

Retention of Nitrogen Following Wildfire in a Chaparral Ecosystem

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ABSTRACT

Wildfires alter nitrogen (N) cycling in Mediterranean-type ecosystems, resetting plant and soil microbial growth, combusting plant biomass to ash, and enhancing N availability in the upper soil layer. This ash and soil N pool (that is, wildfire N) is susceptible to loss from watersheds via runoff and leaching during post-fire rains. Plant and soil microbial recovery may mitigate these losses by sequestering N compounds in new biomass, thereby promoting landscape N retention in N-limited chaparral ecosystems. We investigated the relative balance between wildfire N loss, and plant and soil microbial N uptake and stream N export for an upland chaparral watershed in southern California that burned (61%) in a high-intensity wildfire in 2009 by using a combination of stream,

vegetation, soil microbial, and remote sensing analyses. Soil N in the burn scar was 440% higher than unburned soil N in the beginning of the first post-fire wet season and returned within 66 days to pre-fire levels. Stream N export was 1480% higher than pre-fire export during the first post-fire rain and returned within 106 days over the course of the following three rainstorms to pre-fire levels. A watershed-scale N mass balance revealed that 52% of wildfire N could be accounted for in plant and soil microbial growth, whereas 1% could be accounted for in stream export of dissolved nitrogen.

Key words: disturbance; wildfire; chaparral; nitrogen; soil; stream.

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Data used in this work can be accessed at the SBC LTER Watershed Data Collection repository: <http://sbc.lternet.edu//data/dataCollectionsPortal.html>.

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INTRODUCTION

Wildfires alter nitrogen (N) cycling in Mediterranean-type ecosystems, such as chaparral, where summer drought and dense contiguous fuels contribute to high-intensity, stand-replacing wildfires (Moreno and others 1994). Combustion releases a portion of N contained in plants and litter to the atmosphere, while much of the remaining N is deposited on soil surfaces as ash and converted to biologically available N in surface soils (Christensen

1973; Neary and others 1999). This wildfire-altered N contains ammonium and organic N (Marion and others 1991; Knicker 2007), resulting in increased mineralization and nitrification during early post-fire recovery (Dunn and others 1979; Hanan and others 2016a). Ammonium, nitrate, and dissolved organic N are vulnerable to leaching and runoff during rains following wildfire (Rundel 1983; Meixner and others 2006). As a result, wildfire can enhance landscape N loss to streams for prolonged periods (that is, months to up to 4 years) (Verkaik and others 2013). Thus, N acquisition and retention mechanisms are critical for N-limited chaparral ecosystems to be resilient to recurrent wildfires that cause potentially large ecosystem N loss (Rundel and Parsons 1984).

Plant and soil microbial recovery following wildfire may play a crucial role in mitigating hydrologic N export by sequestering N in biomass, providing dual ecosystem functions: retaining landscape N and mitigating N export to downstream aquatic ecosystems (Rundel and Parsons 1984; Guo 2001; Hanan and others 2016a, 2017). However, the extent to which plant and soil microbial regrowth regulates stream export depends on how quickly plants and soil microbes re-establish after wildfire, which in turn depends on plant and soil microbial functional type and precipitation following the wildfire (Hanan and others 2017). These factors vary over space and time, making it difficult to evaluate the balance between plant and soil microbial N uptake and stream N export at watershed scales. Quantifying this balance is an important step toward understanding the factors that determine the resilience of Mediterranean-type ecosystems to N loss following wildfire.

Because streams integrate upslope hydrologic and N dynamics, stream export should reflect landscape-level N recovery processes, such as plant and soil microbial recovery and biomass N sequestration. We investigated these potential ecosystem functions for an upland chaparral watershed in southern California that burned (61%) in a high-intensity wildfire in 2009. Using a combination of remote sensing, soil and vegetation sampling, and hydrologic and hydrochemical analyses, we evaluated the resilience of this semiarid Mediterranean watershed to N export. Specifically, we addressed the following questions:

1. Following wildfire, how long was required for stream N export to recover to pre-fire levels?
2. Over the recovery period, what was the balance between estimated wildfire N loss, plant N up-

take, soil microbial N uptake, and stream N export?

As the severity, frequency, and extent of wildfire continues to increase under a changing climate and with expanding human populations (McKenzie and others 2004; Westerling and others 2006; Westerling and Bryant 2008), it is crucial to understand intrinsic ecosystem resilience and recovery following these large-scale disturbances.

METHODS

Study Area

Coastal watersheds in the Santa Barbara region are characterized by undeveloped, mountainous headwater regions in the north, and lower elevation coastal plains in the south with urban, suburban, and agricultural land use (Goodridge and Melack 2012). The region experiences a semiarid Mediterranean climate with cool, wet winters and warm, dry summers, and high inter-annual rainfall variability (Beighley and others 2008; Goodridge and Melack 2012). Vegetation in the upper watershed is dominated by *Ceanothus megacarpus* (big pod ceanothus), an N₂-fixing species, on lower slopes, and *Arctostaphylos* spp. (manzanita) on upper slopes, with *Adenostoma fasciculatum* (chamise) mixed throughout (Hanan and others 2016a).

Our study focused on the Rattlesnake Canyon watershed (hereafter Rattlesnake), a 6.9-km² undeveloped, mountainous chaparral watershed for which measurements of stream discharge and N chemistry were available from 2002. Rattlesnake is located along the south-facing Santa Ynez Mountains (Santa Barbara County, California, USA) (Figure 1) and is characterized by high relief and steep terrain, with elevations ranging between 270 and 1262 m and slopes between 20% to 50%, though some regions can reach 100% (Hanan and others 2016a). Soils are predominantly sandy loams, classified as Typic Dystraxepts from the Maymen series (Hanan and others 2016a). Bedrock is highly fractured, primarily marine Cretaceous through Miocene arkosic sandstones and shales (Diblee 1966). Two fires occurred within Rattlesnake from 2008 to 2009: the Tea fire burned 7% of lower Rattlesnake from November 13 to 17, 2008, and the Jesusita fire burned 61% of Rattlesnake from May 5 to 18, 2009. We focus on the Jesusita fire in this study, which burned an over eight times larger area than the Tea fire.

