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Mixed-conifer understory response to climate change, nitrogen, and fire

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Abstract

California's Sierra Nevada mountains are predicted to experience greater variation in annual precipitation according to climate change models, while nitrogen deposition from pollution continues to increase. These changes may significantly affect understory communities and fuels in forests where managers are attempting to restore historic conditions after a century of altered fire regimes. The objective of this research was to experimentally test the effects of increasing and decreasing snowpack depth, increasing nitrogen, and applying prescribed fire to mixed-conifer forest understories at two sites in the central and southern Sierra Nevada. Understory response to treatments significantly differed between sites with herb biomass increasing in shrub-dominated communities when snowpack was reduced. Fire was a more important factor in post-treatment species richness and cover than either snowpack addition or reduction. Nitrogen additions unexpectedly increased herbaceous species richness. These varied findings indicate that modeling future climatic influences on biodiversity may be more difficult than additive prediction based on increasing the ecosystem's two limiting growth resources. Increasing snowpack and nitrogen resulted in increased shrub biomass production at both sites and increased herb production at the southern site. This additional understory biomass has the potential to increase fuel connectivity in patchy Sierran mixed-conifer forests, increasing fire severity and size.

Keywords: biomass, climate change, disturbance, diversity, fire, forest fuels, mixed-conifer, nitrogen deposition, Sierra Nevada

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Introduction

Global climate change is expected to have significant direct effects on terrestrial plant communities by altering temperature and precipitation conditions. It is difficult to predict how these changes will alter disturbance regimes and whether new disturbance patterns will compound or ameliorate climate changes. Predictions of plant community response to climate change have been made with different models (Miller & Urban, 1999; Bergengren *et al.*, 2001) and a limited number of field experiments in grasslands (Grime *et al.*, 2000; Shaw *et al.*, 2002; Zavaleta *et al.*, 2003). In temperate forests, most of the plant diversity is in the understory community and is strongly influenced by abiotic conditions and disturbance regime. Changes in climate and increased pollution deposition may have significant direct effects on vegetation by changing biomass and species composition, and these changes in turn can alter disturbance regimes such as fire intensity and extent. The synergy of these changes will be difficult to understand without field experiments that directly manipulate abiotic conditions, apply disturbance treatments, and follow plant response.

Water and nitrogen are the two resources most limiting plant growth in western forests (Fenn *et al.*, 1998; Witty *et al.*, 2003). Expected increases in anthropogenic CO_2 are predicted to result in increasing temperatures and greater annual variation in precipitation in California's Sierra Nevada mountain range. The variation in precipitation directly influences snowpack depth, which has implications for the timing of water release and growing season length. Coupled with these

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changes is a likely increase in nitrogen deposition resulting from fossil fuel combustion (Bytnerowicz *et al*., 1998). Some studies have found an increase in biomass production and/or net primary productivity with precipitation increase (Grime *et al*., 2000; Shaw *et al*., 2002) and a decrease in species diversity with nitrogen deposition (Zavaleta *et al*., 2003). Continuous high level nitrogen deposition also has the potential to alter N : P ratios, which may result in a shift in the limiting nutrient (Koerselman & Meuleman, 1996). A forecasted increase in late winter/early spring precipitation coupled with hotter, dry summers (Field *et al*., 1999; Kim, 2005) is likely to increase fire frequency and intensity in the Sierra Nevada (Miller & Urban, 1999). Increases in plant productivity resulting from increased precipitation and nitrogen deposition will likely yield higher fuel loads in Sierran forests. These higher fuel loads coupled with predicted hotter, dry summers provide a scenario for increased fire activity in the Sierra Nevada.

While working in Jeffrey pine (*Pinus jeffreyi*) forests of the Tahoe basin, Taylor & Beaty (2005) found that historically, fire years were associated with drought, that drought intensity influenced the extent of fires, and that years with widespread fire events were preceded by 3 years of wet conditions. Fire scar studies in the Southwest have also suggested that widely recorded fires are preceded by 1 or 2 wet years, which increase understory fuel biomass. In the mid-1980s, the western United States experienced a shift to more frequent and longer burning fires, a shift which corresponded to earlier snow melt dates (Westerling *et al*., 2006). With predicted overall drying (Brown *et al*., 2004), earlier snow melt, and warmer temperatures resulting from climate change, western forests may experience increases in seasonal severity rating (Flannigan *et al*., 2000), fire size and frequency (Fagre *et al*., 2003), and land area experiencing high to extreme fire danger (Stocks *et al*., 1998).

