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Impacts of climate and disturbance on nutrient fluxes and stoichiometry in mixed-conifer forests

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Abstract Elucidating climatic impacts on stream nutrient export and stoichiometry will improve the understanding of forest carbon (C) storage in a warmer world. We analyzed C, nitrogen (N), and phosphorus (P) cycles in four watersheds within a rain-snow transition site and another four within a higher-elevation, snow-dominated site, in California's mixed-conifer zone. We used these two sites in a space-for-time substitution to assess the potential warming impacts on nutrient cycles in currently snow-dominated areas that will become more rain-dominated. During a non-drought period (water year (WY) 2004–2011), mean annual stream exports of C and N in particulate forms at the transition site were twice that at the snow-dominated site, suggesting sediment-associated nutrient losses may increase with warming. The transition site had 12% lower N but twice P content in mineral horizons, lower N:P mass ratios in organic horizons, and lower stream export of dissolved inorganic N than the snow-dominated site. These differences suggest montane forests may have lower inputs of available N relative to P with warming. In addition, given strong interests in forest thinning to

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increase drought resiliency, we examined changes in stream nutrient export after thinning and during a major drought period (WY 2013–2015). Stream exports of C, N, and P were similar between unthinned and thinned watersheds during drought, suggesting negligible thinning impacts on stream nutrient export during excessively dry periods. Taken together, our results suggest that as the climate warms, California's montane forests may lose more nutrients through erosion and increase their N-P nutritional imbalance.

Keywords Critical zone · Elemental stoichiometry · Global warming · Sierra Nevada · Soil erosion · Space-for-time substitution

Introduction

Carbon (C) exchange between the atmosphere and forest ecosystems has long been measured to evaluate changes in ecosystem C storage with climate warming (Ballantyne et al. 2017; Fernández-Martínez et al. 2019; Pilegaard and Ibrom 2020). However, forest C storage does not always follow changes in net ecosystem C exchange due to other sources of C loss, such as stream export, that are not accounted for in these measurements (Lovett et al. 2006). In mountainous areas, warming is known to decrease the fraction of precipitation as snow and increase input of energy to the soil surface (Klos et al. 2014; Goulden and Bales 2014; Dutta and Dutta 2016). Those warming-induced changes in hydro-meteorological conditions are expected to alter stream C export by influencing both water yield and soil C inputs and mobilization (Meingast et al. 2020). Hence, evaluating the climatic controls on stream C export in the context of net ecosystem C exchange is central for improving our understanding of C storage as the climate continues to warm in montane forests.

Studies have observed greater annual stream export of dissolved C in warmer years, driven by increases in both dissolved C concentration and annual water yield (e.g., Sebestyen et al. 2009; Leach et al. 2016). Increased dissolved C concentrations with warming has been attributed to increased rates of soil organic matter decomposition (Wang et al. 2013; Ritson et al. 2014; Velthuis et al. 2018). However, changes in stream export of dissolved C do not always mirror changes in their concentrations within the stream. For example, increases in volume-weighted concentrations of dissolved organic C (DOC) between 1980 and 2001 have been observed in boreal forests but accompanied by unchanged rates of stream C export (Eimers et al. 2008). This has been attributed to the predominant influence of unchanged annual water yield on DOC export. Given inconsistent changes in annual water yield with warming among sites within a climatic region (e.g., Null et al. 2010) and across climatic regions (Creed et al. 2014), it is important to examine the impact of warming on water yields and dissolved C concentrations together to help understand changes in stream C export with warming. Additionally, streams can export C in suspended and bedload sediments that are naturally derived from bank, splash, and hillslope erosion, and mass movement from adjacent upland soils (Leonard et al. 1979; Gomi et al. 2005). The impact of warming on the export of sediment-associated C (alternatively called particulate C) is relatively less studied even though particulate C export can be greater than dissolved C export (Argerich et al. 2016; Turowski et al. 2016). To gain a more comprehensive understanding of stream C export with warming, both particulate and dissolved C export must be considered.

Change in forest C storage with warming will likely be constrained by the availability of soil nitrogen (N) and phosphorus (P; Hungate et al. 2003; Tang et al. 2018; Terrer et al. 2019). A global meta-analysis of long-term trends in foliar N suggests that terrestrial rooted plants are experiencing N "oligotrophication" with warming (Craine et al. 2018). For example, based on long-term measurements in northern hardwood forests of the United States, lower rates of soil net N mineralization, soil net nitrification, and dissolved inorganic N (DIN) export from streams were observed in warmer years, suggesting N oligotrophication (Bernal et al. 2012; Durán et al. 2016; Groffman et al. 2018). Meanwhile, soil P availability is also expected to change with warming. For instance, in a global analysis of the impact of mean annual air temperature, mean annual precipitation, and soil texture on soil available P pools, Hou et al. (2018) reported that soil P availability decreased with increasing temperature in finer textured soils, but increased with increasing temperature and decreased with increasing precipitation in coarser textured soil (sand content > 50% by weight). Thus, climate warming will potentially alter the availability of N and P in forest soils, indirectly influencing the forest C cycle.

Montane forests are experiencing more severe and frequent droughts with increasingly warmer temperatures, particularly in the western United States (Diffenbaugh et al. 2015; Williams et al. 2015, 2020). Stream export of nutrients commonly decreases under drought due to low water yield and lower transfer rates of dissolved organic matter and sediments from forest soils to streams (Stacy et al. 2015; Szkokan-Emilson et al. 2017). However, the relative degree by which C, N, and P stream exports change under drought conditions, and the relative role of different forms (dissolved vs. particulate) of these nutrients as mechanisms of nutrient export from forests, are unknown.

In many forests of the western United States, forest thinning has been implemented to increase the forest resilience to drought (Agee and Skinner 2005; D'Amato et al. 2013), which may influence nutrient losses in streamflow. In years with near-average precipitation, stream export of dissolved C and N can be greater in thinned than unthinned watersheds due to increases in concentrations and runoff (Dung et al. 2012; Bäumler and Zech 1999; Wang et al. 2006). However, in drought years, influences of thinning on water yields are often negligible (Saksa et al. 2017; Bart et al. 2021), which may result in similar rates of stream export of nutrients between the thinned and unthinned watersheds. With frequent drought conditions and increasing forest thinning (Graham et al. 1999; Agee and Skinner 2005), an improved understanding of how thinning impacts stream nutrient export in drought years is essential.

Elevational changes in forest nutrient cycles capture the climatic effects over decadal to centennial time scales. They also reflect an integrated response to a changing climate because air and soil temperatures, annual precipitation amount, vegetation composition, and soil properties typically covary along the elevational gradient (Körner 2007). The Kings River Experimental Watersheds in California's Southern Sierra Nevada consists of two sites in close proximity along an elevation gradient: a lower-elevation rain-snow transition site and a higher-elevation snow-dominated site. Because of the observed shift from snow-dominated to rain-dominated regimes with warming (Clifton et al. 2018), comparing these two sites can provide insights into long-term warming effects on nutrient cycles (Williams et al. 2011). Watersheds in those two sites were also selectively thinned in 2012. This occurrence coincided with the onset of a severe drought in California (2012–2016), providing an opportunity to study the impact of drought and forest thinning on stream nutrient export. Our research questions were:

1. What is the proportion of stream nutrient export in particulate versus dissolved form, and does this vary between the two sites prior to drought and thinning?
2. How different are nutrient pools in plants and soils, and stoichiometric ratios in soils and stream water between the two sites prior to drought and thinning?
3. How does stream export of nutrients change under drought alone (in unthinned watersheds) and with drought combined with thinning (in thinned watersheds)?