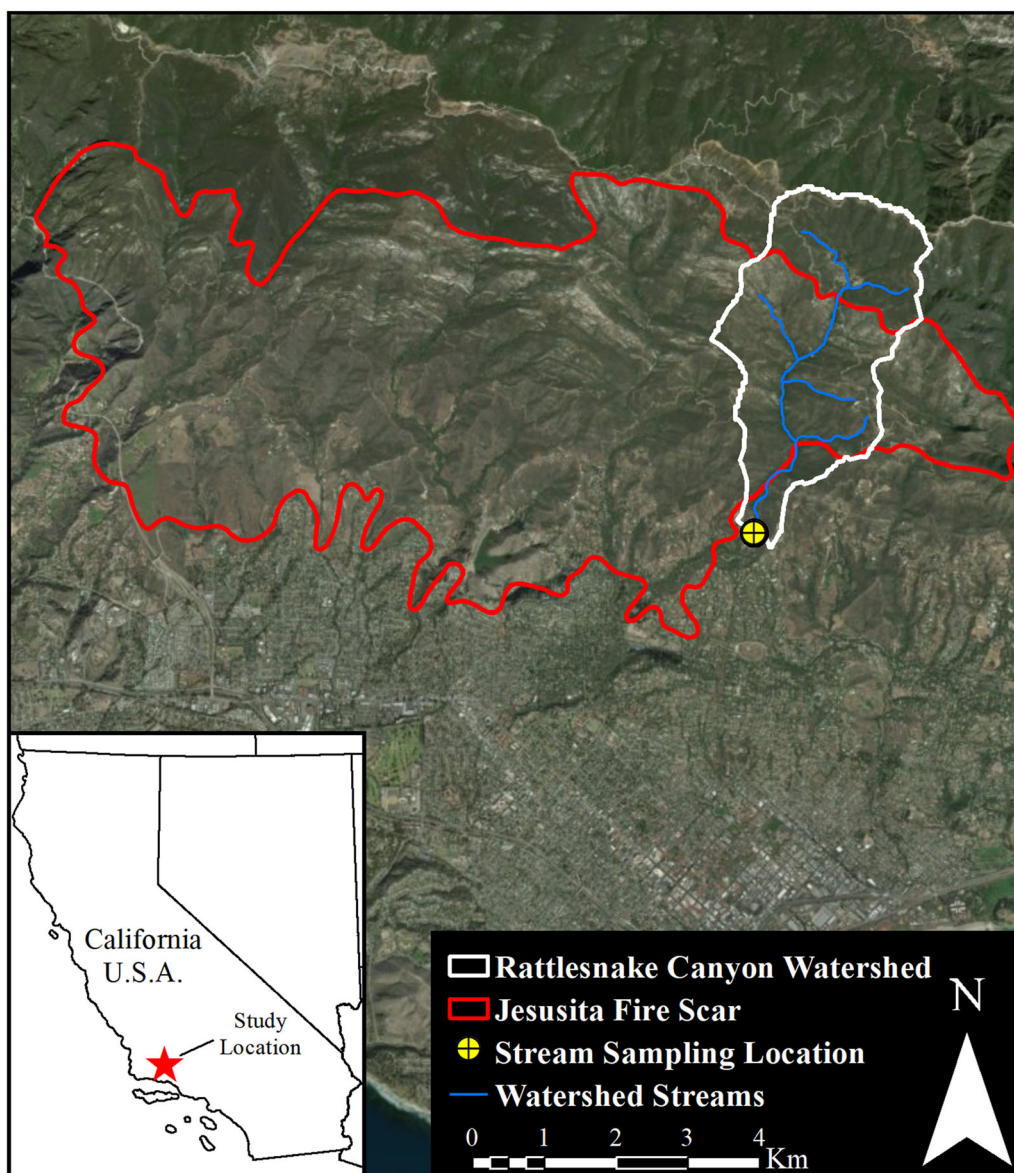


Figure 1. Pre-fire satellite image of study location (Lat: 34.4576, Long: -119.6922) with Rattlesnake Canyon study watershed, Rattlesnake Creek and hydrologic and hydrochemical sampling location, and Jesusita fire scar identified.

Remote Sensing Land Cover Classification

Land cover was characterized using multiple end-member spectral mixture analysis (MESMA) to estimate fractions of green vegetation (GV), non-photosynthetic vegetation (NPV), and ash (Roberts and others 1998). We used imagery acquired by the Airborne Visible Infrared Imaging Spectrometer (AVIRIS) (Figure 2), a platform that has been used to map vegetation and fuel loads in chaparral ecosystems with high accuracy (Roberts and others 1998, 2003). Four AVIRIS images were used to define pre-fire land cover (March 2009), fractional

land cover changes following wildfire (June and August 2009), and fractional land cover changes following the first post-fire wet season (April 2010) in Rattlesnake (Figure 2). Because GV identifies the areal coverage of the photosynthetically active plant community, we used this metric to quantify post-fire plant recovery over the wet season as the GV difference between August 2009 (pre-wet season) and April 2010 (post-wet season) images (Figure 2). Cloud cover obscured 9.8% of the watershed area in the June 2009 image, and non-overlapping AVIRIS flightlines resulted in missing 2 and 2.9% of the watershed area in August 2009

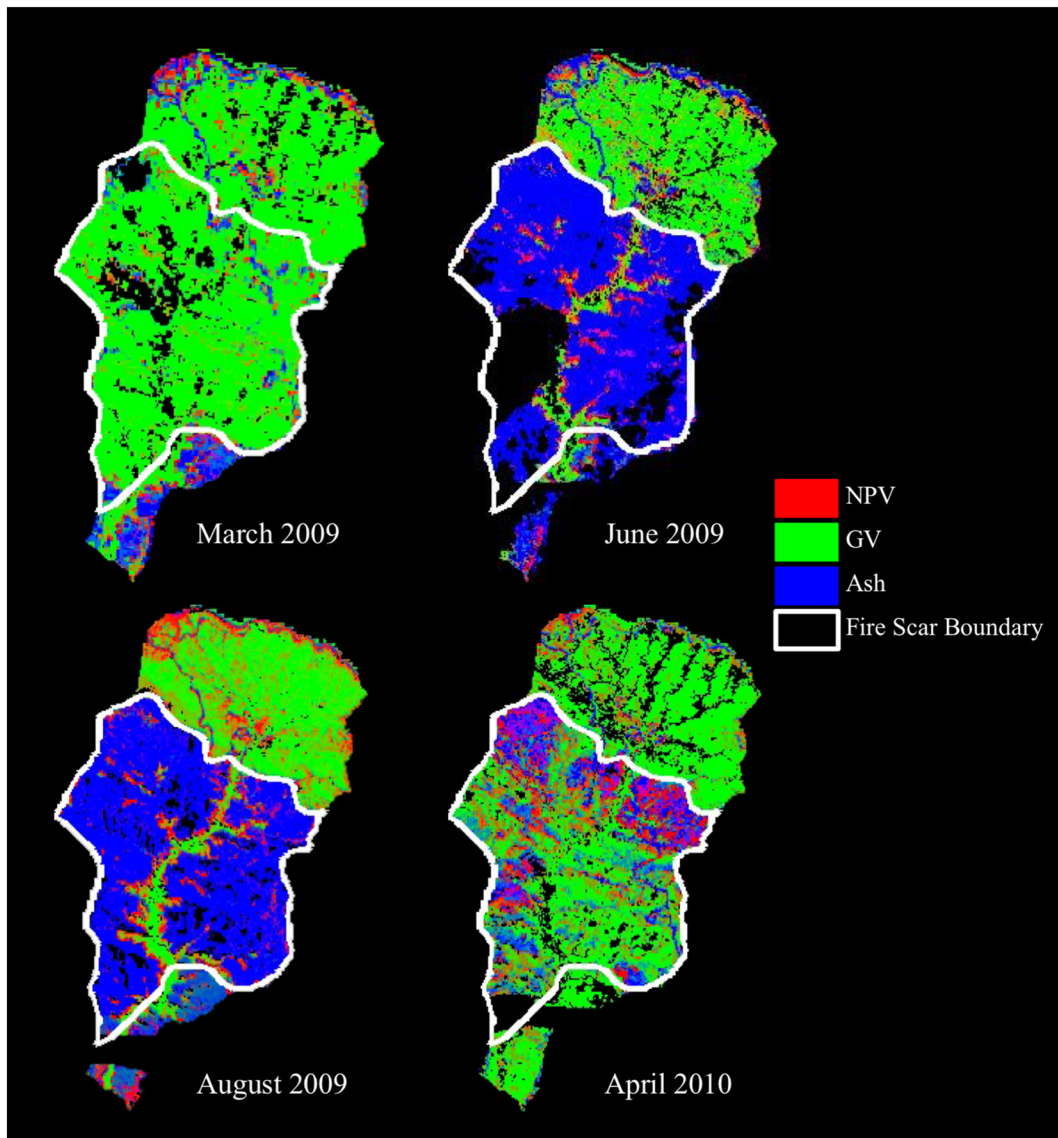


Figure 2. Remote sensing image classification of green vegetation (GV), non-photosynthetic vegetation (NPV), and ash land cover in Rattlesnake Canyon watershed for pre-fire, pre-wet season (March 2009), post-fire, pre-wet season (June and August 2009), and post-fire, post-wet season (April 2010) time periods.

and April 2010 images (Figure 2). We assumed that land cover fractions in obscured or missing regions were the same as the rest of the fire scar and watershed areas.