To date, there have been no field studies in the mixed-conifer forest of the Sierra Nevada that experimentally manipulated precipitation, nitrogen deposition, and fire. Determining how these factors will influence the forest's understory and biomass production is important not only for fuels management but also for maximizing diversity, which may increase ecosystem resilience to climate change (Noss, 2001). The objectives of this study were to determine how altered snow depth, increased levels of nitrogen deposition and fire affect mixed-conifer understory diversity and biomass production. Specific hypotheses were (1) increases in snowpack, nitrogen, and their interaction would increase both herb and shrub percent cover and biomass, (2) nitrogen treatments would decrease the number of species, and (3) fire would increase herb species richness. We focused on manipulating snowpack depth because in the Sierra Nevada it supplies almost all of the soil moisture used by plants during the growing season.

Materials and methods

Study site

This study was conducted in mixed-conifer forests at the Teakettle Experimental Forest (http://teakettle.ucdavis.edu) in the southern Sierra Nevada and at Yosemite National Park in the central Sierra Nevada at 2100 m elevation (Fig. 1). The Teakettle site comprised five principle overstory species including white fir (*Abies concolor*), red fir (*Abies magnifica*), incense cedar (*Calocedrus decurrens*), Jeffrey pine (*P. jeffreyi*), and sugar pine (*Pinus lambertiana*). The Yosemite site's five principle overstory species are the same with the exception of ponderosa pine (*Pinus ponderosa*) replacing Jeffrey pine. Of the 120 understory herbs cataloged at Teakettle alone, the most common at both the sites are *Monardella odoratissima*, *Viola pinetorum*, *Arabis repanda*, *Collinsia torreyi*, and *Kelloggia galioides* (North *et al*., 2002, personal observation). The understory at Teakettle had a larger shrub component than at Yosemite, with average plot biomass being 10 times greater than at Yosemite. Yosemite had a larger herb component averaging 2.7 times higher biomass than at Teakettle. Plots at each site were located within the same forest stand, with the maximum distance between any two plots being 1000 m. At each site, 40 potential plot locations were identified that occurred in forest gaps that were a minimum of 144 m^2 and had a maximum of 40% canopy cover (determined by averaging four moose horn measurements).

Experimental design

We used a $3 \times 2 \times 2$ full factorial design with three replicates per treatment combination at each site. The treatments included additions of nitrogen (NH_4), increases and reductions of snowpack depth, and prescribed fire. In Sierra Nevada mixed-conifer, more than 85% of the annual precipitation occurs as snow, and vegetation relies on soil moisture supplied by the winter snowpack. Thirty-six plots were established at each location and followed for 4 years; 1-year pretreatment (2003), 2 years of snowpack and N treatment (2004–2005), prescribed fire was applied to half of the plots (summer 2005) and 1 year post-treatment (2006). Plot size was determined from earlier studies at Teakettle (North *et al*., 2002, 2005a), which had suggested

No burn				Burn			
	Snowpack				Snowpack		
Nitrogen	None	Addition	Reduction	Nitrogen	None	Addition	Reduction
None	Control	+S	− S	None	Burn only	+ S	− S
Addition	+ N	+ S +N	− S+N	Addition	+ N	+ S+N	− S+N

	Treatments		
Location	Snowpack reduction	Snowpack addition	Nitrogen
Yosemite	−60%	+ 60%	+ 12 kg ha^{-1}
Teakettle	−30%	+ 30%	+ 24 kg ha^{-1}

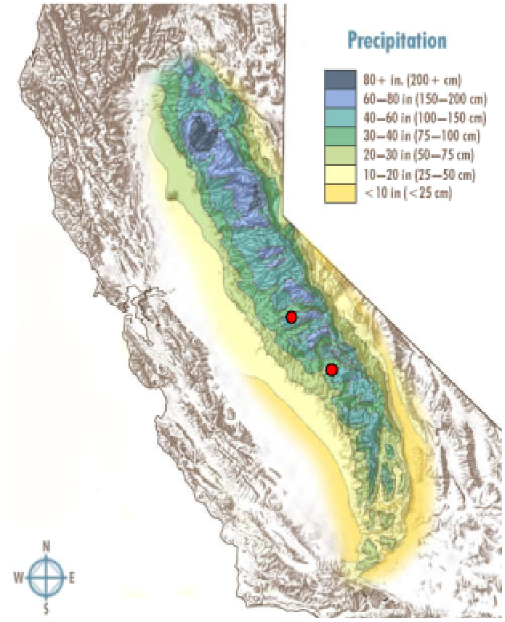

Fig. 1 California map indicating the location of the two study sites, Yosemite National Park (northern dot) and Teakettle Experimental Forest (southern dot). The upper table shows the different treatments in the experimental design and the lower table indicates treatment amounts by study site.

