

Elevation-dependent influence of snow accumulation on forest greening

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Rising temperatures and declining water availability have influenced the ecological function of mountain forests over the past half-century. For instance, warming in spring and summer and shifts towards earlier snowmelt are associated with an increase in wildfire activity and tree mortality in mountain forests in the western United States^{1,2}. Temperature increases are expected to continue during the twenty-first century in mountain ecosystems across the globe^{3,4}, with uncertain consequences. Here, we examine the influence of interannual variations in snowpack accumulation on forest greenness in the Sierra Nevada Mountains, California, between 1982 and 2006. Using observational records of snow accumulation and satellite data on vegetation greenness we show that vegetation greenness increases with snow accumulation. Indeed, we show that variations in maximum snow accumulation explain over 50% of the interannual variability in peak forest greenness across the Sierra Nevada region. The extent to which snow accumulation can explain variations in greenness varies with elevation, reaching a maximum in the water-limited mid-elevations, between 2,000 and 2,600 m. *In situ* measurements of carbon uptake and snow accumulation along an elevational transect in the region confirm the elevation dependence of this relationship. We suggest that mid-elevation mountain forest ecosystems could prove particularly sensitive to future increases in temperature and concurrent changes in snow accumulation and melt.

Recent studies have documented a shift from energy to water limitation across forested ecosystems of western North America^{5,6}. This transformation has reversed the response of these ecosystems to increases in temperature where before the early 1990s increases in air temperature increased terrestrial carbon uptake. Following the early 1990s an apparent shift from energy to water limitation resulted in reduced carbon uptake with increased temperature and coincident decreases in water availability⁵. In the western United States, increases in regional spring–summer temperatures and earlier snowmelt since the mid-1980s strongly correlate with increases in forest wildfire activity¹ and increases in tree mortality rates². A consistent message has emerged from these studies: the combined effects of increases in temperature and decreases in water availability over the past half-century have impacted the ecological function of mountain forests.

The sensitivity of mid-latitude mountain forests to water availability and the associated importance of snowmelt water has been well documented at the plot scale^{7–10}. However, the effects of variations in snowpack accumulation on vegetation activity

have not been observed at the ecosystem scale across elevational gradients. Modelling studies suggest that ecological sensitivity to water and energy limitation varies markedly with elevation^{11,12}. In the western United States, wildfire frequency has increased since the mid-1980s, especially at elevations between 1,700 and 2,600 m. In this regard, maximum increases in fire frequency have occurred around 2,100 m in response to earlier spring snowmelt associated with increases in temperature¹. Such results illustrate the sensitivity of mountain ecosystems to elevational variations in water availability (for example, rain/snow) and climatic forcings (for example, temperature and solar radiation).

Temperature increases are expected to continue during the twenty-first century in mountain environments across the globe^{3,4}, affecting the timing of spring arrival and snowmelt^{13,14}, and plant and animal species displacement and/or extinction¹⁵. Observed and projected changes in temperature, snowfall versus rainfall apportionment, and snowmelt timing vary considerably with elevation. As a consequence, understanding the feedbacks between ecological function and snowpack dynamics across elevational gradients is of paramount importance to evaluate ecosystem sensitivities to climate change.

We analyse the effect of snowpack accumulation on the greenness of vegetation through the combined analysis of annual peak forest greenness (that is, the normalized difference vegetation index (NDVI)) and annual maximum snowpack accumulation in the Sierra Nevada Mountains, USA (Fig. 1a). We focus on regional and elevational variations in these relationships to identify the most sensitive areas to interannual variations in snowpack accumulation. Furthermore, we analyse *in situ* measurements of gross CO₂ ecosystem exchange (GEE) and snow water equivalent (SWE) across an elevational transect in the Sierra Nevada (Fig. 1) for the water years (WY, October–September) 2009–2011 to provide further and independent evidence of the mechanisms that lead to the patterns observed from the analysis of NDVI and SWE. The Sierra Nevada region was selected for this analysis given the relatively uniform orientation of the mountain front to prevailing storms and well organized ecotones arranged across elevational gradients¹⁶. Most of the annual precipitation at high elevations in the region falls in the form of snow during winter and spring¹⁷, with little contributions from summer rainfall, and therefore the ecosystem relies heavily on water availability from snowmelt.

In the Sierra Nevada, the interannual variations in vegetation greenness in summer resemble those in maximum snowpack accumulation in spring during the period 1982–2006 (Fig. 1). Spatially, peak growing season NDVI increases significantly following