Materials and methods

Site description

The Kings River Experimental Watersheds (KREW) is a long-term research area established by the United States Department of Agriculture, Forest Service. It consists of two sites, each with four watersheds (zero- and first-order), and both located on the western slope of the southern Sierra Nevada, California: a rain-snow transition site (37° 3.120′ N, 119° 12.196′ W, 35–60% of precipitation as snow) and a snow-dominated site (36° 58.631′ N, 119° 4.917′ W, 75–90% of precipitation as snow, Fig. 1). The rain-snow transition site has an elevation of 1485–2115 m, and the snow-dominated site has an elevation of 2050–2490 m (Table 1). Both sites experience a Mediterranean-type climate, with an average of 90% of the annual precipitation occurring between October and June (Safeeq and Hunsaker 2016). Soils at both sites are derived primarily from granitoid parent materials. They are classified as coarse-loamy, mixed, superactive, mesic Humic Dystroxerepts at the transition site and mixed, frigid Dystric Xeropsamments at the snow-dominated site (Johnson et al. 2011). Overstory vegetation at the transition site is dominated by white

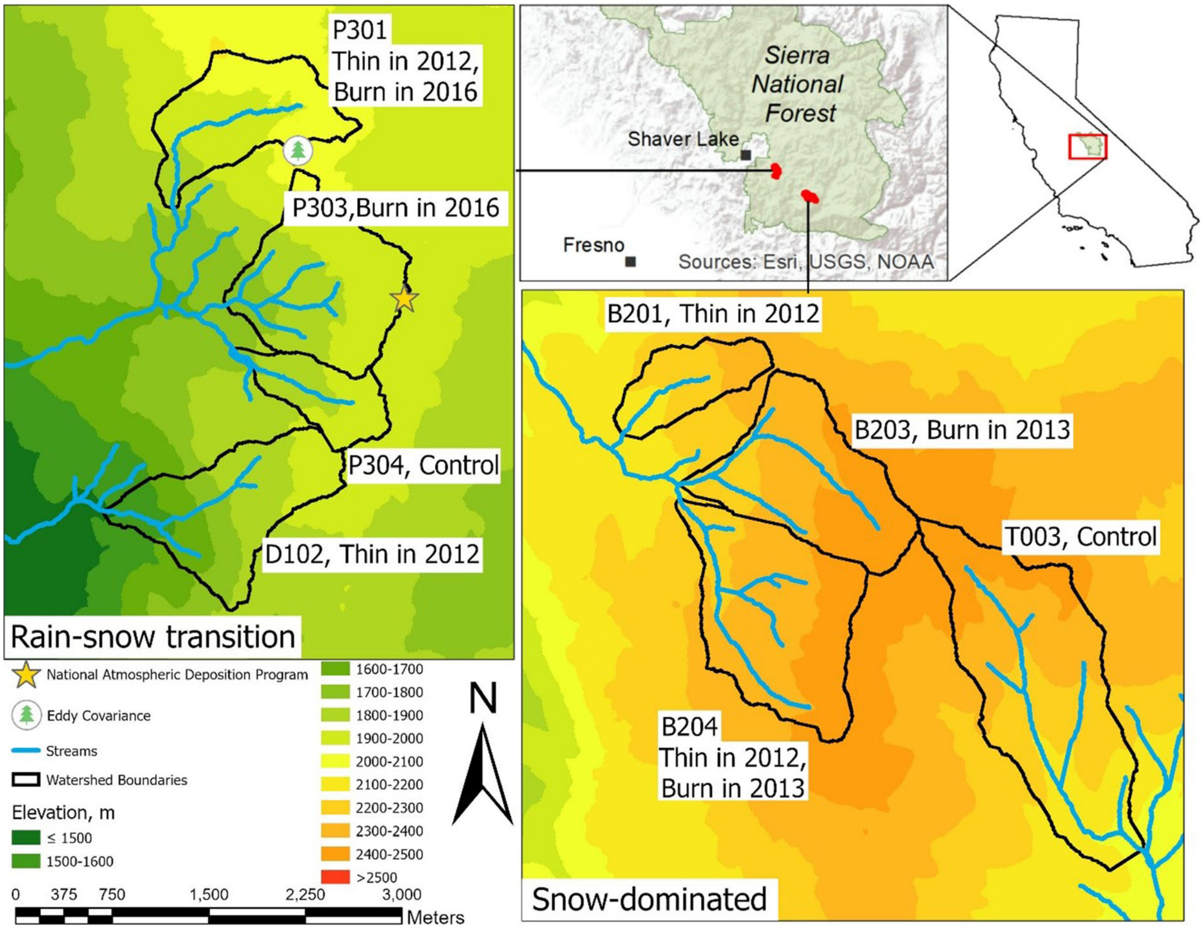

Fig. 1 Location of eight watersheds at the rain-snow transition and snow-dominated sites at the Kings River Experimental Watersheds. The map shows the elevation designated by green to orange colors, denoting low to high elevations, respectively. Atmospheric nitrogen deposition (star symbol; National Atmospheric Deposition Program) and ecosystem carbon exchange rates (tree symbol; eddy flux) were measured at the rain-snow transition site. Forest thinning was applied in 2012 to two watersheds at each site (B201 and B204 at the snow-dominated site and P301 and D102 at the transition site). Prescribed burns were applied to two watersheds at the snow-dominated site (B203 and B204) in 2013 and two watersheds at the transition site (P301 and P303) in 2016. The delayed application of the prescribed burns within the ''thin and burn'' and ''burn only'' treatments at the transition site allowed us to include the P301 watershed as an additional ''thin only'' treatment and the P303 watershed as an additional control in the analysis of data from water year 2003–2015

fir (*Abies concolor* (Gordon) Lindl. ex Hildebr.) and incense cedar (*Calocedrus decurrens* (Torr.) Florin) based on the proportion of the total stand basal area (Table 1). Overstory vegetation at the snow-dominated site is dominated by red fir (*Abies magnifica* A. Murray bis) and white fir (Lydersen et al. 2019).

In summer and fall 2012, thinning treatments were applied in two watersheds each at the transition (P301, D102) and snow-dominated sites (B201, B204). Prescribed burns were applied to two watersheds at the transition site in 2016 (P301 and P303) and two watersheds at the snow-dominated site in 2013 (B203 and B204) to ultimately generate a thin only, burn only, thin and burn, and control watershed at each site. The burned watersheds were excluded from this study because stream nutrient concentrations were not measured after water year (WY) 2015; however, the delayed application of the prescribed burns at the transition site allowed us to include the P301 watershed as an additional thin only treatment, and the P303 watershed as an additional control during the study period of WY 2004–2015 (Table 1). The snow-dominated site had one watershed as a control (T003). Experimental treatments were assigned based

Table 1 Mean elevation, watershed area, and tree composition in the eight watersheds at the Kings River Experimental Watersheds (watersheds ordered from the highest to the lowest elevation)

Site	Watershed	Mean elevation, m	Area, ha	Species composition prior to drought and thinning, % basal area	Treatment assignment during a drought period (water year 2013–2015)
Snow-dominated	B203	2373	138	78% ABMA, 15% ABCO, 3% PICO, 3% PIJE and PIPO, 1% PILA	Not used due to a burn treatment in 2013
	B204	2365	167	93% ABMA, 6% ABCO, 1% PILA	Not used due to a burn treatment in 2013
	T003	2289	228	52% ABCO, 42% ABMA, 3% PILA, 2% CADE	Control
	B201	2257	53	57% ABMA, 22% ABCO, 11% PILA, 10% PICO	Thinned
Rain-snow transition	P301	1979	99	46% ABCO, 29% CADE, 23% PILA, 2% PIJE and PIPO	Thinned
	P303	1905	132	51% ABCO, 42% CADE, 7% PILA	Control
	P304	1899	49	49% ABCO, 33% CADE, 18% PILA	Control
	D102	1782	121	33% CADE, 30% ABCO, 22% PILA, 13% PIJE and PIPO, 2% QUKE	Thinned

