fig. 3**. Trophic transfer efficiency as the % sage-derived 15N from a two-source mixing model as a metric for plant-based subsidies in treatments receiving burned and unburned plant material at Days-10 and 31. Lines represent best-fit generalized additive models (GAMs) with treatment-level 95% confidence intervals.



**Fig. 4**. Greenhouse gas concentration for (**A**) carbon dioxide (CO2) and (**B**) methane (CH4) at the beginning of the study before plant material was added (Day-0) and across three experimental time points. Lines represent best-fit generalized additive models (GAMs) with treatment-level 95% confidence intervals. Black lines with gray confidence intervals indicate global smoothers across all data points; solid (*burned*) and dotted (*unburned*) black lines together represent treatment-level intercepts with global smoothers; colored lines indicate factor-smooths that vary between treatments.