that understory communities were clumped between forest gaps. At our study sites, clumps varied but were generally about 100 m^2. We used 9 m × 9 m plots, which were each subdivided into nine contiguous subplots. The number of individuals by species was tallied in each subplot using a 1 m × 1 m quadrat. Percent cover of each herb and shrub species was inventoried by visual estimation of aerial cover in each subplot using a 1 m × 1 m quadrat by the same individual each year. For each of the first 3 years, two subplots were randomly selected and clipped. Dry weights were determined for herbaceous plants and shrubs for each subplot. The entire 9 m × 9 m plot was clipped during the final year. Live fuels were measured via clipping, drying (70 °C for 48 h), and weighing the biomass. Dead fuels were measured pre- and post-prescribed fire using a modified version of the US Forest Service fuel inventory system (Brown, 1974; Hurteau *et al*., 2001).

Treatments

We selected the two study locations to bracket a range of projected changes in snowpack and nitrogen deposition. The two locations have similar forest and understory vegetation but in the future will have contrasting precipitation and nitrogen conditions indicative of changes predicted to occur over the Sierra range in the next 50 years. The Yosemite site within the central Sierra is expected to have a dramatic increase in snow from more winter storms tracking down from the Pacific Northwest. The Teakettle site in the southern Sierra is expected to have a significant increase in pollution inputs but a less dramatic increase in snow. Both locations are expected to experience increased frequency of El Niño and La Niña events increasing annual variation in winter snowpack depth. The two locations were selected by comparing Sierran west slope climate (Hetch Hetchy and Huntington Lake stations, Western Regional Climate Center) and air sampling stations (Camp Mather and Shaver Lake Stations, see Fenn *et al*., 2003). These data suggest that there is a significant transition zone between the two study sites due to different predominant weather and deposition patterns. Yosemite experiences higher precipitation and lower pollution inputs typical of the northern and central Sierra, while Teakettle is typical of the drier, more polluted conditions of the southern Sierra. To bracket a range of these projected changes, a greater increase/decrease in snowpack was presumed for Yosemite and a greater nitrogen addition for Teakettle. Snowpack additions and reductions were made by measuring snowpack depth at each site during the first week in March, (following California State's Department of Water Resources sample timing). Snow was shoveled onto/off of snowpack treatment plots (plot area plus a 1 m buffer), until snowpack depth was increased/decreased by 30% (Teakettle) or 60% (Yosemite) of the average snowpack for the site. These treatment level changes were determined by examining March snow depth records for stations nearest to the field sites in El Niño and La Niña years against each station's 30-year average. Current NH_4-N deposition rates taken from the nearest sampling station to each site are $3.6\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ at Teakettle (Shaver Lake station) and $1.2\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ at Yosemite (Camp Mather station) (Fenn *et al.*, 2003). Nitrogen (NH_4) additions of 9.7 (Yosemite) and 19.4 g (Teakettle) (equivalent to 12 and $24\,\mathrm{kg\,ha^{-1}}$, respectively) were hand spread on each plot at the beginning of the growing season, following snow melt. Given the relatively short duration of our experiment, we selected ammonium over nitrate because it is more readily available to plants. Nitrogen additions were determined by examining the relationship between population growth in the Los Angeles basin and nitrogen deposition in the San Bernardino Mountains and making a conservative estimate based on population growth predictions for the Central Valley of California (Duane, 1996). Fire treatments were applied during the 2005 growing season, each plot was lit using drip torches by fire personnel at each site.

Each year, we recorded the date of complete snow melt using Hobo data loggers (Kreuzer & Ray, 2003), and measured soil moisture content for all snow-free months using time domain reflectometry (TDR, Gray & Spies, 1995). In each subplot, all vegetation was clipped at ground level, dried (70 °C for 48 h), weighed, and returned to the site. We measured N : P ratios to determine if adding nitrogen on the plots would increase this ratio, resulting in a transition to phosphorous becoming a limiting nutrient. Work by Koerselman & Meuleman (1996) found that when N : P is >16, phosphorous can become limiting. Plant nitrogen to phosphorous ratios were determined using standard methodologies (N-nitrogen gas analyzer, P-microwave acid digestion/dissolution) conducted by the U.C. Davis DANR Analytical lab.