Percent species composition by basal area represented the pretreatment conditions for trees ≥ 1 cm diameter at breast height (~ 1.4 m). Species codes are ABCO, white fir (*Abies concolor* (Gordon) Lindl. ex Hildebr.); ABMA, red fir (*Abies magnifica* A. Murray bis); CADE, incense cedar (*Calocedrus decurrens* (Torr.) Florin); PICO, lodgepole pine (*Pinus contorta* Loudon ssp. *murrayana* (Grev. & Balf.) Critchf.); PILA, sugar pine (*Pinus lambertiana* Douglas); PIJE, Jeffrey pine (*Pinus jeffreyi* Balf.); PIPO, ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson); QUKE, black oak (*Quercus velutina* Lam.). Treatment assignment is shown for the six of the eight watersheds used to examine the impact of drought and thinning on stream nutrient export

on forest conditions and habitat for wildlife species of concern (Lydersen et al. 2019). Thinning treatments in mature stands were conventional timber harvest (i.e., chainsaw-felling, slash left in the stand, logs skidded to a landing) that removed trees across all diameter classes to a target basal area of 27–55 m^2 ha^{-1} (target basal areas varied by predetermined aspect and topographic position classes; Lydersen et al. 2019). California black oak (*Quercus kelloggii* Newb.), sugar pine (*Pinus lambertiana* Douglas), and ponderosa pine were retained preferentially. Trees removed from US National Forest land had a maximum Diameter at Breast Height (DBH, ~ 1.4 m) of 76 cm, but some trees up to a DBH of 117 cm were cut on a portion of privately owned land within the thinned watersheds at the transition site. Thinning treatments in young (< 30 years old) and even-aged stands were precommercial, and shrub cover was reduced to below 10% by mastication in stands with shrub cover > 50%. Approximately 10–25% of the area planned for thinning (or mastication) within thinned watersheds was excluded from operation due to slope steepness (generally > 30% slope) and lack of existing roads (especially in D102).

From 2012 to 2016, California experienced a historic multi-year drought, with near-record low precipitation combined with above-average temperatures (Diaz and Wahl 2015; Robeson 2015). Comparing the climatic conditions during the drought period (WY 2013–2015) to the non-drought period (WY 2004–2011) at KREW, mean annual temperature (± standard deviation, SD) increased from 9.4 ± 0.7 to 10.6 ± 0.6 °C at the transition site, and from 7.1 ± 0.6 to 8.1 ± 0.5 °C at the snow-dominated site (Hunsaker and Safeeq 2018; Yang et al. 2021). Mean annual precipitation decreased from 1438 ± 516 to 755 ± 192 mm $year^{-1}$ at the transition site, and from 1450 ± 510 to 809 ± 189 mm $year^{-1}$ at the snow-dominated site (Hunsaker and Safeeq 2018; Yang et al. 2021). The drought also contributed to extensive forest mortality at KREW, ranging from a 12–44% reduction in tree basal area observed across the eight watersheds (Lydersen et al. 2019).

Atmospheric nutrient inputs

We acquired the net ecosystem C exchange (NEE) measured every half hour in years prior to drought and thinning (WY 2010–2012) from the eddy covariance flux tower at the transition site (https://www.ess.uci.edu/~california/; Fig. 1). Ecosystem respiration (ER) was determined as the y-intercept of a linear fit to the half-hour NEEs during turbulent periods where incoming solar radiation was less than 200 W m^{-2}. The half-hour gross ecosystem C exchange (GEE) was calculated as the difference between observed NEE and ER. Gross primary production (GPP) and net ecosystem production (NEP) were the annual cumulative GEE and NEE, respectively (Goulden et al. 2012; Kelly 2014). We reported the pre-drought GPP and NEP by averaging annual values in WY 2010–2012. Net ecosystem C exchange was not measured at the snow-dominated site. However, annual rates of GPP and ER were correlated to elevation based on the eddy covariance measurements at the transition site and three additional elevation sites on the same western slope of southern Sierra Nevada (Supplementary Fig. S1). Hence, we estimated the annual rates of GPP and ER at the snow-dominated site based on regression equations between these variables as a function of elevation and the mean elevation of that site (2320 m). At the snow-dominated site in years prior to drought and thinning, the estimated mean annual GPP and ER were 9452 and 2631 kg ha^{-1} year^{-1}, respectively, resulting in a mean annual NEP of 6821 kg ha^{-1} year^{-1}.

The annual rate of total atmospheric N deposition in years before drought and thinning (WY 2009–2012) was acquired from the National Atmospheric Deposition Program (http://nadp.slh.wisc.edu/committees/tdep/tdepmaps/) using coordinates of the two sites. Atmospheric dry deposition of P was measured by collecting dust samples at the transition site in summer 2014 using passive collectors (Aciego et al. 2017). Annual rate of total P deposition was then calculated as 1.6 times the dry deposition rate based on measurements at a similar elevation in the Sierra Nevada, 68 km away (i.e., the Lower Kaweah monitoring station at 1905 m, Vicars and Sickman 2011). We assumed the snow-dominated site and the transition site had similar rates of atmospheric P deposition, as atmospheric P deposition was similar at another two mixed-conifer sites along the western slopes of the Sierra Nevada (approximately 0.15 kg ha^{-1} year^{-1}, Jassby et al. 1994; Vicars and Sickman 2011).

Stream nutrient export in dissolved forms

Stream water grab samples were collected manually every two weeks in each watershed from the two sites in years prior to drought and thinning (WY 2004–2011) and in years during drought and after thinning (WY 2013–2015), with one sample from each month used for chemical analyses and the other for archiving. Concentrations of dissolved inorganic N (DIN) and dissolved inorganic P (DIP, orthophosphate) were determined for samples collected in all watersheds at the Forest Service's Riverside Fire Sciences Laboratory, Riverside, California. We acquired concentrations of DIN and DIP in those years from Hunsaker and Padgett (2019). Concentrations of total dissolved N (TDN) and DOC were determined for samples collected in all watersheds in WY 2009 and 2010, and six watersheds in WY 2013–2015 (Table 1). We acquired these datasets from Yang et al. (2021), and calculated DON concentration by subtracting DIN from TDN.

Concentrations of dissolved inorganic C (DIC) were not measured. We estimated DIC concentrations using measured DOC concentrations and the equation: [DIC mg L^{-1}] = − 0.38*[DOC mg L^{-1}] + 10.03 (n = 740, $p < 0.01$, $R^2 = 0.15$). We developed this equation based on the measured concentrations of stream DIC and DOC in Santa Catalina Mountains in Arizona, USA from WY 2010–2017 (Chorover et al. 2020), where the streams drained granitoid watersheds similar to those within the KREW. From the Santa Catalina dataset, we chose 740 observations with DOC concentrations ranging from 1 to 10 mg L^{-1}, similar to the range of DOC concentrations from our sites (Yang et al. 2021). Concentrations of DOP were not measured; hence, we estimated DOP to be one-third of DIP concentrations, based on a study of 20 streams (second- and third-order streams) in California's Central Valley derived from the headwater basins (zero- and first-order streams) in the Sierra (Sobota et al. 2011). Stream discharge rates (L s^{-1}) were measured in all watersheds, using a combination of nested flumes and weirs (Hunsaker et al. 2012; Safeeq and Hunsaker 2016). We calculated the annual stream export of each dissolved solute by multiplying the concentration by the monthly discharge rate (weighted by watershed area, mm year^{-1}), and then summed these values for each water year, for each watershed.

Stream nutrient export in particulate forms

Particulate materials (i.e., suspended and bedload sediments) were collected in each watershed from the two sites in years prior to drought and thinning (WY 2005–2011) and in years during drought and after thinning (WY 2013–2015). Suspended sediments were measured using a combination of bi-weekly manual and automated sampling methods (Teledyne ISCO, Lincoln, NE, USA), with the latter triggered by a combination of stage and turbidity thresholds periodically adjusted to account for seasonal variation of the water table; thresholds were higher in winter and lower in summer. Water samples were processed for suspended sediment concentration (mg L^{-1}) using vacuum filtration with 1 μm glass fiber filters (Hunsaker 2007). Bedload sediments, including coarse mineral material (> 2 mm) and fine organic matter (< 2 mm), were captured in settling ponds constructed downstream from the water discharge measurements once a year. Bulk bedload sediments were then dried and weighed in the laboratory. Multivariate suspended sediment concentration–discharge rating curves for each watershed (adjusted R^2 between 0.53, [$n = 71$, watershed P301] and 0.75 [$n = 86$, watershed T003]) were applied to create a continuous record of sediment flux to calculate annual sediment yields (Safeeq et al. 2018).