Watershed Rainfall and Runoff

Hourly rain-gauge data were obtained from five gauges in or near the Rattlesnake watershed operated by the Santa Barbara County Flood Control District (<http://countyofsb.org/pwd/water.sbc>). Integrated watershed-wide rainfall was determined by spatial interpolation based on rain-gauge elevation and watershed topography using geographic

weighted regression (Fotheringham and others 2002). Stream water level was measured at a 5-min frequency near the watershed outlet using a pressure transducer (Solinst Canada Ltd., Georgetown, Ontario) corrected for atmospheric pressure. These water-level records were converted to stream discharge using geomorphic profiles and a hydraulic computation program, Hydrologic Engineering Center-River Analysis Program (HEC-RAS) (USACE 2005). Runoff was calculated as discharge divided by watershed area. Runoff was calibrated using manual wading rod measurements with an electromagnetic flow meter (Hach Company, Loveland, CO) and the velocity-area method (Bu-

chanan and Somers 1969), and was re-calibrated following changes in stream morphology at the sampling location.

To understand rain event-based runoff change pre- and post-fire, we estimated the expected runoff for pre- and post-fire periods from the relationship between log-transformed rainfall and log-transformed runoff during pre-fire conditions. The differences in runoff are calculated using the following equation:

$$dR = \frac{(R_{\text{obs}} - R_{\text{exp}})}{R_{\text{exp}}} \quad (1)$$

where dR = change in runoff relative to expected runoff (dimensionless), R_{exp} = expected storm runoff based on the rainfall–runoff model (mm), and R_{obs} = measured storm runoff (mm) (Figure 3).

Stream N Chemistry

Storm samples were collected hourly on the rising limb of the hydrograph, and every two to four hours on the falling limb for every storm event. Storm samples were collected either manually in rinsed 500-ml high-density polyethylene (HDPE) bottles or automatically using ISCO 6712C portable water samplers (Teledyne Isco, Inc., Lin-

coln, Nebraska). Autosampler deployments typically lasted about 24 h, and samples were iced during this period and stored at 4°C after retrieval.

Samples analyzed for ammonium (NH_4^+), nitrate (NO_3^-), and dissolved organic nitrogen (DON) were filtered through Gelman A/E glass fiber filters (1- μm nominal pore size) into 60-ml HDPE bottles rinsed with filtered stream water. NH_4^+ and NO_3^- concentrations were determined on a Lachat flow injection autoanalyzer (Hach Company, Loveland, Colorado). NH_4^+ was measured by adding base to the sample stream, which converted NH_4^+ to NH_3 . NO_3^- was measured using the Griess–Ilosvay reaction after cadmium reduction. The detection limit for NH_4^+ and NO_3^- was $7.0 \mu\text{g L}^{-1}$, sensitivity was $2.8 \mu\text{g L}^{-1}$, and accuracy was $\pm 5\%$. Filtered samples were assayed for total dissolved N (TDN) by alkaline persulfate digestion in an autoclave for 25 min followed by determination as NO_3^- product on the Lachat. The detection limit for TDN was $14 \mu\text{g L}^{-1}$, sensitivity was $2.8 \mu\text{g L}^{-1}$, and accuracy was $\pm 10\%$. Dissolved organic N (DON) was calculated as the difference between TDN and the sum of NO_3^- and NH_4^+ .

Particulate nitrogen (PN) samples were filtered through 25-mm pre-combusted (450°C for 4 h) Pall Type A/E glass fiber filters and stored at -20°C . Prior to analysis, samples were acidified

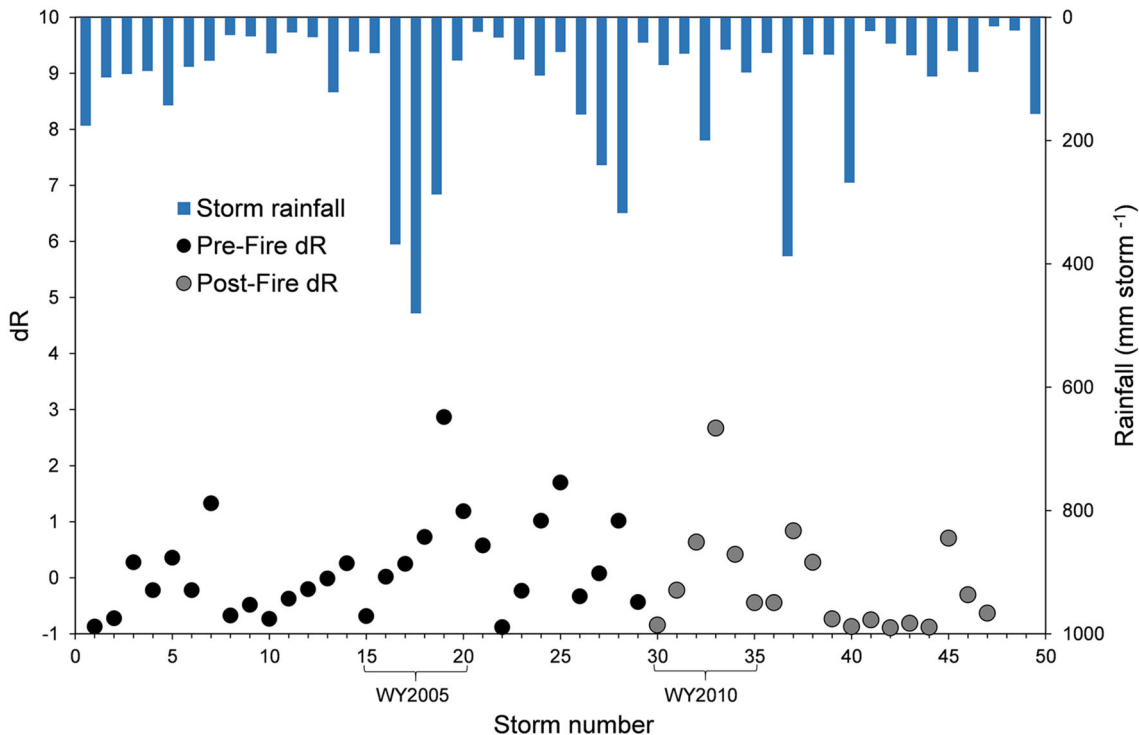


Figure 3. Magnitude differences in observed runoff relative to expected runoff (dR ; dimensionless) for pre- and post-fire periods calculated according to equation 1. Rainfall (mm) per storm event is plotted on the top x - and right y -axes.

(10% HCl) and heated in a drying oven overnight at 60°C, and temporarily stored at 4°C until being analyzed using the Dumas combustion method on a Control Equipment Corporation model 440 HA automated organic elemental analyzer. Precision and accuracy were ± 0.3 weight % N.