Data analysis

Vegetation data were divided into two functional groups, herbs and shrubs. Both the functional groups were analyzed independently for treatment differences in species richness, biomass, and percent cover using a split-plot ANOVA with time as the within-subject factor. If a treatment variable was not significant, we pooled data from plots across that treatment. Targeted contrasts were made against the control for each treatment combination. We analyzed treatment as one factor with 12 levels to efficiently use the limited number of degrees of freedom and used contrasts to compare individual treatments to the control. We used Fisher's least significant difference mean separation to compare variation between years. When there was a significant time × treatment interaction, we tested the treatment effects within time. When the assumption of sphericity was violated, data were transformed using $\sqrt{X}$. In the case of shrub cover and shrub biomass at the Teakettle site, after transformation, the data still violated the sphericity assumption and significance was determined using conservative degrees of freedom (Von Ende, 2001). Differences in N : P ratios between sample years were determined using paired *t*-tests. Differences between pre- and post-prescribed fire fuel levels were determined using paired *t*-tests. Differences between post-treatment fuel levels were determined using ANOVA. Mean comparisons by treatment were made using Fisher's least significant differences mean separation.

We used multi-response permutation procedure (McCune & Grace, 2002) to test for differences in species composition between the treatments. To examine species-specific growth response to the treatments, we identified six species that were present at both the sites and on at least 80% of the plots. In this analysis only, we pooled the sites by treatment and compared pre- and post-treatment species cover using a paired *t*-test.

Results

Treatments

Paired *t*-test results for pre- and postfire fuel levels were significant ($P \leq 0.05$) for all replicates that included fire at both sites. Mean prefire fuel depths by treatment at Teakettle ranged from 6.1 to 10.3 cm and at Yosemite ranged from 5.3 to 7.5 cm. Mean postfire fuel depths by treatment at Teakettle ranged from 0.3 to 0.5 cm and at Yosemite ranged from 0.6 to 1.6 cm. There were no posttreatment differences in fuel level at either site (Teakettle: $F = 1.23$, $P = 0.3558$, df = 5; Yosemite: $F = 1.26$, $P = 0.3409$, df = 5).

Snow reduction treatments melted out an average of 5.0 days earlier than ambient snow plots at Teakettle and an average of 6.5 days earlier at Yosemite. Snow increase treatments melted out an average of 6.5 days later than ambient snow plots at Teakettle and 3.3 days later at Yosemite. For herbs, which complete their life cycle between late-May and early-July, these changes represent approximately a 10–20% increase or decrease in the growing season length. Although snowpack duration differed, there were no significant differences in soil moisture between treatments at either site.

N : P ratios were not significantly different for plots that did not include an increase in nitrogen at Teakettle (paired *t* test, $P = 0.063$) or Yosemite ($P = 0.361$). N : P ratios significantly increased in nitrogen addition plots at both Teakettle ($P = 0.008$) and Yosemite ($P = 0.019$) compared with untreated plots. At Teakettle, there was a 1.18% increase from pretreatment levels, resulting in a 6.05 : 1 ratio. At Yosemite there was a 1.26% increase from pretreatment levels, resulting in an 8.13 : 1 ratio.

When comparing herb and shrub results, we used the following abbreviations for each treatment; control (C), nitrogen (N), fire (F), nitrogen–fire (NF), snowpack increase (S+), snowpack increase–fire (S+F), snowpack increase–nitrogen (S+N), snowpack increase–nitrogen–fire (S+NF), snowpack decrease (S−), snowpack decrease–fire (S−F), snowpack decrease–nitrogen (S−N), and snowpack decrease–nitrogen–fire (S−NF).

Herbs

At both the sites, there were no significant time × treatment interactions; however, there were significant differences between years. At Teakettle, the post-treatment year was significantly different from all the other years. At Yosemite, the post-treatment year was not significantly different from the other years; however, 2005 was significantly different from 2003 (pre-treatment) and 2004. The two experimental sites had similar response in herb species richness, but had contrasting herb cover response in their controls. At Teakettle, species richness and cover increased in the control plots by 2.8% and 20.2%, respectively, between 2002 and 2006 (Fig. 2). During the same period, control richness increased and cover decreased at Yosemite by 5.4% and 22.5%, respectively (Fig. 2). At Teakettle, there was no difference in richness response between the snowpack treatments, so plots were pooled. From 2002 to 2006, species richness had significant decreases in the fire treatment ($P = 0.01$). Herb cover varied by treatment. Compared with the control, there were nonsignificant decreases in herb cover for the S+F and S+N treatments and