We acquired concentrations of particulate C (PC) and particulate N (PN) in years prior to drought and thinning (WY 2005–2011) using the measurements of bedload sediments from Stacy et al. (2015). Concentrations of PC and PN were not measured in years during drought and after thinning (WY 2013–2015). We estimated concentrations (%) in unthinned watersheds in years during the drought period using the measured annual discharge rate (mm year^{-1}) and the linear relationships between discharge rate and concentrations based on the pre-disturbance dataset (n = 7 water years) for each site (the transition site: [PC] = − 0.0106*[annual discharge] + 12.7780 ($p < 0.01$, $R^2 = 0.78$), [PN] = − 0.0004*[annual discharge] + 0.5157 ($p = 0.02$, $R^2 = 0.71$); the snow-dominated site: [PC] = − 0.0067*[annual discharge] + 12.1730 ($p = 0.04$, $R^2 = 0.62$), [PN] = − 0.0003*[annual discharge] + 0.5290 ($p = 0.08$, $R^2 = 0.48$)). Concentrations of particulate P (PP) were not measured in this study and were estimated as two times the DIP concentrations on a volumetric basis (mg L^{-1}; based on the study of 20 streams in California's Central Valley, Sobota et al. 2011). We calculated the annual stream exports for PC and PN by multiplying concentration by the annual sediment yield (kg ha^{-1} year^{-1}) in the eight watersheds in those years. Annual stream export of PP was calculated using the estimated concentrations (mg L^{-1}) multiplied by annual discharge rate (weighted by watershed area, mm year^{-1}) in years prior to drought and thinning (WY 2004–2011).

Nutrient concentrations and pools in tree biomass

Tree survey plots (10 m × 20 m) were established in the upland of each watershed within the two sites based on the stream length and watershed size, resulting in 10–20 plots per watershed (Dolanc and Hunsaker 2017). Within each plot, all live trees with diameters > 1 cm at DBH were measured and identified for species annually from 2003 to 2006 prior to drought and thinning (Dolanc and Hunsaker 2017). Total aboveground biomass (AGB) was calculated using species-specific allometric equations (Matchett et al. 2015) based on the DBH measured for the eight main species (Table 1). Biomass of foliage, branches, stem bark, stem wood, coarse roots, and fine roots were then calculated based on their proportions to AGB developed for each species (Jenkins et al. 2003 for aboveground components and Chojnacky et al. 2014 for coarse and fine roots).

We collected fully developed leaves from 6 to 12 individuals (i.e., field replicates) of four species found at our research sites (i.e., black oak, Jeffrey pine, ponderosa pine, and lodgepole pine; Barnes 2020). Green leaves were collected from the outer, sunlit portion of the upper third crown of each individual and composited to measure C concentration using dry combustion in an elemental analyzer (Costech Analytical ECS 4010 Elemental Analyzer, Costech Analytical Technologies, Inc., Valencia, CA). Concentrations of N and P in composite samples were measured using the Kjeldahl digestion with a Lachat AE Flow Injection Auto Analyzer (Methods 13-107-06-2-D and 13-115-01-1-B, Lachat Instruments, Inc., Milwaukee, WI, USA). We did not sample green leaves for incense cedar, sugar pine, white fir and red fir. Hence, we used foliar concentrations of C, N, and P reported from the literature for these unmeasured species (Supplementary Table S1). Woody components were not sampled for determining nutrient concentrations. We considered C concentrations to be 50% in all woody components of all tree species (Fahey et al. 2005), and used N and P concentrations in these tree components from the literature (Supplementary Table S1). Nitrogen and P concentrations in woody components without actual measurements or that were unavailable from the literature were estimated as the mean value of available conifer species for each component. Nutrient pools in tree biomass were estimated by multiplying nutrient concentrations of biomass components by the mass of these components. We summed the nutrient content of all trees within a plot, and averaged plots for each watershed (kg ha^{-1}). Mean annual nutrient pool in tree biomass was reported as the average value of four watersheds over the four years for each site.

Nutrient concentrations and pools in soils

Quantitative soil pits (7–12 per watershed based on area) were excavated at the two sites in 2004 prior to drought and thinning. At each soil pit, surficial organic horizons (i.e., O) were collected in paper bags using a ring (0.0638 m^2), and mineral horizons were sampled down to 1 m depth. Soils in organic horizons were measured for mass and concentrations of total N and total P. Soils in mineral horizons < 2 mm were measured for mass, concentrations of total C, total N, and Bray-extractable P (2 g soil in 20 mL of 0.5 M HCl plus 1 M NH_4F, Johnson et al. 2011). Concentrations of total C and total N were analyzed using a dry combustion C and N analyzer (LECO, St. Joseph, MI). Bray-P concentrations were analyzed colorimetrically on a Gilford Stasar III, Visible Spectrophotometer. We did not measure total C concentrations in organic horizons from the soil pits; instead, we used concentrations measured in 2011 for pool calculations (Stacy et al. 2015), where total C concentrations in organic horizons were measured in one watershed at the transition site (P303) and one watershed at the snow-dominated site (B203).

Analyses of datasets prior to drought and thinning

We compared stream nutrient export, nutrient pools in tree biomass and soils, and nutrient stoichiometric ratios between the two sites to provide insights of potential warming effects, using measurements in years prior to drought and thinning (WY 2004–2011). We calculated the mean and SD of annual stream export for nutrients in dissolved and particulate forms (i.e., DOC, DIC, PC, DON, DIN, PN, DOP, DIP, PP) using a Monte Carlo simulation. Briefly, at each site, we randomly sampled one value of annual stream export across four watersheds and in different years for 1000 iterations, and then calculated the mean and SD. The mean annual export of total C, N, and P were calculated as the sum of its components (i.e., dissolved organic, dissolved inorganic, particulate), and errors were propagated assuming that they were independent and normally distributed (Taylor 1997). Next, we calculated the stoichiometric mass ratios of C, N, and P in organic horizons, mineral horizons, and stream water in each watershed. We compared these values between the two sites using two-sample t-tests, with watersheds serving as replicates.

Data analyses for studying the impact of drought and forest thinning

We examined the impacts of drought alone and drought combined with thinning on stream export of measured nutrients, including DOC, DON, DIN, DIP, PC, and PN. We grouped the two sites for these analyses because of the limited replicates: one control and one thinned watersheds at the snow-dominated site and two control and two thinned watersheds at the transition site. To examine the impact of drought alone, we compared annual stream export of nutrients in control watersheds (i.e., P303, P304, T003) in years prior to drought (WY 2004–2011) to those during the drought period (WY 2013–2015). We used two-sample t-tests to identify the differences in annual export between pre-drought and drought periods, with watersheds across years within each period serving as replicates. To examine the impact of drought combined with thinning on stream nutrient export, we used a Before-After-Control-Impact framework in linear mixed-effects models (BACI; Smith 2014). This framework compared differences between the control and thinned watersheds during the drought period after "normalizing" these differences prior to drought and thinning. Briefly, the class variables *CI* (Control for three control watersheds and Impact for three thinned watersheds, Table 1) and *BA* (Before for WY

2004–2011 and After for WY 2013–2015) and their interaction term ($CI \times BA$) were included as fixed effects, while the actual *watersheds* and *water years* were random effects. A significant interaction term implies changes in stream export of nutrients occur in the thinned watersheds but not in the control watersheds.

For statistical comparisons above, all values were log-transformed to meet the assumption of normality and homoscedasticity of the residuals. All statistical analyses were conducted in SAS 9.4 (SAS Institute, Inc. 2013). We used an a priori alpha level of 0.10 to evaluate statistical significance because of the great variation typically found in field studies (Amrhein et al. 2019).