Pre-fire and Post-fire Stream N Fluxes

Dissolved N (ammonium, nitrate, and DON) is directly available for plant and soil microbial uptake, in contrast to particulate N which requires hydrolysis and/or oxidation into smaller compounds before plant and soil microbial uptake can occur. Therefore, we focus on the plant- and soil microbial-available dissolved N compounds. Accordingly, stream dissolved N flux (that is, ammonium, nitrate, and DON) is calculated using the following equations:

$$DWC_{N,f} = \frac{\sum_{i=1}^n N_{i,f}(Q_i)}{\sum_{i=1}^n Q_i} \quad (2)$$

$$F_N = \sum_{f=1}^3 DWC_{N,f}(Q_S) \quad (3)$$

where $DWC_{N,f}$ = storm discharge-weighted concentration for dissolved N form f (g L^{-1}), $N_{i,f}$ = stream concentration of dissolved N form f at time i of storm (g L^{-1}), Q_i = watershed stream discharge at time i of storm (L s^{-1}), F_N = storm stream N flux (g storm^{-1}), and Q_S = storm watershed stream discharge (L storm^{-1}). All Q_S values were converted to runoff (R_S) by dividing by watershed area.

We fit power models to storm flux (F_N) versus storm runoff (R_S) relationships for the 2002–2008 pre-fire time period in Rattlesnake watershed:

$$F_{\text{exp}} = \sum_{f=1}^3 F_{N,0,f}(R_S)^{m_f} \quad (4)$$

where F_{exp} = modeled pre-fire F_N (g storm^{-1}), $F_{N,0,f}$ = modeled pre-fire F_N of dissolved N form f at $R_S = 0$ (g storm^{-1}), and m_f = power slope for f

(Table 1). This approach enabled us to estimate expected stream flux (that is, F_{exp}) for post-fire storm events under the assumption of pre-fire watershed conditions. Since storm runoff (R_S) is the independent variable in the calculation of F_{exp} , which is a product of DWC_N and R_S (equation 3), the proportion of variability in F_{exp} explained by (1) watershed hydrology (that is, R_S) versus (2) the watershed biogeochemical processes responsible for collectively determining stream N concentration (that is, DWC_N) is given by R^2 and $R^2 - 1$, respectively. By calculating F_{exp} as a function of R_S , we control for inter-annual variability in the timing and magnitude of storm runoff events, which is variable in Santa Barbara's Mediterranean climate (Beighley and others 2008; Goodridge and Melack 2012). This allows us to estimate the effect of wildfire in altering the magnitude of stream N fluxes, which can be calculated as the normalized difference between observed, post-fire stream N export and expected stream N export under pre-fire watershed conditions for any given post-fire storm event:

$$wfe = \frac{(F_N - F_{\text{exp}})}{F_{\text{exp}}} \quad (5)$$

where wfe = change in post-fire stream N export due to wildfire (dimensionless). Therefore, changes in watershed N export due to a wildfire effect will manifest as deviations in wfe from 0, with the magnitude of the effect given by wfe .

Recovery Time of Stream N Fluxes

We identified the time to recovery of stream N fluxes to pre-fire levels by fitting a first-order exponential decay model to the wfe time series:

$$wfe_{\text{mod}} = wfe_0 e^{k_{wfe} t} \quad (6)$$

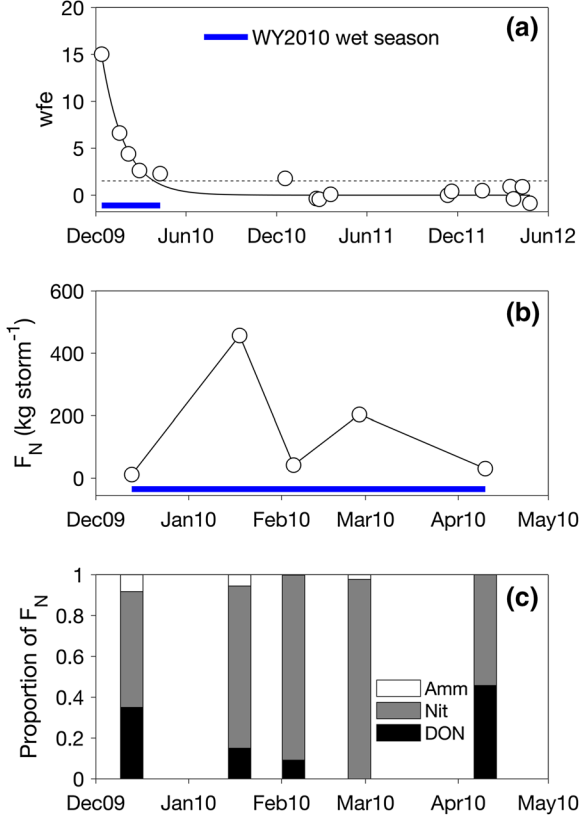
where wfe_{mod} = modeled wfe time series, wfe_0 = wfe at $t = 0$ (that is, initial post-fire rainstorm), k_{wfe} = decay constant (d^{-1}), and t = time elapsed since first post-fire rainstorm (d) (Table 2).

Table 1. Power Model Parameters [95% Confidence Intervals] for Storm Ammonium, Nitrate, and Dissolved Organic Nitrogen (DON) Flux vs. Runoff Relationships for the Pre-fire Period (2002 – 2008)

	$F_{N,0}$ (g storm^{-1})	m (dimensionless)	R^2	n
Ammonium	0.01 [– 0.004, 0.03]	1.25 [0.99, 1.50]	0.94	24
Nitrate	3.2 [– 0.1, 6.5]	1.23 [1.04, 1.42]	0.95	26
DON				
$R_S < 15$ mm	1.6 [– 0.3, 3.4]	1.28 [0.77, 1.80]	0.83	19
$R_S > 15$ mm	27.0 [– 2.4, 56.4]	0.48 [0.25, 0.71]	0.87	7

Table 2. Exponential Decay Model Parameters [95% Confidence Intervals] for Soil N (Ammonium, Nitrate, Extractable Organic Nitrogen) Levels and Stream N (Ammonium, Nitrate, Dissolved Organic Nitrogen) Wildfire Effects (wfe) for the WY2010 Wet Season

	$N_{\text{fire},0}$ (g m ⁻²)	k_{Nfire} (d ⁻¹)	t_{rec} (d)	R^2	n
Soil N	17 [13, 20]	- 0.04 [- 0.07, - 0.02]	66	0.98	5
	wfe ₀ (dimensionless)	k_{wfe} (d ⁻¹)	t_{rec} (d)	R^2	n
Stream N	15 [13, 16]	- 0.02 [- 0.03, - 0.02]	106	0.97	18

**Figure 4.** Time series of (A) stream wildfire effects (wfe) with recovery wfe level (dotted line = + 2σ pre-fire wfe time series) (B) stream N export (F_N), and (C) compositional proportions of F_N (Amm = ammonium, Nit = nitrate, DON = dissolved organic nitrogen) for the WY2010 wet season.

We then defined the time to recovery as the post-fire day on which wfe_{mod} equaled the two standard deviation (+2σ) wfe for all rainstorms during the pre-fire time period:

$$t_{\text{rec}} = \ln\left(\frac{wfe_{2\sigma,\text{pre}}}{wfe_0}\right) \left(\frac{1}{k_{\text{wfe}}}\right) \quad (7)$$

where t_{rec} = time to recovery of stream N flux to pre-fire level (d), and $wfe_{2\sigma,\text{pre}}$ = +2σ of pre-fire wfe time series (Figure 4a).