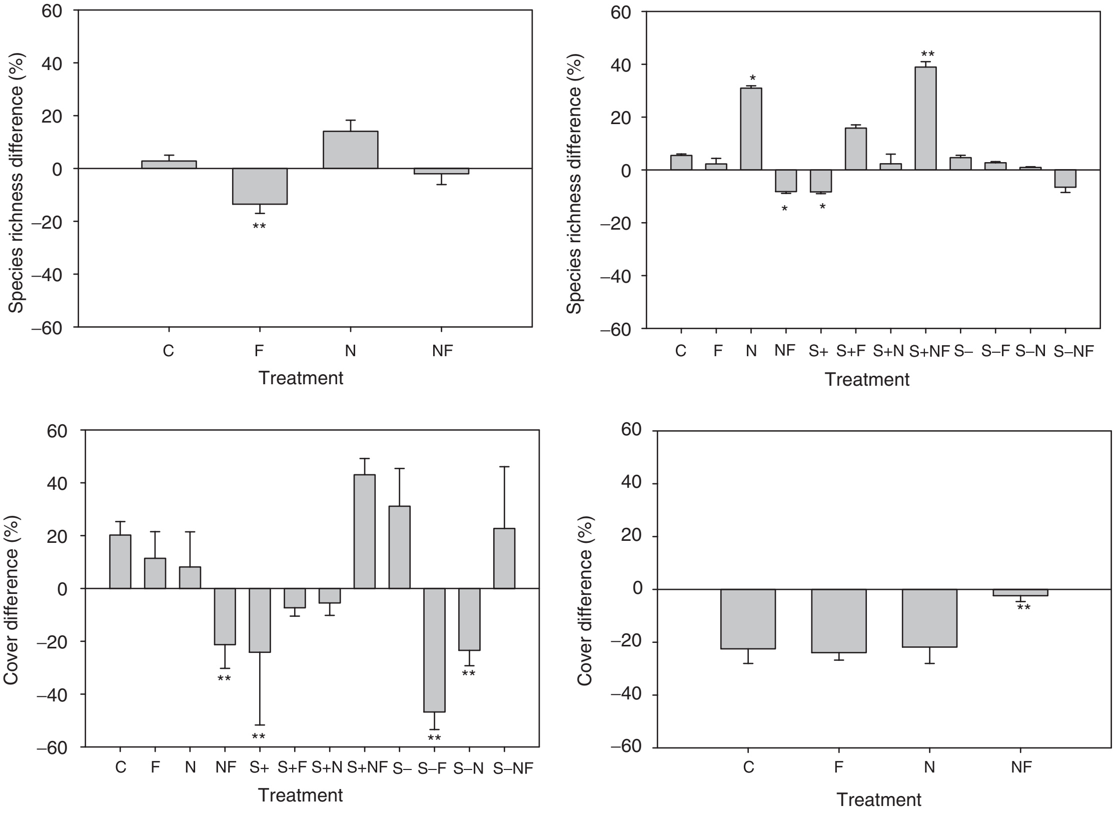

Fig. 2 Teakettle (left column) and Yosemite (right column) percent change in mean herb species richness and mean percent cover response to treatments from their pretreatment values with standard error bars. Treatments with an asterisk are significantly different from the control (*$P<0.1$; **$P<0.05$).

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significant decreases in NF, S + , S−F, and S−N. Nonsignificant increases in herb cover were observed for the remainder of the treatments. At Yosemite, species richness significantly decreased in the nitrogen + fire and snow increase treatments as compared with the control. The nitrogen and snow + nitrogen + fire treatments had significant increases in richness compared with the control. At Yosemite, there was no significant difference in herb cover between snowpack treatments, so these plots were pooled. Compared with the control, the NF treatment had a significantly lower percent change from the pretreatment cover values.

At Teakettle, herb biomass was greatest for the nitrogen, fire, and snow–nitrogen and fire treatments, which were all significantly greater than the control (Table 1). At Yosemite, with the exception of the S + F and S−NF, all treatments had significantly lower herb biomass than the control (Table 1).

Shrubs

We found the same significant differences between treatment years for shrub cover at Teakettle and shrub richness and cover at Yosemite. There was a significant time × treatment interaction for the Teakettle shrub cover, so we examined treatment differences within 2006. At Teakettle, shrub cover increased over pretreatment values and was significantly different from the control for S + , S + F, S + N, and S−NF (Fig. 3). All treatments at Teakettle that included fire had a significantly greater reduction in shrub cover as compared with the control. At Yosemite, shrub data were pooled across snow treatments because there was no significant response to snow addition or reduction. At Yosemite, species richness was highest and significantly greater than the control for the NF treatment. All treatments decreased from their pretreament shrub cover values at Yosemite, but none were significantly different from the control.

At Teakettle, the snowpack reduction treatment yielded the greatest shrub biomass, but was not significantly greater than the control (Table 1). The snowpack + nitrogen and fire treatment had the lowest shrub biomass and was significantly different from the control. All the treatments that included fire had higher shrub biomass than the control, but only the S−F treatment was significantly different from the control. At Yosemite, the S + F treatment had the highest post-treatment shrub biomass; however, none of the treatments were significantly different from the control for shrub biomass (Table 1).