Results

Stream export of C, N, and P prior to drought and thinning

Stream export of total C was similar at the transition and snow-dominated sites, with respective fluxes of 89 ± 32 and 98 ± 11 kg ha^{-1} year^{-1} (mean and SD of Monte Carlo simulation) corresponding to 1% of the NEP at each site (Fig. 2a). The proportion of PC to total C stream export at the transition site was twice that at the snow-dominated site, with respective fluxes of 52 ± 31 and 26 ± 9 kg ha^{-1} year^{-1} (58% and 27%) as PC, 23 ± 4 and 52 ± 5 kg ha^{-1} year^{-1} (26% and 53%) as DIC, and 14 ± 3 and 20 ± 3 kg ha^{-1} year^{-1} (16% and 20%) as DOC.

Stream export of total N was greater at the transition site than the snow-dominated site, with respective fluxes of 3.2 ± 1.5 and 1.6 ± 0.4 kg ha^{-1} year^{-1} corresponding to 40% and 21% of atmospheric N deposition, respectively (Fig. 2b). At both sites, approximately two-thirds of total N stream export was as PN. Fluxes for the transition and snow-dominated sites were 2.1 ± 1.4 and 1.0 ± 0.3 kg ha^{-1} year^{-1} (66% and 63%) as PN, 1.0 ± 0.5 and 0.4 ± 0.1 kg ha^{-1} year^{-1} (31% and 25%) as DON, and 0.1 ± 0.0 and 0.2 ± 0.1 kg ha^{-1} year^{-1} (3% and 12%) as DIN.

Stream export of total P was similar at the transition and snow-dominated sites, with respective fluxes of 0.22 ± 0.06 and 0.19 ± 0.03 kg ha^{-1} year^{-1}, comparable to atmospheric P deposition (0.17 kg ha^{-1} year^{-1} at both sites; Fig. 2c). At both sites, approximately 60% of total P stream export was as PP. Fluxes for the transition and snow-dominated sites were 0.13 ± 0.05 and 0.11 ± 0.03 kg ha^{-1} year^{-1} (60% and 58%) as PP, 0.07 ± 0.03 and 0.06 ± 0.01 kg ha^{-1} yr^{-1} (32% at both sites) as DIP, and 0.02 ± 0.01 and 0.02 ± 0.00 kg ha^{-1} year^{-1} (8% and 10%) as DOP.

Nutrient pools and stoichiometric ratios prior to drought and thinning.

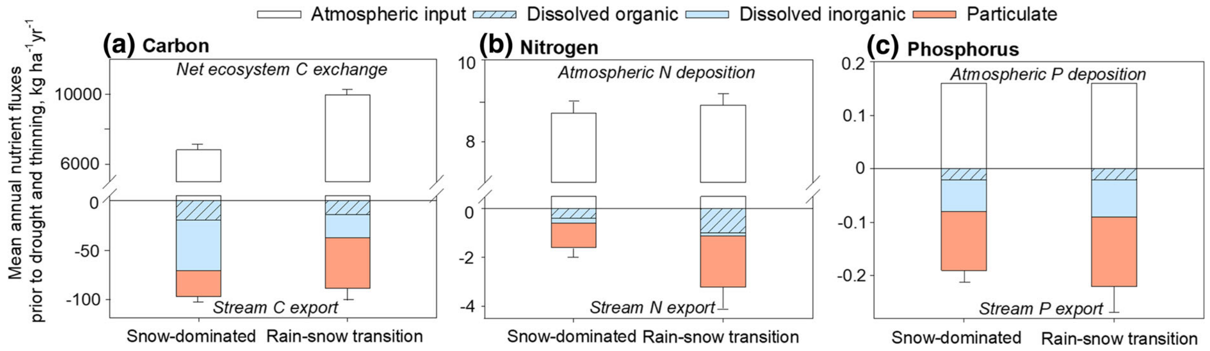

Fig. 2 Potential climatic impact (comparison of snow-dominated site vs. rain-snow transition site) on atmospheric input and stream export for **a** carbon (C), **b** nitrogen (N), and **c** phosphorus (P) at the Kings River Experimental Watersheds. Stream export of nutrients were reported in forms of dissolved organic, dissolved inorganic, and particulate. Based on Monte Carlo simulations, the transition site had similar export of total C and P but twice the export of total N in stream water compared to the snow-dominated site. Error bars for stream nutrient export were standard deviations of 1000 iterations of annual export averaging four watersheds at each site using Monte Carlo simulations. Error bars for net ecosystem C exchange and atmospheric N deposition were standard deviations of three water years (WY 2010–2012, see methods for details). Atmospheric P deposition was only available in one water year (WY 2014)

The tree biomass C pool was 39% less at the transition versus snow-dominated site, with respective values of 100.4 ± 20.9 and 160.8 ± 56.5 Mg ha^{-1} (mean annual value and SD of four years, Fig. 3a, p = 0.09). Tree biomass N pool was similar between the two sites ($p = 0.22$), and tree biomass P pool was 50% lower at the transition versus snow-dominated site ($p = 0.01$; Fig. 3b and c). The total N pool in mineral horizons was 12% lower at the transition than snow-dominated site, with respective values of 5.77 ± 0.61 and 6.57 ± 0.53 Mg ha^{-1} (mean value and SD of four watersheds, $p = 0.09$, Fig. 3b). Bray-P pool in mineral horizons was 103% greater at the transition site than at the snow-dominated site, with respective values of 0.27 ± 0.03 and 0.11 ± 0.03 Mg ha^{-1} ($p = 0.01$, Fig. 3c). The two sites had similar amounts of total C, total N, and total P in organic horizons and similar amounts of total C in mineral horizons ($p \geq 0.11$, Fig. 3).

Nutrient stoichiometric mass ratio in soils and stream water varied between the two sites. The transition site had lower ratios of total N:total P in organic horizons, total C:Bray-P, and total N:Bray-P in mineral horizons, and DIN:DIP in stream water than the snow-dominated site ($p \leq 0.03$, Table 2). The two sites had similar ratios of total C:total N in mineral horizons, and DOC:DON, TDN:TDP, and PC: PN in stream water ($p \geq 0.17$).

Nutrient fluxes under drought and after thinning

Comparing a drought with a non-drought period, stream export in control (not thinned) was approximately 89% lower for DOC, PC, and PN (, $p < 0.01$ for all three nutrients), and 78% lower for DON and DIN ($p = 0.07$ for DON and $p < 0.01$ for DIN, Fig. 4). However, stream export of DIP was similar prior to and during the drought period in control watersheds ($p = 0.15$, Fig. 4d). During drought, stream exports of DOC, DON, DIN, DIP, PC, and PN from control watersheds were similar to those observed from the thinned watershed, based on the BACI analysis ($p \geq 0.43$, Supplementary Fig. S2).