Plant Biomass N

Plant biomass recovery in the region was measured in the field as reported in Hanan and others (2016a). We use their results from Rattlesnake for the first post-fire growing season. Following the Jesusita fire, aboveground biomass, carbon, and N content of recovering vegetation were determined for fifteen 15 m × 15 m wildfire-burned plots. Plots were delineated at random points in eight large (> 500 m²) polygons, which were established prior to burning for a separate vegetation analysis (Roth and others 2012). Vegetation was sampled during times of peak biomass (June) during the 2010 water year (WY) growing season. To determine plant biomass (carbon; C) and N content, aboveground plant biomass was harvested from twelve 1-m² subplots located at random distances along three evenly spaced transects within each 15 m × 15 m plot. Weights for all shrub and herbaceous species within each subplot were measured, and subsamples were used for dry weight corrections and nutrient analyses. Plant total C (TC) and total N (TN) concentrations were measured using a Carlo Erba/Fisons NA 1500 Series 2 elemental analyzer, and dry weights were normalized to area (g m⁻²).

Soil Microbial Biomass N

Soil microbial biomass N was measured using the chloroform slurry-extraction method (Fierer and Schimel 2002). The efficiency of biomass extraction using this method is not significantly different from traditional chloroform vapor extraction methods (Fierer and Schimel 2002). Soil subsamples (10 g) were extracted with 40 ml of 0.5 M K₂SO₄ and 0.5 ml of CHCl₃ and filtered. Non-purgeable total nitrogen (TN) contents of CHCl₃-fumigated and CHCl₃-unfumigated extracts were measured on a Shimadzu Corporation, Series V Model CSN analyzer. Extractable microbial biomass N was calculated as the difference in organic N between the

CHCl₃-treated and the untreated subsamples. Because CHCl₃ releases a fraction of total microbial biomass N, a conversion factor of 0.54 for N was used to estimate total N (Brookes and others 1985). Extractable organic nitrogen (EON) was calculated as extracted TN minus inorganic N (NH₄⁺ + NO₃⁻). Results were normalized to g g⁻¹ dry weight soil and further normalized to area (g m⁻²).

Soil N

In the same 15 × 15 m plots where vegetation and soil microbial biomass were sampled, four soil cores (5 cm diameter by 15 cm depth) were collected on an approximate monthly basis during the 2009–2010 and 2010–2011 growing seasons (that is, November 2009 to June 2010, and December 2010 to May 2011). Soils were returned to the laboratory for analysis. All soil samples were homogenized and run through a 4-mm sieve. Bulk densities were determined as oven-dry mass divided by core volume. Water content was determined by weighing 10 g wet subsamples and then reweighing after drying at 65 °C for 72 h. Extractable NH₄⁺ and NO₃⁻ were extracted from 10 g of soil (wet weight) in 0.5 M K₂SO₄ (40 ml) for 4 h and then vacuum-filtered through a glass fiber filter (Pall Gelman Type A/E 1.0 µm), and extracts were frozen until analysis. Inorganic N concentrations were analyzed using a Lachat autoanalyzer (Lachat 1989). For NH₄⁺, this involves increasing the pH of the flow stream to convert NH₄⁺ to NH₃, which diffuses across a Teflon membrane into an acidic medium that contains a pH indicator. NH₄⁺ in the sample is calculated from the pH change in the indicator solution (Lachat method 31-107-06-5-A, Milwaukee, WI). NO₃⁻ was reduced by cadmium followed by a Griess-Ilosvay reaction and analyzed colorimetrically (Lachat method 12-107-04-1-B, Milwaukee, WI). Total nitrogen (TN) content was measured for all soil extracts using a Shimadzu Corporation, Series V Model CSN analyzer, and extractable organic nitrogen (EON) was calculated as extracted TN minus inorganic N. Results were normalized to µg cm⁻³ dry weight using bulk density and water content and further normalized to area (g m⁻²).

Recovery Time of Soil N

Soil N produced by the Jesusita wildfire was calculated as the difference between the burned soil N time-series values in WY2010 and the mean unburned soil N for Rattlesnake (3.8 g m⁻²) in WY2011 (N_{fire}; Figure 5). The time to recovery of soil N to pre-fire levels was then estimated by fit-

ting a first-order exponential decay model to the N_{fire} time series:

$$N_{\text{fire,mod}} = N_{\text{fire,0}} e^{k_{\text{Nfire}} t} \quad (8)$$

where N_{fire,mod} = modeled N_{fire} time series (g m⁻²), N_{fire,0} = N_{fire} at t = 0 (that is, initial soil sampling of the wet season), k_{Nfire} = N_{fire} decay constant (d⁻¹), and t = time elapsed since first soil sampling of the wet season (d) (Table 2). We then defined the time to recovery as the post-fire day on which N_{fire,mod} equaled the two standard deviation (+2σ) of unburned soil N for Rattlesnake:

$$t_{\text{rec}} = \ln\left(\frac{N_{2\sigma,\text{unburn}}}{N_{\text{fire,0}}}\right) \left(\frac{1}{k_{\text{Nfire}}}\right) + 31 \text{d} \quad (9)$$

where t_{rec} = time to recovery of soil N to the pre-fire level (d), N_{2σ,unburn} = +2σ of the unburned soil N time series, and 31 d is the time difference between the initial soil sampling (January 13, 2010) and initial rainstorm (December 13, 2009) of the wet season (Figure 5b).

Watershed N Mass Balance

To identify the roles of plant and soil microbial N uptake in landscape N retention and mitigation of stream N export following wildfire, we estimated a watershed mass balance for the WY2010 wet season for the Rattlesnake soil N pool created by the Jesusita fire. We calculated total N loss as:

$$L_{\text{fire}} = 0.61(A_w)(AL_{\text{fire}}) \quad (10)$$

where L_{fire} = total wildfire N loss during the wet season (g), 0.61 is the proportion of burned area of Rattlesnake, A_w = Rattlesnake watershed area (m²), and AL_{fire} = N_{fire} areal mass loss (15.1 g m⁻²), calculated as the difference between the initial (16.8 g m⁻²) and final (1.7 g m⁻²) soil N (that is, N_{fire}) values measured during the wet season (Figure 5).

Plant recovery was based on August 2009 and April 2010 remote sensing images, with the change in the GV cover fraction (that is, difference between post-fire and pre-fire GV) representing plant recovery (Figure 2). During the first growing season following the Jesusita fire, all aboveground biomass was considered new growth, as the plots were initially bare. To constrain the range in potential plant uptake of soil N, we estimated the belowground biomass of herbs and shrubs using the product of estimated root:shoot N ratios of 0.55 and 0.60, respectively (Kummerow and others 1977), and measured aboveground biomass N

(Table 3). Chaparral herbs germinate from soil seed banks following wildfire, so we assumed that 100% of biomass was derived from soil N, calculating herb N uptake as:

$$AU_{\text{herb}} = 0.55(N_{\text{herb,above}}) + N_{\text{herb,above}} \quad (11)$$

where AU_{herb} = herb N areal uptake for estimated belowground and measured aboveground biomass (g m^{-2}), $N_{\text{herb,above}}$ = measured aboveground herb N (g m^{-2}), and 0.55 = root:shoot N ratio (Klimeš and Klimešová 1994). In contrast, many chaparral

shrubs re-sprout from surviving root structures following wildfire, a primary mode of regrowth during early post-fire recovery (Keeley and Keeley 1981). Since an estimated 44% of shrub root N was lost due to wildfire (Debano and Conrad 1978; Hanan and others 2017), we calculated shrub N uptake as:

$$AU_{\text{shrub}} = 0.44(0.60)(N_{\text{shrub,above}}) + N_{\text{shrub,above}} \quad (12)$$

where AU_{shrub} = shrub N areal uptake for estimated belowground and measured aboveground biomass (g m^{-2}), 0.44 = proportion of root N loss due to wildfire, $N_{\text{shrub,above}}$ = measured aboveground shrub N (g m^{-2}), and 0.60 = root:shoot N ratio (Kummerow and others 1977). The amount of N sequestered in new plant biomass is then estimated as:

$$U_p = A_w (\Delta GV) (AU_p) \quad (13)$$

where p = plant class (herb, shrub, and litter), U_p = plant N sequestered over the wet season for each plant class p (g), ΔGV = change in GV cover fraction during the wet season (%), and AU_p = plant N areal uptake for measured aboveground (Hanan and others 2016a) and estimated belowground (except litter) biomass for each plant class p (g m^{-2}). Litter represents the accumulation of dead plant material on the soil surface from herb and shrub growth and is therefore included in plant N uptake due to sequestration of N in previously living plant matter (Tables 3 and 4).