Changes in community composition

Multiple response permutation procedure comparisons of species composition by treatment within each site indicate there were significant differences among all the treatments (Teakettle $a = 0.156$, $P = 0.0001$; Yosemite $a = 0.376$, $P < 0.0001$). We examined how treatments affected the most common herb and shrub species ($\geq 80\%$ of the plots) between 2002 and 2006 (Table 2). Perennial herbs had both positive and negative responses to treatments, typified by *A. repanda*, with significant cover increases in the S + F and S + N treatments, and *K. galioides*, with significant decreases in F, S + F, and S−NF treatments. Annuals such as *C. torreyi* usually had a significant positive response to all treatments that included fire. Shrubs decreased in most

Table 1 Post-treatment herb and shrub biomass at Teakettle and Yosemite experimental sites

	Teakettle (g/81 m^2)		Yosemite (g/81 m^2)	
Treatment	Herb (SE)	Shrub (SE)	Herb (g)	Shrub (g)
Snowpack + nitrogen + fire	10.5 (22.9)	987.4 (285.1)**	65.7 (31.2)**	189.8 (697.3)
Snowpack−fire	17.8 (7.6)	2051.1b (709.8)	84.8 (4.5)**	136.4b (234.1)
Nitrogen + fire	43.3 (22.6)	1832.7 (478.7)	76.4 (35.9)**	462.5 (641.8)
Snowpack−nitrogen	25.3 (7.3)	2933.5 (38.0)	97.2 (32.3)**	145.9 (500.0)
Fire only	127.5 (17.9)**	2578.1 (786.1)	60.3 (24.4)**	300.0 (104.3)
Nitrogen +	88.1 (22.6)**	4070.0 (225.7)	85.4 (18.1)**	87.6 (218.6)
Snowpack−	39.2 (16.4)	4692.4 (1305.9)	98.1 (48.6)**	80.5 (274.2)
Snowpack−nitrogen + fire	77.0 (29.1)**	2935.6 (494.0)	98.0 (160.1)	95.7 (326.0)
Control	**17.6 (22.9)**	**2900.0 (171.8)**	**322.7 (32.2)**	**336.2 (433.5)**
Snowpack + nitrogen	30.6 (12.0)	3500.2 (567.8)	93.8 (70.7)**	929.1(195.4)
Snowpack + fire	48.4 (10.7)	2611.5 (1112.8)	275.5 (16.1)	385.3 (535.2)
Snowpack +	16.7 (9.3)	4221.8 (496.9)	139.2 (60.9)**	580.7 (326.6)

Treatments are ordered from lowest to highest mean rank, where the average is calculated across a row using the rank of the value within each column. Values within the same column with an asterisk indicate significant difference from the control (**$P < 0.05$).