Discussion

Importance of sediment export to stream nutrient losses

Large fractions of total C, total N, and total P in stream export were in particulate forms prior to drought and thinning (43%, 65%, and 58% averaging two sites, respectively), suggesting that sediment export contributes significant amounts to forest nutrient losses. The mixed-conifer forests in the Sierra Nevada experience a Mediterranean-type climate with little

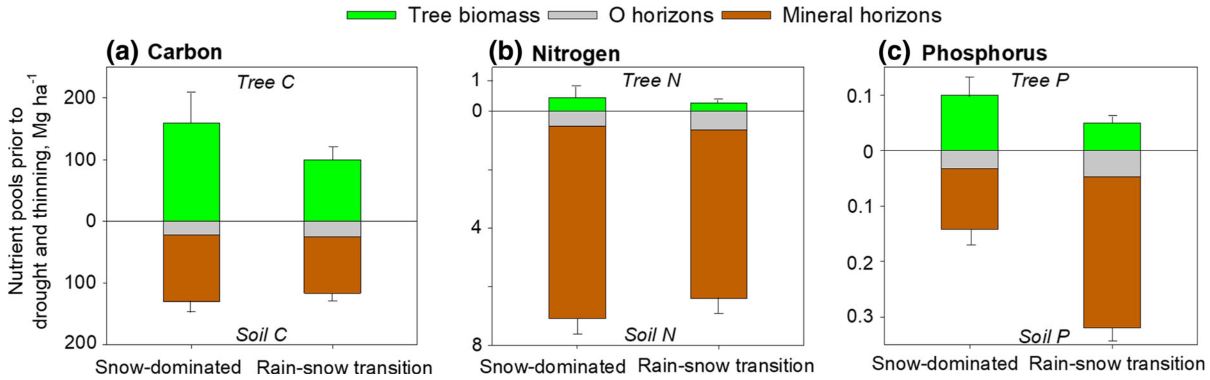

Fig. 3 Potential climatic impact (comparison of snow-dominated site vs. rain-snow transition site) on tree biomass and soil contents of **a** carbon (C), **b** nitrogen (N), and **c** phosphorus (P) at the Kings River Experimental Watersheds. Based on two-sample t-tests with watersheds serving as replicates, the transition site had lower biomass contents of total C ($p = 0.09$) and P ($p = 0.01$), lower mineral soil contents of total N ($p = 0.09$), and greater mineral soil contents of Bray-P ($p = 0.01$) compared to the snow-dominated site. Error bars for tree nutrient contents were standard deviations of four watersheds and four sampling years (year 2003–2006) at each site. Error bars for soil nutrient contents were standard deviations of four watersheds at each site; soil measurements only occurred in year 2004. Phosphorus concentration was measured as total P in the organic horizon and Bray-extractable P in the mineral horizons (2 g soil in 20 mL of 0.5 M HCl plus 1 M NH_4F, Johnson et al. 2011)

Table 2 Potential impact of climate (comparison of snow-dominated site vs. rain-snow transition site) on nutrient stoichiometric mass ratios in soils and streams at the Kings River Experimental Watersheds

Site	Watershed	Organic horizons	Mineral horizons			Stream water			
		Total N:Total P	Total C:Total N	Total C:Bray-P	Total N:Bray-P	DOC:DON	DIN:DIP	TDN:TDP	PC:PN
Snow-dominated	B203	14.8	17.6	953.5	54.1	41.5	4.2	5.7	28.1
	B204	14.9	17.4	764.5	43.9	23.1	6.0	11.5	25.5
	T003	16.4	20.6	1711.5	82.9	41.0	3.4	7.8	25.6
	B201	17.9	13.5	1180.0	87.4	34.2	3.3	10.5	17.6
	Mean and standard deviation	**16.0 ± 1.5**	17.3 ± 2.9	**1152.4 ± 409.6**	**67.1 ± 21.4**	34.9 ± 8.6	**4.2 ± 1.3**	8.9 ± 2.6	24.2 ± 4.6
Rain-snow transition	P301	12.4	19.2	422.7	22.1	15.5	1.4	16.4	25.6
	P303	13.9	18.6	419.5	22.5	18.1	1.7	10.0	25.7
	P304	14.0	16.1	321.3	20.0	49.2	2.2	4.0	24.2
	D102	14.3	15.3	359.9	23.5	7.9	1.4	29.7	24.5
	Mean and standard deviation	**13.6 ± 0.9**	17.3 ± 1.9	**380.8 ± 49.1**	**22.0 ± 1.5**	22.7 ± 18.2	**1.7 ± 0.4**	15.0 ± 11.0	25.0 ± 0.8

Values in bold indicate significant differences between the two sites based on two-sample t-tests with watersheds as replicates (n = 4). Nutrient codes are total C (carbon), total N (nitrogen), total P (phosphorus), Bray-P (Bray-extractable phosphorus using 2 g soil in 20 mL of 0.5 M HCl plus 1 M NH_4F), DOC (dissolved organic carbon), DON (dissolved organic nitrogen), DIN (dissolved inorganic nitrogen), DIP (dissolved inorganic phosphorus), TDN (total dissolved nitrogen), TDP (total dissolved phosphorus), PC (particulate carbon), and PN (particulate nitrogen)

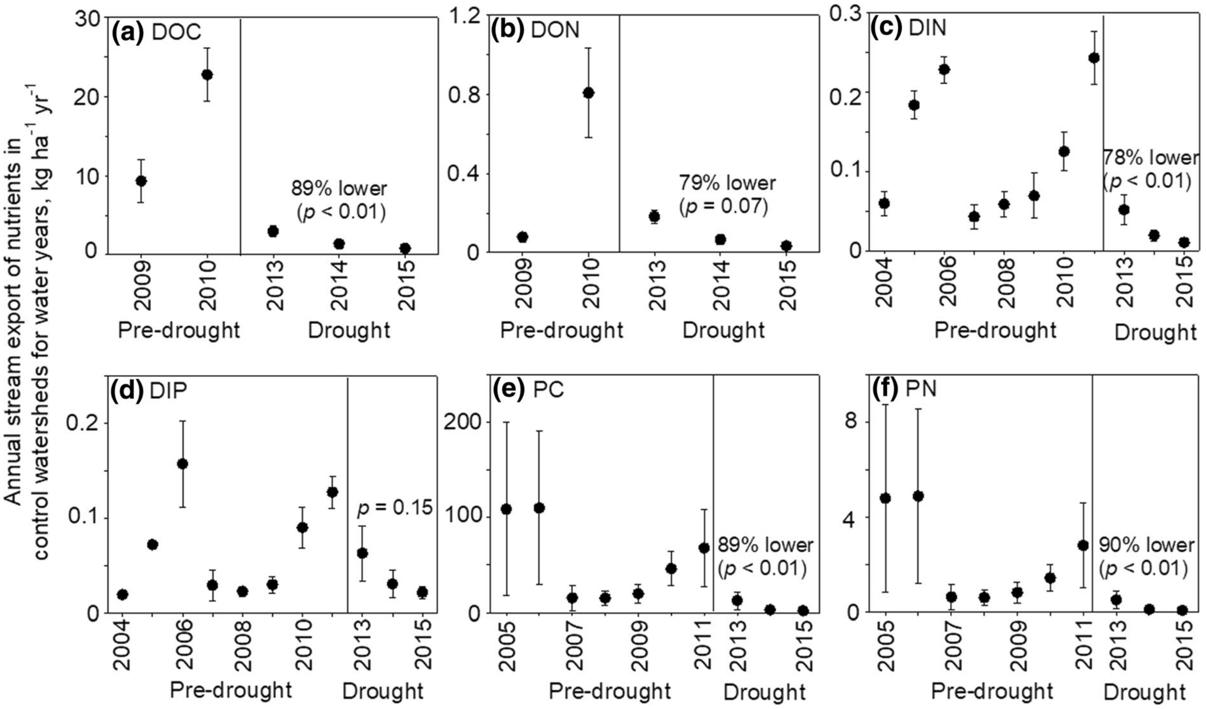

Fig. 4 Drought impact on annual stream exports of **a** DOC (dissolved organic carbon), **b** DON (dissolved organic nitrogen), **c** DIN (dissolved inorganic nitrogen), **d** DIP (dissolved inorganic phosphorus), **e** PC (particulate carbon), and **f** PN (particulate nitrogen) in control watersheds (unthinned) at the Kings River Experimental Watersheds. Differences in annual stream export of nutrients between pre-drought (water year (WY) 2004–2011) and drought periods (WY 2013–2015) were examined using two-sample t-tests with measurements in control watersheds (i.e., P303, P304, T003) across water years within each period serving as replicates (indicated by p values and percent change, if significant, within each panel). Error bars were standard errors of three watersheds within each water year

precipitation during the summer months, resulting in warm and dry soils. This antecedent dry condition before infrequent and often intense precipitation events during the winter season pose a high risk of erosive events and flooding (Zuazo et al. 2006; Panagos et al. 2015). However, in the subalpine/alpine forests in the Sierra (Sickman et al. 2001), stream export of PN was < 15% of total N export, much lower than proportions at our sites (66% at the transition site and 63% at the snow-dominated site). The lower amount of PN in stream water reported by Sickman et al. (2001) compared to our values can be attributed to lower erosion rates at higher elevations with bare-rock landscapes (Aciego et al. 2017). In most mature and intact temperate forests, particulate nutrients are commonly a small fraction of the total stream export (e.g., 30% for C, Argerich et al. 2016; 36% for N, Vanderbilt et al. 2003; 33% for P, Kunimatsu et al. 2001). Bormann et al. (1974) concluded that sediment export is negligible in intact and mature humid forests mainly because of the biotic protection during water flows. Unlike temperate forests in relatively humid regions, soil erosion has long been recognized as an important issue in forests in Mediterranean-climate regions (Ruiz et al. 2021). Our study emphasizes that nutrient loss by soil erosion may exceed that in water-soluble forms in mountain forests with a Mediterranean-type climate.