Soil microbial biomass N uptake for the WY2010 wet season is calculated as:

$$U_{\text{microbe}} = 0.61(A_w)(MBN_{\text{wet,final}} - MBN_{\text{wet,pre}}) \quad (14)$$

where U_{microbe} = soil microbial biomass N uptake (g), $MBN_{\text{wet,final}}$ = soil microbial biomass N for the final soil sampling of the wet season (g m^{-2}), and $MBN_{\text{wet,pre}}$ = soil microbial biomass N for the soil

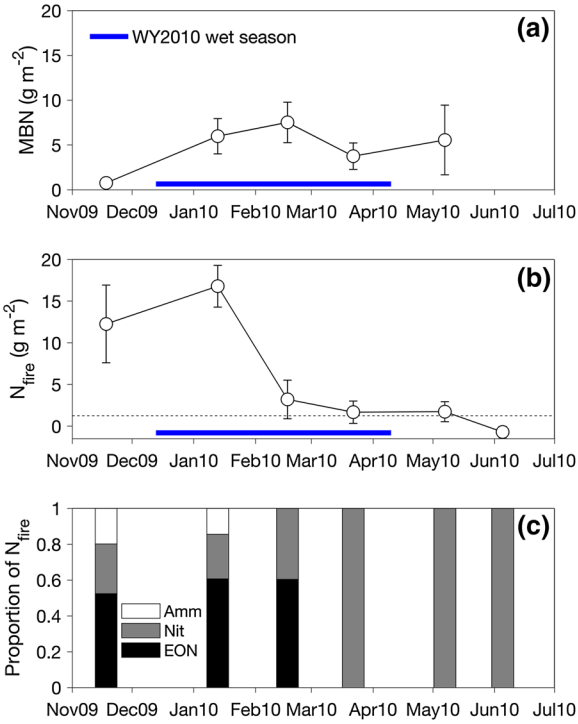


Figure 5. Time series of (A) soil microbial biomass N (MBN), (B) wildfire soil N (N_{fire}) with recovery N_{fire} level (dotted line = $+2\sigma$ unburned soil N), and (C) compositional proportions of N_{fire} (Amm = ammonium, Nit = nitrate, EON = extractable organic nitrogen) for the WY2010 wet season.

Table 3. Measured (1 S.E.) Plant Aboveground Carbon (C) and N Uptake (U_{above}), Estimated Belowground N Uptake (U_{below}), and Plant Areal N Uptake (AU) for the WY2010 Wet Season

	U_{above} (g C m^{-2})	U_{above} (g N m^{-2})	U_{below} (g N m^{-2})	AU (g N m^{-2})
Herb	82.3 (15.3)	2.5 (0.4)	1.4 ^a	3.9
Shrub	115.1 (54.5)	3.8 (1.8)	1.0 ^b	4.8
Litter	18.0 (4.8)	0.5 (0.2)	—	0.5
Soil microbial	—	—	5.7 (0.4)	3.0

^aCalculated using root:shoot N ratio of 0.55 (Klimeš and Klimešová 1994).

^bCalculated using root:shoot N ratio of 0.60 (Kummerow and others 1977).

Table 4. Watershed Mass Balance for Wildfire N Loss (L_{fire}), Plant N Uptake (U_{herb} , U_{shrub} , U_{litter}), Soil Microbial N Uptake (U_{microbe}), Stream N Export (L_{stream}), and Combined Plant N Uptake, Soil Microbial N Uptake, and Stream N Export (UL_{comb}) for the WY2010 Wet Season

	L_{fire}	U_{herb}	+	U_{shrub}	+	U_{litter}	+	U_{microbe}	+	L_{stream}	=	UL_{comb}
Mg ^a	63.2	8.6		10.5		1.1		12.6		0.7		33.5
% of L_{fire}	–	14		17		2		20		1		53

^aMg = 10⁶ g.

sampling immediately preceding the wet season (g m^{-2}) (Tables 3 and 4; Figure 5a).

Stream N export is calculated as:

$$L_{\text{stream}} = \sum_{s=1}^5 F_{N,s} - F_{\text{exp},s} \quad (15)$$

where s = storm number (total of 5 storms). We calculated residual flux (that is, $F_N - F_{\text{exp}}$) instead of absolute flux (that is, F_N), as residual stream N flux describes the excess N pool from the wildfire (Table 4).

With the six terms specified—wildfire N loss (L_{fire}), herb N uptake (U_{herb}), shrub N uptake (U_{shrub}), litter N uptake (U_{litter}), soil microbial N uptake (U_{microbe}), and stream N loss (L_{stream})—the watershed wildfire N mass balance is:

$$L_{\text{fire}} = U_{\text{herb}} + U_{\text{shrub}} + U_{\text{litter}} + U_{\text{microbe}} + L_{\text{stream}} \quad (16)$$

In addition, plant N uptake, soil microbial N uptake, and stream N loss terms are calculated as percentages of wildfire N loss as (Table 4):

$$\% \text{ of } L_{\text{fire}} = \frac{U_p | U_{\text{microbe}} | L_{\text{stream}}}{L_{\text{fire}}} \times 100 \quad (17)$$

RESULTS

Watershed Landscape Recovery

The pre-fire (March 2009) image showed that Rattlesnake land cover was 86% green vegetation (GV) with a minor ash component, which was residual from the Tea Fire (Figure 2). In June 2009, following the Jesusita fire in May 2009, GV areal cover had dropped to 33% and ash areal cover had increased to 47% (Figure 2). Over the summer dry period (between June and August 2009 images), there was 1% GV loss and no apparent ash loss, although we visually observed wind redistribution within and export from the watershed. Over the following wet season (that is, between August 2009 and April 2010 images), GV areal cover increased to

64%, and ash areal cover declined to 11% (Figure 2).

Watershed Rainfall and Runoff

Total annual rainfall in Rattlesnake varied between 230 mm in 2014 and 1740 mm in 2005, with an average value of 661 mm during our study period (2002 to 2014). Rainfall for the first wet season following the Jesusita fire was 837 mm. Rainfall and runoff ranged from 15 to 480 mm storm⁻¹ and from 0.15 to 197 mm storm⁻¹, respectively. Maximum rainfall and runoff were recorded during the same storm in WY2005. Lowest values were recorded in WY2012, coinciding with the onset of a prolonged drought. There was no significant difference between dR values for pre- and post-fire periods ($t(45) = 1.1$, $p = 0.29$) and for the pre-fire period and the first post-fire wet season ($t(32) = -0.8$, $p = 0.42$) (Figure 3).