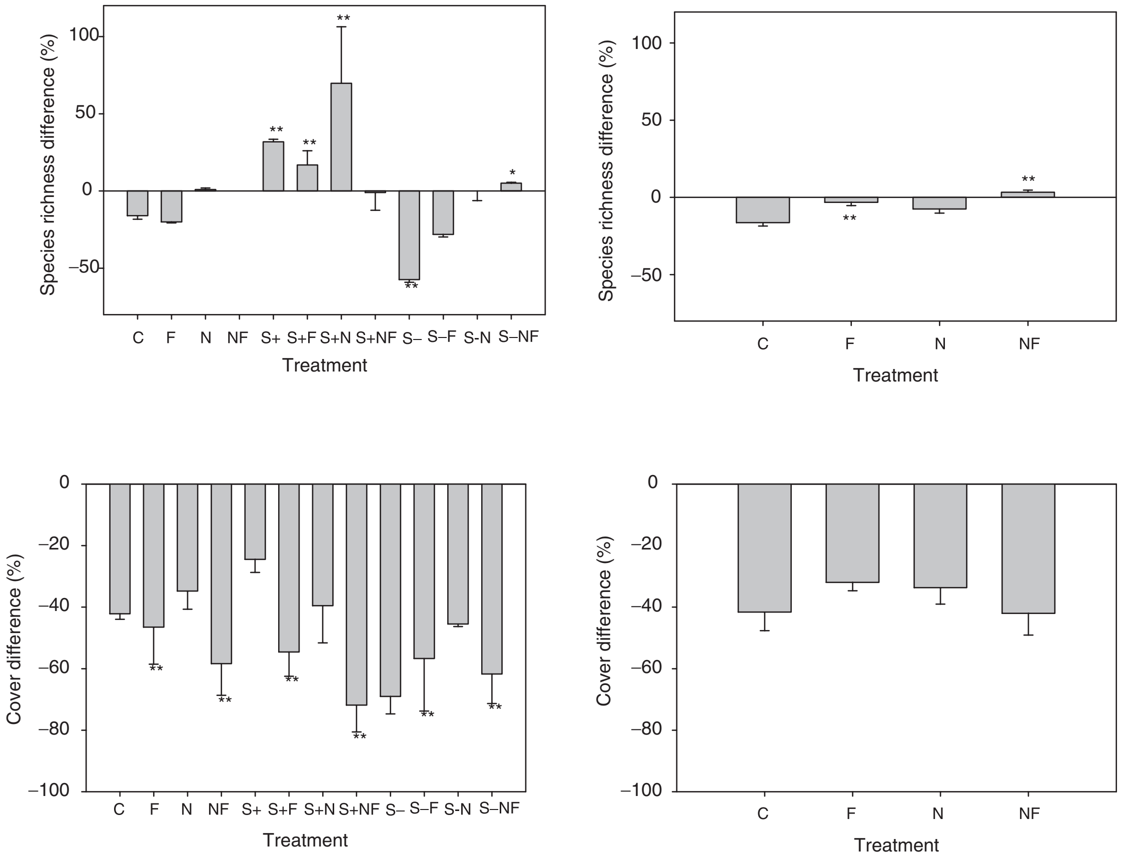

Fig. 3 Teakettle (left column) and Yosemite (right column) percent change in mean shrub species richness and mean percent cover response to treatments from their pretreatment values with standard error bars. Treatments with an asterisk are significantly different from the control ($^*P<0.1$; $^{**}P<0.05$).

treatments, typified by *Symphoricarpus mollis* with a decrease of 11–135% in cover.

Discussion

Our field experiment highlights the difficulty in experimentally determining how climate change, nitrogen inputs, and disturbance may affect forest understory communities. In the absence of any treatment (i.e. in the controls), there were still changes at both the sites in herb richness and cover, and shrub cover over the 4-year study period. The herbaceous community, which typically contains most of the plant diversity in temperate coniferous forests, unexpectedly had an increase in richness with the nitrogen-only treatment and a decrease with fire (Teakettle) and NF treatments. Average ranking (Table 1) indicates snowpack-addition treatments generally increased shrub biomass, but herb response varied between sites, possibly due to an interaction between snow removal and length of growing season (discussed below). The combination of additional snowpack and nitrogen, followed by fire, produced the lowest herb and shrub biomass at Teakettle. These findings suggest that pollution input and climate change effects on snowpack influence understory biomass, potentially increasing fire intensity and extent.

Our results, however, are limited by the complex response of the understory, suggesting that it may be difficult to accurately model climate change effects on these dynamic communities. Some of the 'noise' in our field experiment resulted from low sample size and only 4 years of data, arising from management (delayed application of the prescribed burn due to weather) and practical (remote site snow manipulation) constraints. Over the course of the field experiment, however, we have noted two interacting factors that may be affecting our results and that should be considered in modeling understory response. Changes in precipitation may have significantly different effects on vegetation depending on dominant vegetation, and whether precipitation occurs as snow or rain. There was no significant difference in soil moisture with snow manipulations probably because water rapidly percolates through the extremely porous decomposed granitic soils found at both the sites. The influence of the snowpack may be more a matter of shading, particularly for the herbs that germinate (annuals) or re-sprout (perennials) only after snow melt. At Teakettle, where shrubs dominate understory biomass, averaging 10 times that of Yosemite, snow reduction treatment (NS) and the snow reduction + nitrogen and fire lengthened the herb growing season, producing an increase in herb biomass in a system otherwise dominated by shrubs. Yosemite's understory community, dominated by herbs, with an average biomass 2.7 times that of Teakettle's, had significant immediate decreases in biomass with almost any treatment that altered *status quo* growing conditions. Some research has suggested that understory response to changes in resource conditions is strongly affected by which functional groups dominate a community's composition (Pausas & Austin, 2001; Grime, 2002). The role of dominant functional groups is one possible explanation for the variation in treatment response between the sites. This varied response lends a cautionary tale to modeling vegetation community response to predicted changes in climate. Models that predict changes in understory communities may need to distinguish shrub from herb-dominated systems and whether future precipitation patterns favor rain or snow.