Stream export of particulate and dissolved nutrients with warming

We observed stream export of PC and PN at the transition site to be twice that at the snow-dominated site prior to drought and thinning (Fig. 2), suggesting that C and N losses through sediment export may be amplified with warming. The greater exports of PC and PN at our warmer, transition site were driven by the higher annual sediment yield (Supplementary Fig. S3b, c); concentrations of PC and PN in stream water were similar between the two sites (Supplementary Fig. S3h, i). In subalpine forests in Switzerland, warming-induced increases in annual sediment yield have been attributed to increases in both water yield and sediment availability (Micheletti and Lane 2016), and increases in sediment availability alone (Costa et al. 2018). In the Sierra Nevada, the annual water yield was lower at the warmer, transition site in all water years (Supplementary Fig. S3a), likely due to reduced snowpack and higher evapotranspiration rates under a warmer condition (Berghuijs et al. 2014; Goulden and Bales 2014). Thus, the higher sediment yield at our warmer, transition site, mainly in wet years, was driven by increases in sediment availability alone (Supplementary Fig. S4c, S4d); Warming will likely enhance erosion rates by amplifying wet-dry cycles and flooding events (Goudie 2006; Rodeghiero et al. 2011; Swain et al. 2018). In relatively humid forests, increases in sediment export of nutrients with warming have also been projected to accompany increases in the frequency and magnitude of large storm events, which transport disproportionate amounts of sediments into streams (e.g., the Catskill Mountains in New York, Mukundan et al. 2020). Whether the forest is limited by moisture seasonally or not, sediment availability and sediment-associated nutrient losses will likely increase with warmer temperatures and similar annual precipitations.

Differences in stream export of dissolved nutrients between our two sites prior to drought and thinning may indicate a mixed hydrological and biogeochemical processes response to warming. Annual stream export of DOC was 30% lower at the transition than snow-dominated site (Fig. 2), which was driven by the lower annual water yield offsetting higher volume-weighted DOC concentrations (Supplementary Fig. S3a and d). The lower annual water yield at the warmer, transition site also offset the higher volume-weighted DIP concentrations found at this site (Supplementary Fig. S3g), resulting in similar stream exports of DIP between the two sites. However, the lower annual water yield at the transition site accompanied 19% lower volume-weighted DIN concentrations, resulted in 50% lower stream DIN export from the transition site than from the snow-dominated site (Supplementary Fig. S3c, f). These observations suggest that stream export of dissolved nutrients may decrease with warming in Mediterranean-climate regions mainly because of longer growing seasons and thus greater evapotranspiration and reduced water yield. In contrast, in relatively humid forests, increases in annual stream export of dissolved nutrients are often observed and projected with warming (Morales-Marín et al. 2018; Mukundan et al. 2020; Shogren et al. 2020). This has been attributed to no change or moderate increases in annual water yield associated with marked increases in dissolved nutrient concentrations. We observed stream export of DON at the transition site to be twice that at the snow-dominated site, which was driven by the substantially higher volume-weighted DON concentration at the transition site observed in a single water year (Supplementary Fig. S3e). Overall, changes in annual water yield and dissolved nutrient concentrations are both important to total nutrient export via streamflow with warming.

Based on our study, a climatic impact on total C losses through stream export is not a major concern regarding forest C storage in the Sierra Nevada, as stream export of total C was only approximately 1% of the NEP at both sites (Fig. 2a). The high NEPs measured at our mixed-conifer zone were because of year-round photosynthesis with relatively high nutrient availability and adequate supplies of stored water in soils (Kelly and Goulden 2016; Klos et al. 2018). A low proportion of stream C export to NEP has also been observed at H.J. Andrews Forests in Oregon (approximately 6%, Argerich et al. 2016); stream C export at the Andrews was comparable to the values at the snow-dominated site of our region (114 vs. 98 kg ha^{-1} year^{-1}, sum of DOC, DIC, and PC). In contrast, stream export of total C can reach nearly half of NEP in boreal forests where the cold climate limits net primary production (18 vs. 41 kg ha^{-1} year^{-1}, Leach et al. 2016). Thus, in non temperature-limited forests (e.g., Mediterranean and temperate), C losses from stream export are not a major component of the overall ecosystem C budget. However, it is still important to characterize stream C export in these forests to clarify their contributions to the global C budget, as stream C exports at our sites were more than half of the global mean terrestrial NEP (143 kg ha^{-1} year^{-1}, Koffi et al. 2012).

Nitrogen-Phosphorus imbalance with warming

Our study suggests that mixed-conifer montane forests may receive lower inputs of available N relative to P with warming. We observed higher concentrations and amounts of soil available P, and lower soil N:P ratios at the warmer, transition site than the snow-dominated site (Table 2, Supplementary Fig. S5g and S5h), suggesting a potential shift in the relative availability of N and P in soils with warming. In northern hardwood forests, lower exports and concentrations of stream DIN has been observed in warmer years (Sickman et al. 2001; Groffman et al. 2018), which was attributed to the observed higher decomposition rates and lower soil net N mineralization rates with warming (Durán et al. 2016; Melillo et al. 2017; Groffman et al. 2018). Similarly, we observed lower exports and volume-weighted concentrations of stream DIN at the warmer site, suggesting decreases in net N mineralization rates and available N in soils with warming. Thus, ecosystem production in the mixed-conifer zone of the Sierra Nevada will likely be influenced by a potential N-P imbalance with warming, especially if atmospheric inputs of P from the Central Valley of California and trans-Pacific sources continue to increase while atmosphere inputs of N remain stable or decline (Aciego et al. 2017).

The lower storage of N than P in soils at our transition site compared to the snow-dominated site may also be attributed to more frequent historical wildfire events with warmer and drier conditions in this region (Schwartz et al. 2015). Wildfire has been estimated to remove substantial amounts of N relative to P (Johnson and Turner 2014; Johnson et al. 2007). As climate continues to warm, increases in fire severity and frequency at higher elevations (Alizadeh et al. 2021) will likely further enhance the N deficiency in the higher elevation forests of the Sierra Nevada. However, this may be offset somewhat regionally by smaller N deficiencies at lower elevations due to less frequent and severe fire caused by reductions in vegetation productivity from water limitation (Kennedy et al. 2021). Overall, the potential N-P nutritional imbalance with warming in the Sierra Nevada will be further enhanced under disturbances such as wildfire.

Stream nutrient export during drought and after thinning

Very few studies have evaluated drought impacts on stream export simultaneously for multiple nutrient elements and nutrients in different chemical forms in forested watersheds. We observed that, although export of dissolved C and N in control watersheds both decreased during drought (Fig. 4), changes in the volume-weighted concentrations were different; DOC concentrations decreased, whereas DON and DIN concentrations slightly increased during drought (Supplementary Fig. S6d, S6e, and S6f). Similar decreases in stream export of dissolved C and N during drought were driven by the substantial reduction in annual water yield (Supplementary Fig. S6a). We observed similar DIP export prior to and during drought (Fig. 4), driven largely by the increased DIP concentrations offsetting the reduced annual water yield (Supplementary Fig. S6g). During non-drought periods, water often flows through upper soil horizons and contributes C and N mostly derived from soil organic matter to streams (Raymond and Saiers 2010; Vose et al. 2016). During a major drought period, soil–water interflow is usually limited. Still, groundwater flow continues to travel in deep regolith and contribute more nutrients such as P derived from geological weathering to streams. Thus, decreases in DOC concentrations and increases in DIP concentrations in our control watersheds during drought may be attributed to the switch of hydrologic coupling between topsoil/subsoil and streams to that between substratum and streams. We did not observe decreases in DON and DIN concentrations during drought, likely due to drought decreasing in-stream metabolism and dilution capacity to a greater degree than source supply from soils. Overall, the negative impacts of drought on nutrient concentrations and total nutrient export in streamflow may be less significant for P than for C and N due to the continued supply of P from the deep regolith.