Stream N Recovery

Post-fire stream dissolved N flux (F_N) increased with respect to what would have been expected under pre-fire conditions. For the initial post-fire storm, F_N was 1480% higher than the F_{exp} value (Table 2; Figure 4a and b). This wildfire effect (wfe) was short-lived, as F_N returned to pre-fire levels within 106 days of the first storm of the wet season (Figure 4a).

Soil N Recovery

Burned soil N (N_{fire}) was 320 and 440% higher than unburned soil N based on our initial soil sampling immediately before the wet season and initial sampling of the wet season, respectively (Table 2; Figure 5b), but returned to pre-fire levels within 66 d of the initial post-fire storm of the wet season (Table 2; Figure 5). Extractable organic nitrogen (EON) was the dominant fraction of N_{fire} , comprising 52% of N_{fire} , with nitrate and ammonium comprising 28 and 20% of N_{fire} (Figure 5). For the first soil sampling of the wet season (Jan-

uary 2010) N_{fire} increased by 4.5 g m^{-2} , from 12.3 to 16.8 g m^{-2} (Figure 5). The dominant N fraction remained EON at 61% of N_{fire} , with ammonium and nitrate comprising 25 and 14% of N_{fire} (Figure 5). Ammonium was not detected by the second soil sampling of the wet season, with EON and nitrate comprising 60 and 40% of N_{fire} (Figure 5). By the final soil sampling of the wet season, EON was not detected, with nitrate comprising all of N_{fire} (Figure 5).

Plant and Soil Microbial N Uptake

Herbaceous species, primarily the short-lived perennial vine *Calystegia macrostegia*, comprised 42% of aboveground biomass and sequestered 3.9 g N m^{-2} in measured aboveground and estimated belowground (except litter) biomass (AU_{herb}) (Table 3). Shrub species comprised 58% of aboveground biomass and sequestered 4.8 g N m^{-2} in measured aboveground and estimated belowground biomass (AU_{shrub}) (Table 3). Plant litter derived from new herb and shrub growth sequestered an estimated 0.5 g N m^{-2} (AU_{litter}) (Table 3). Mean soil microbial biomass N was 5.7 g m^{-2} with net N uptake of 3.0 g m^{-2} for the wet season (Table 3).

Wildfire N Mass Balance

Estimated wildfire N decline over the wet season was 63.2 Mg (L_{fire} ; Table 4). Plant N uptake for all new plant growth over the wet season, herb (U_{herb}) and shrub (U_{shrub}), was 8.6 and 10.5 Mg , respectively, and 1.1 Mg for plant litter derived from new plant growth (U_{litter}), equivalent to 14, 17, and 2% of L_{fire} (Table 4). Soil microbial N uptake (U_{microbe}) over the wet season was 12.6 Mg , equivalent to 20% of L_{fire} (Table 4). Stream N export (L_{stream}) was 0.7 Mg , equivalent to 1% of L_{fire} (Table 4). Combined plant N uptake, soil microbial N uptake, and stream N loss (U_{Lcomb}) was 33.5 Mg , equivalent to 53% of L_{fire} (Table 4).

DISCUSSION

During wildfire, heating of the upper few centimeters of soil transforms soil organic N to ammonium, nitrate, and simpler organic N compounds, with partially combusted plant biomass depositing as a N-containing ash layer across the watershed surface (Christensen 1973; DeBano and Conrad 1978; Raison 1979; Knicker 2007). As a result, N availability for potential plant and soil microbial uptake is often enhanced in the upper soil following wildfire, both by soil heating and by

solubilized ash infiltration during initial rainstorms of the post-fire wet season (Christensen and Muller 1975; Rundel 1983; Fenn and others 1993; Carreira and others 1994). However, hydrologic N export can be pronounced in chaparral watersheds during the first wet season following wildfire, causing N loss via overland runoff and shallow soil interflow to streams (Riggan and others 1994; Earl and Blinn 2003; Coombs and Melack 2013; Verkaik and others 2013; Bixby and others 2015).

The topography and soils of Rattlesnake watershed are characteristic of California chaparral and Mediterranean-type ecosystems: steep slopes and shallow soils with high infiltration capacity and hydraulic conductance (Beighley and others 2005; Li and others 2006). Together, these factors make shallow soil interflow a dominant runoff mechanism (Beighley and others 2005). Despite these favorable geomorphic and hydrologic conditions for large hydrologic N losses, our study shows that soil N and stream N export returned to pre-fire levels within 66 and 106 days, respectively, after the onset of the first wet season following wildfire (Table 2; Figures 4 and 5). This recovery coincided with the establishment of ephemeral herbs and regrowth of shrub and soil microbial biomass, which sequestered 32.8 Mg of N, or an amount equivalent to 52% of wildfire N loss over the WY2010 wet season (Table 4). Hence, we discuss watershed N changes in Rattlesnake during this initial wet season, and how those changes were influenced by plant and soil microbial recovery, two potentially important N retention mechanisms during the initial wet season following wildfire, when hydrologic N loss is expected to be maximal. This hypothesized plant and soil microbial N retention has important implications for chaparral ecosystem resilience to post-fire N loss and mitigation of downstream effects on aquatic ecosystems.

Wildfire N: Ash, Soil, and Stream

Ash clogging of soil pores and hydrophobic resins can impede rainfall infiltration into the soil during initial post-fire rains, increasing overland runoff and rapidly transporting ash N to streams (DeBano 2000; Coombs and Melack 2013). However, differences between observed and expected runoff (that is, dR) for pre-fire and post-fire periods were not significantly different, indicating no detectable hydrologic alteration due to wildfire (Figure 3). Therefore, the largest increase in stream wildfire effect (that is, wfe) for the initial post-fire rainstorm likely resulted from an increase in the N

concentration of surface runoff and/or shallow soil interflow as the ash layer was mobilized (Figure 4). In addition, because soil infiltration capacity was relatively unchanged as indicated by nonsignificant differences between pre- and post-fire dR values (Figure 3), we attribute the increase in soil N between the pre-wet season (November 2009) and initial wet season (January 2010) soil N samplings to infiltration of ash N resulting from the first two rainstorms of the wet season (December 2009 and January 2010). A majority of the ash cover decline over the wet season, from 47% to 11% (Figure 2), occurred during these initial rainstorms based on our observations. This allows us to obtain an integrated ash N estimate of 4.5 g m^{-2} , which is within the range of other ash N measurements in wildfire studies of Mediterranean ecosystems: 2.1 and 5.8 g m^{-2} in California chaparral (Christensen and Muller 1975; Rundel and Parsons 1984), 8.9 g m^{-2} in California bishop pine forest (Grogan and others 2000), and 6.6 g m^{-2} in South African coastal shrub fynbos (Stock and Lewis 1986). The 320% increase in soil N following the Jesusita fire in Rattlesnake (Figure 5) is higher than the range of soil N increase in other wildfire studies (65% to 310%; Smithwick and others 2005). However, the recovery timescales of soil N (66 days) and stream N export (106 days) to pre-fire levels are among the most rapid reported for fire-adapted ecosystems (Verkaik and others 2013).