In a model examining herb and shrub biomass response, parameterized with these data, Hurteau *et al.* (in review) found that nitrogen was the primary driver of herb biomass production followed closely by snowpack increase-nitrogen combinations. Specifically, nitrogen deposition at a rate of $12\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ produced a greater amount of biomass than the $24\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ rate. While this finding is contrary to what one might expect in a nitrogen limited system, the increasing N : P ratio on nitrogen treatment plots indicates that when subjected to continuously high levels of nitrogen deposition, phosphorous may become a limiting nutrient. Model results for shrub biomass indicated mixed results in response to nitrogen deposition level. When coupled with increasing snowpack, the level of nitrogen deposition did not produce different biomass results. When coupled with decreasing snowpack, the $24\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$ level produced more shrub biomass than the lower nitrogen level. Model results indicate that fire reduces shrub cover and biomass, opening growing space, and allowing herb biomass and cover to increase.

Several field studies have examined the impact of predicted increases in precipitation resulting from climate change. Grime *et al.* (2000) found that increasing summer rainfall in two UK grasslands resulted in significantly more biomass production than control plots. Shaw *et al.* (2002) reported that increasing precipitation in a California grassland resulted in increased net primary productivity. Increases in understory biomass can alter the intensity and extent of fire. In climate and fire reconstruction studies in the Southwest, the most extensive fires were recorded in years that were preceded by several wet years that may have built grass and herb biomass. In an earlier study at Teakettle (North *et al*., 2005b), we did not find this wet/dry cycle associated with fires. If ENSO events, however, become more frequent or intense, Sierran forests might experience periodic fuel building similar to that found in the Southwest. In our experiment, snow and nitrogen treatments that were burned had some of the lowest biomass of any treatments at both Teakettle and Yosemite (Table 1). The Sierra Nevada has generally been considered to be more influenced by forest fuel accumulation in the form of woody material, tree litter, and semi-decomposed tree litter (duff) (Keifer *et al*., 2006) than by grass and forbs needed to carry fire in drier ponderosa pine forests. Our experiment suggests that understory biomass does respond to changes in snow and nitrogen conditions, and that these changes may be sufficient to increase fire intensity reducing postburn biomass. Such a change could move Sierran fire patterns toward larger, more regionally synchronous fire events that have been documented in several southwest studies (Swetnam & Betancourt, 1990; Grissino-Mayer & Swetnam, 2000; Swetnam & Baisan, 2003).

Table 2 Percent cover in each of the 12 experimental treatments for the four most abundant species at both sites that occurred in ≥80% of the plots. Using a paired *t*-test, means that are significantly different from their pretreatment values are represented by $^{*}P<0.1$ and $^{**}P<0.05$

Species	F	N	NF	S +	S + F	S + N	S + NF	S–	S–F	S–N	S–NF
Arabis repanda	2.5	0.8	1.3	1.3*	1.5**	1.6**	0.6	0.6	NP	−1.8	2.5
Collinsia torreyi	27**	0.8	2.8**	−1.3	1.0*	1.0**	3.1**	2.6	2.5**	2.0	3.3**
Kelloggia galioides	−1.0**	−18	−1.6	−5.8	−1.8**	9.6	−1.8	3.8	−0.1	−4.3	−1.3**
Symphoricarpos mollis	−21**	−135*	−19**	−124**	−34**	−105*	−11	−119*	−5.1**	−113**	18**

Means with a negative sign indicate a reduction in cover from the pretreatment value. An 'NP' signifies that the species was not present in the plots that received a particular treatment.

At the Yosemite site, snowpack increase coupled with fire and nitrogen produced the greatest herb species richness, while at Teakettle, it was the nitrogen addition treatment. Field studies examining the impacts of increasing nitrogen deposition have found that increasing nitrogen increases productivity (Foster & Gross, 1998; Shaw *et al*., 2002) and decreases species richness and/or diversity (Foster & Gross, 1998; Zavaleta *et al*., 2003; Bowman *et al*., 2006). Our findings are somewhat contrary to these as the treatments that had the greatest species richness all included nitrogen addition. The disparity in findings between our study and those of others may in part be due to the heterogeneous growing conditions in forests compared with grassland ecosystems. Laughlin *et al*. (2007) found that understory species' richness was lowest where the overstory density was greatest in a ponderosa pine forest. The variable forest canopy cover in Sierran mixed-conifer forest (North *et al*., 2002, 2004), which influences other abiotic factors such as light availability and precipitation interception/throughfall, may have influenced our findings.

Changes in climate and pollution inputs will have significant effects on forest communities directly altering resource conditions and indirectly affecting disturbance regimes. Our study suggests that these changes are complex and may vary depending on present community composition and the timing and form of changes in precipitation patterns. Treatments that increased preburn understory biomass increased fire intensity reducing shrub biomass and exposing more mineral soil, conditions that may have been more common with historically frequent fire. Before climate models can accurately predict changes in forest understory communities, more field experiments are needed which follow long-term response in forest understories, which have different community compositions.

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