We did not find significant changes in stream export of C, N, and P in dissolved and particulate forms in thinned watersheds compared to control watersheds during a drought period (Supplementary Fig. S2), which could be due to the limited hydrologic connections between soils (as a source) and streams, or the low-intensity thinning implemented at our sites (removal of $\sim$ 10% basal area). In contrast, increases in stream export of dissolved nutrients have been observed for high-intensity thinning (removal of $>$ 40% basal area) and in years with near-average annual precipitations (Bäumler and Zech 1999; Schelker et al. 2016). Under drought combined with thinning, increases in volume-weighted concentrations of DOC and DIN observed previously at the same sites (Yang et al. 2021) did not result in a similar increase in stream export of DOC and DIN. This is likely due to the similar annual water yield between the thinned and control watersheds during drought (63 mm year^{-1} vs. 87 mm year^{-1} averaged over three watersheds and three water years). Thus, annual water yield but not nutrient concentrations predominantly influence the total nutrient export by streamflow under disturbance.

Study limitations

Not all nutrient inputs and exports were measured in this study. For example, N inputs from biological N fixation (i.e., symbiotic and non-symbiotic) were not characterized, but these unmeasured inputs may have been significant at our study sites. At the snow-dominated site, soil patches with elevated N content have been observed and attributed to biological N fixation by actinorhizal shrubs such as *Ceanothus cordulatum* and *Ceanothus prostratus* (Erickson et al. 2005). Our transition site likely has biological N fixation rates similar to the snow-dominated site because of their similar percentages of cover and frequency for *Ceanothus* species (the dominant symbiotic N fixing genus) prior to drought and thinning (Dolanc and Hunsaker 2017). We estimated the biological N fixation at our two sites to be approximately 10.2 kg ha^{-1} year^{-1} prior to drought and 8.6 kg ha^{-1} year^{-1} following the drought, using an equation developed from a global synthesis (Cleveland et al. 1999) and measurements of ET for the entire Upper Kings River basin (43 cm year^{-1} for WY 2004–2011, Goulden et al. 2012 and 36 cm year^{-1} for WY 2016, Bales et al. 2018; [biological N fixation, kg ha^{-1} year^{-1}] = 0.234 × [annual evapotranspiration rate, ET, cm year^{-1}] + 0.172). These estimated rates were approximately 30% higher than atmospheric N deposition at our sites (8.0 and 7.7 kg N ha^{-1} year^{-1} at the transition and snow-dominated site, respectively), suggesting that biological N fixation is an important N input to mixed-conifer forests in the Sierra Nevada. Soil emission of N_2O was measured to be approximately 0.02 kg N ha^{-1} year^{-1} at the two sites (Blankinship et al. 2018). However, total N losses from soil emissions (i.e., N_2 and N_xO) were not measured at our sites. Assuming emission rates of gaseous N at our sites were similar to that at the Sierra's Emerald Lake basin (0.14 kg N ha^{-1} year^{-1}, Williams et al. 1995) that has a comparable soil types and climate, N emission losses from soils were only approximately 4% and 9% of the stream N losses at the transition site and the snow-dominated site, respectively. Thus, N losses via soil emission may not be important to the overall N balance in these ecosystems.

We did not measure P inputs to soils from rock weathering, which are known to be important to the forest P cycle (Gu et al. 2020). In a previous study at the Kings River basin, net release of total P from the regolith was estimated to be ten times higher than losses of dissolved P from stream export (Uhlig et al. 2017). However, the bedrock P input can be outpaced by dust deposition of P, at least during drought (Aciego et al. 2017; Aarons et al. 2019). Thus, measurements of P input through bedrock weathering and dust deposition are both important for studying forest P cycle given increased drought events under rising temperatures.

We collected stream water samples for chemical analyses every other week because of the difficult accessibility of these sites, particularly during winter and early spring periods with deep snowpacks. This sampling frequency likely miss some major events (e.g., storm, snowmelt) and result in biases in our estimates of stream nutrient export. Stream DIC and DOP concentrations were estimated based on our measured DOC and DIP (respectively) and empirical equations derived from the sites that have similar climatic and geological conditions. Hence, these values do not meet accuracy standards from a purely nutrient budgetary perspective. However, we use these estimations simply for comparing relative nutrient fluxes between the two elevation sites to infer the potential warming impact on these fluxes. Further, differences in nutrient fluxes and pools between the two sites may be attributed to the potential differences in historical management activities and climatic variation. Compared with the snow-dominated site, the transition site often receives more human disturbance, such as timber harvesting (Martin 2009; Hunsaker and Neary 2012). Unfortunately, the full management history in each watershed from the two sites is not well documented.

Conclusions

We used space-for-time substitution to examine warming impacts on C, N, and P cycles in California's mixed-conifer montane forests, focusing on stream nutrient export in particulate and dissolved forms and nutrient stoichiometry status. During a non-drought period, stream export of nutrients in particulate forms at the rain-snow transition site was twice that at the higher-elevation snow-dominated site despite the lower annual water yield. This suggests that sediment availability and sediment-associated nutrient losses may increase with warming. Compared with the snow-dominated site, the transition site had lower stream export of DOC and DIN, greater export of DON, and similar export of DIP, which was driven by a mixed response of water yield (hydrological) and nutrient concentrations (biogeochemical processes) to a warmer environment. We further observed higher concentrations and contents of soil P, lower mass ratios of soil N:P, and lower concentrations and total export of DIN in streams at the transition site than the snow-dominated site. These observations combined with recent findings from long-term trends in N cycles suggest that N storage and availability in temperate forests will decrease with warming, especially relative to the availability of P.

Given the strong interests in forest thinning to increase drought resiliency, we compared stream export of nutrients during a non-drought period to that following a forest thinning and during a major drought period by grouping watersheds from the two sites. In unthinned watersheds, stream export of C and N decreased, whereas P export remained similar when we compared the drought with the non-drought periods. Stream export of C and N is more sensitive to drought than P because of the limited source supply under minimal soil interflow; groundwater continues to travel in deep regolith during drought and contributes more P derived from geological weathering to streams. Stream exports of C, N, and P were similar between thinned and unthinned watersheds during drought despite differences in volume-weighted nutrient concentrations. Thinning impacts on water yield and stream nutrient export are negligible during drought because of the limited flow conditions. Our study emphasizes the importance of monitoring nutrient losses from streamflow when evaluating the potential impact of a warmer and drier climate on ecosystem nutrient cycles, and demonstrates the potential for a climate-driven N-P nutritional imbalance.

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Author contributions YY, SCH, and AAB developed the concept of this manuscript. YY, CTH, DWJ, MS, EPM, EMS, and SCH conducted laboratory analyses. CTH designed and implemented the KREW study, and CTH and DWJ contributed stream and soil chemistry data. MEB and RRB performed preliminary data analyses. YY conducted the full data analyses and drafted the manuscript. All authors contributed to revisions.

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Data availability The data that support the findings of this study are available at: https://doi.org/10.2737/RDS-2017-0037; https://doi.org/10.2737/RDS-2018-0028; https://doi.org/10.2737/RDS-2017-0040.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that there are no conflicts of interest regarding the content of this article.

Ethical approval Not applicable.

Informed consent Not applicable.

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