Chaparral N Retention: Shrubs, Herbs, and Soil Microbes

Chaparral shrub species and soil microbial biomass comprise dominant fractions of total biomass in mature chaparral ecosystems (Rundel 1983). In contrast, herb species biomass is typically low (Christensen and Muller 1975; Keeley and Keeley 1981). However, during the earliest post-fire successional phase, ephemeral herbs can comprise a large fraction of new plant biomass due to high growth and N uptake rates (Keeley and Keeley 1981; Rundel and Parsons 1984; Hanan and others 2016a). For example, in experimental burns in chaparral watersheds in southern California, ephemeral herbs comprised 5% to 31% of new biomass in the first year following fire and accounted for 55% of N uptake in new biomass (Rundel and Parsons 1984). The ephemeral herb *C. macrostegia* was dominant following wildfire on south-facing slopes in the Santa Monica Mountains of southern California, where it comprised 60% to 70% of biomass regrowth in initial post-fire years (Guo 2001). After the initial few years of post-fire

succession, the ephemeral herb community is displaced by the return of the plant community to shrub dominance (Gray and Schlesinger 1981; Keeley and others 1981).

In our study, ephemeral herbs, predominantly *C. macrostegia*, accounted for 45% of N uptake by new plant growth (Table 3) and took up 8.6 Mg of N, an amount equivalent to 14% of wildfire N loss over the wet season (Table 4). However, ephemeral herbs may also have indirectly promoted additional N uptake by shrubs and soil microbes, which accounted for 17 and 20%, respectively, of wildfire N loss over the wet season (Table 4). Ephemeral herbs contain less lignin and other carbon-rich phenolic compounds and have lower C:N ratios than other chaparral plants (Hanan and others 2017), making ephemeral herb litter more available (that is, labile) to the soil microbial community (Hart and others 2005). This labile herbaceous litter input to soils can enhance soil microbial biomass growth and N turnover (Hart and others 2005). Although there is evidence that plants are able to take up organic N, inorganic N is considered the primary form of N for plant uptake (Näsholm and others 2009). Although plants and soil microbes compete for soil inorganic N, the large fraction of soil organic N (EON) during the first half of the wet season (Figure 5) may have facilitated a mutualistic feedback: labile herb litter inputs promoted soil microbial biomass and EON uptake/growth, and EON mineralization and nitrification (stimulated by increased soil pH; Hanan and others 2016b) in turn enhanced soil ammonium and nitrate availability for shrub uptake/growth. This hypothesized role of ephemeral herbs in direct N uptake and indirect enhancement of shrub and soil microbial N uptake through provision of labile herb litter may be an important mechanism of early post-fire landscape N retention in chaparral ecosystems.

The role of ephemeral herbs in N retention is also characteristic of other terrestrial ecosystems (Muller and Bormann 1976; Blank and others 1980). The “vernal dam” hypothesis proposed that a single herb species, *Erythronium americanum*, which grows in northern hardwood forest during the critical period between snowmelt in winter and forest canopy development in spring, plays a crucial role in reducing stream nitrate export by sequestering N in its biomass during the period of maximal hydrologic flushing (Muller and Bormann 1976). In early summer, as other plants become photosynthetically active, *E. americanum* begins to decompose and release sequestered N (Muller and Bormann 1976). A subsequent study in a mesic hardwood forest provided another example of a

“vernal dam”, where N uptake by a spring ephemeral herb could potentially avert a sizeable fraction (34%) of annual stream N loss (Blank and others 1980). In another study conducted in a northern hardwood forest ecosystem prior to spring canopy closure, ^{15}N isotopic tracing revealed that ammonium uptake by the ephemeral herb *Allium tricoccum* and soil microbial biomass reduced the amount of substrate available for nitrification, thereby reducing nitrate loss that might otherwise occur through denitrification and leaching (Zak and others 1990). Thus, ephemeral herbs facilitate N retention in periods preceding spring canopy closure in hardwood forest and following wildfire in chaparral ecosystems, when watersheds are vulnerable to potentially large hydrologic N losses.

Chaparral N Retention and N Limitation

To place the role of post-fire plant and soil microbial N uptake in context, we examined the relative magnitudes of plant and soil microbial N retention versus the primary N sources in southern California chaparral watersheds: dry and wet atmospheric deposition (N_{dep}), N fixation in soils (N_{fix}), and N from weathering of parent rock (N_{rock}). Although urban and agriculture land uses have markedly enhanced atmospheric N deposition rates in many regions of California (Riggan and others 1985; Padgett and others 1999; Meixner and others 2006), the Santa Barbara region is not downwind of such land uses and does not receive these augmented N inputs. Accordingly, typical N_{dep} is low: $0.01 \text{ g m}^{-2} \text{ year}^{-1}$ for ammonium and $0.02 \text{ g m}^{-2} \text{ year}^{-1}$ for nitrate and DON (Santa Barbara Coastal LTER; <http://sbc.lternet.edu//data/dataCollection.sPortal.html>). In the moisture-limited soils of southern California, N_{fix} is also low ($0.01 \text{ g m}^{-2} \text{ year}^{-1}$) (Kummerow and others 1978). Weathering of parent rock contributes an estimated median subsidy of $0.32 \text{ g m}^{-2} \text{ year}^{-1}$ N to chaparral soils of the Transverse Ranges, which include the Santa Ynez Mountains in the Santa Barbara region (Morford and others 2016). Thus, it would require over 18 years ($U_{\text{plant+microbe}} [N_{\text{dep}} + N_{\text{fix}} + N_{\text{rock}}]^{-1}$) for N sources to replace the amount of N sequestered in plant and soil microbial biomass, assuming that this N pool had instead been lost from the watershed (Table 4). Therefore, prevention of shorter-term N losses via rapid post-fire plant and soil microbial N sequestration has the potential to mitigate longer-term N limiting conditions by promoting watershed N retention in this chaparral ecosystem.

“Missing” N

A significant fraction of L_{fire} (47%) remained unaccounted for in our wildfire N mass balance. While an additional 3% of L_{fire} (3.1 Mg) can be accounted for as stream particulate N export during the wet season, the most probable fate of the other 44% of wildfire N was (1) loss to the underlying fractured bedrock aquifer (Rademacher and others 2002), (2) uptake by riparian plants (Naiman and Decamps 1997), and/or (3) loss via soil denitrification (Hill 1996; Mayer and others 2007). Unless the entirety of the missing N was lost via seepage to the underlying aquifer and/or denitrification, riparian plant uptake would be an additional watershed N retention mechanism. The riparian corridor in Rattlesnake remained relatively unburned (Figure 2), so riparian plants would likely have maintained a pre-fire capacity for N uptake. To provide an approximate estimate of riparian N retention, we use a riparian plant uptake of 10.3 g m^{-2} , measured for a mesic riparian zone (Schade and others 2002), to yield an additional 9% (5.7 Mg) of N uptake, increasing N sequestration to 61% of wildfire N loss, which does not include stream dissolved and particulate N loss (Table 4). The shift toward nitrate dominance in both N_{fire} and F_{N} in the mid- to latter half of the wet season indicated efficient EON mineralization and nitrification of soil ammonium, providing substrate for denitrification (Figures 4 and 5). Given this, we estimate that denitrification would need to have been 5.3 g m^{-2} over the burned area of Rattlesnake to account for the remaining 35% of L_{fire} , which is similar to the mean denitrification rate estimated in a N cycling study of Rattlesnake watershed (Hanan and others 2017) and other terrestrial denitrification studies (Seitzinger and others 2006).

CONCLUSION

We propose that rapid post-fire recovery of the chaparral plant and soil microbial community, particularly ephemeral herbs, following wildfire can function as a “pyrogenic dam”, redirecting ash and soil N produced by wildfire from potential hydrologic export toward watershed N retention. This N retention is not limited to chaparral and wildfire disturbance (Muller and Bormann 1976; Blank and others 1980; Zak and others 1990) and merits future study in chaparral and exploration in other ecosystems, such that the various modes and mechanisms of ecosystem resilience to environ-

mental variability may be better understood under accelerating ecosystem and climate change.

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