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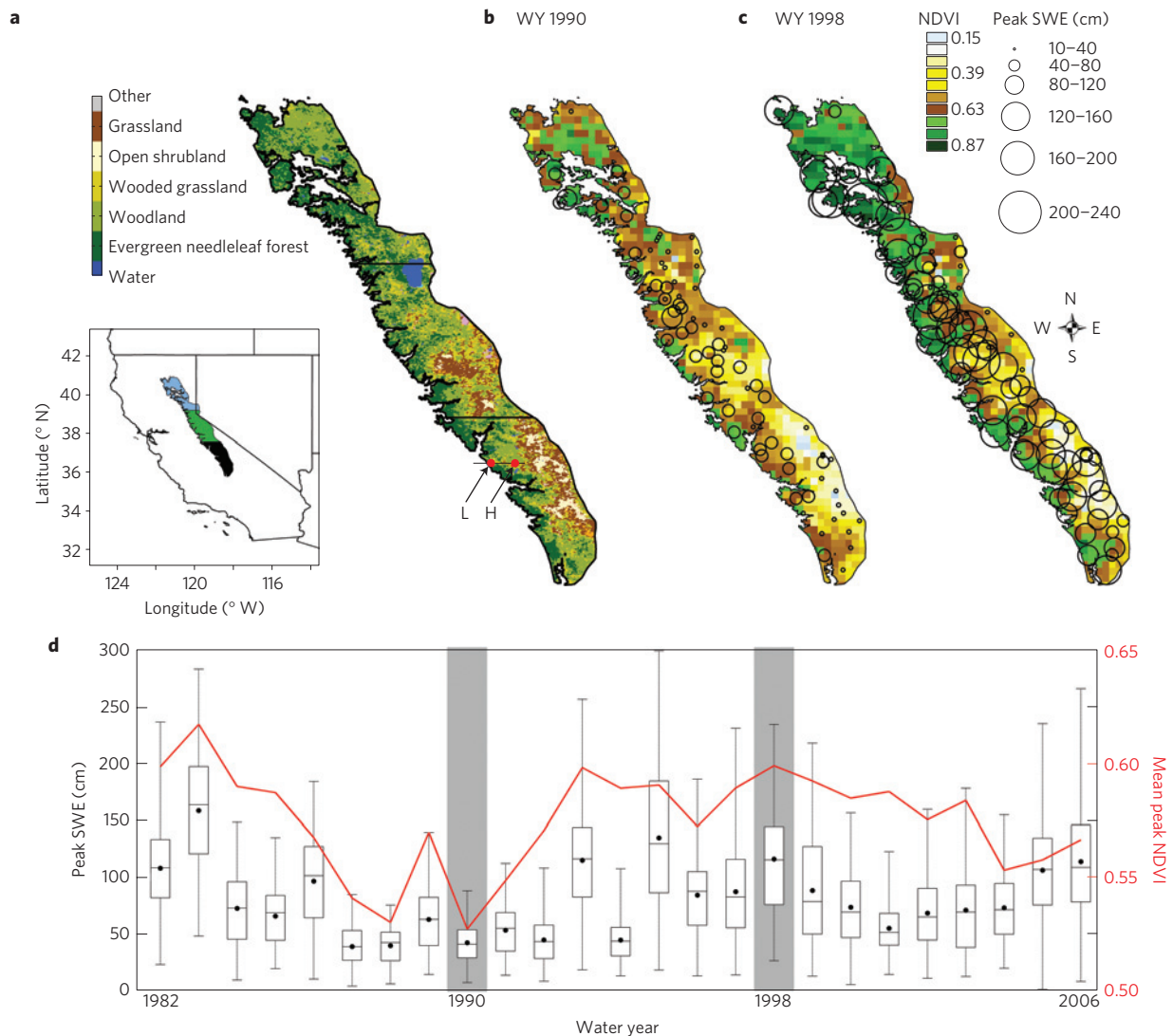


Figure 1 | Study area and correspondence between SWE and NDVI across the Sierra Nevada Mountains. **a**, Location of the study area in the state of California (USA; bottom left) and land cover classification with the predominant cover types^{23,24}. The area is subdivided into northern, central and southern Sierra Nevada subregions (blue, green and black, respectively). The area is subdivided into northern, central and southern Sierra Nevada subregions (blue, green and black, respectively). The lower (L) and higher (H) elevation sites of *in situ* measurements are marked by the red dots in the Southern subregion. **b,c**, Growing season peak NDVI for example dry and wet years, respectively. Greater NDVI (greenness) values are indicated by darker green on the maps. Peak SWE values at the snow pillows are represented by the size of the black circles. Note the correspondence between forest greenness and peak SWE. **d**, Similarities between mean peak NDVI (red) and peak SWE (box plots) for the period WY 1982–2006. Vertical lines indicate the range of peak SWE; boxes indicate the 0.25 and 0.75 percentiles; horizontal lines indicate median values and black dots correspond to mean annual peak SWE values. The years highlighted in grey correspond to **b,c**. The standard deviation of annual peak NDVI within the region for the period 1982–2006 ranges between 0.15 and 0.18, with a mean standard deviation of 0.17.

winters with deep snow cover (for example, Fig. 1b,c), whereas the time series of average peak NDVI follows a trend close to that of maximum seasonal snow accumulation (Fig. 1d). Significant correlations between annual peak NDVI and peak SWE were obtained over the region for evergreen needleleaf forests, woodlands and wooded grasslands for the period 1982–2006 (Fig. 2). The regional-scale documentation of the influence of snowmelt water on vegetation growth complements plot-scale studies that have illustrated the importance of snowmelt water for sustaining transpiration late into the growing season^{7–9}. Relationships between vegetation greenness and maximum accumulation are significantly stronger in the northern Sierra Nevada (Fig. 2a,b), where the elevation range is lower, the dominant vegetation types are evergreen needleleaf forest and woodland, forest extent is greater (Fig. 1a) and maximum snow accumulation tends to be higher than in the central and southern subregions (see Methods). This northern region has

previously been identified as one of the most vulnerable to changes in snowmelt timing in the western United States with respect to forest fire activity¹ and tree mortality rates². Although our analyses make reference to maximum snowpack accumulation, there is a strong relationship between maximum accumulation and snow disappearance date in the Sierra Nevada region, with an R^2 value of 0.84 between the mean yearly values for the period 1982–2006. Hence, the date of snow disappearance also explains significant variability in vegetation greenness.

Relationships between vegetation greenness and snowpack accumulation show significant variations with elevation (Fig. 3). The strongest relationships (that is, highest R^2 values) exist at an elevation range between 1,900 and 2,600 m. R^2 values drop notably above 2,600 m, suggesting a switch from water limitation at the lower and middle elevations (regions I and II, Fig. 3b) to energy limitation at the highest elevations (region III, Fig. 3b). Relationships also drop

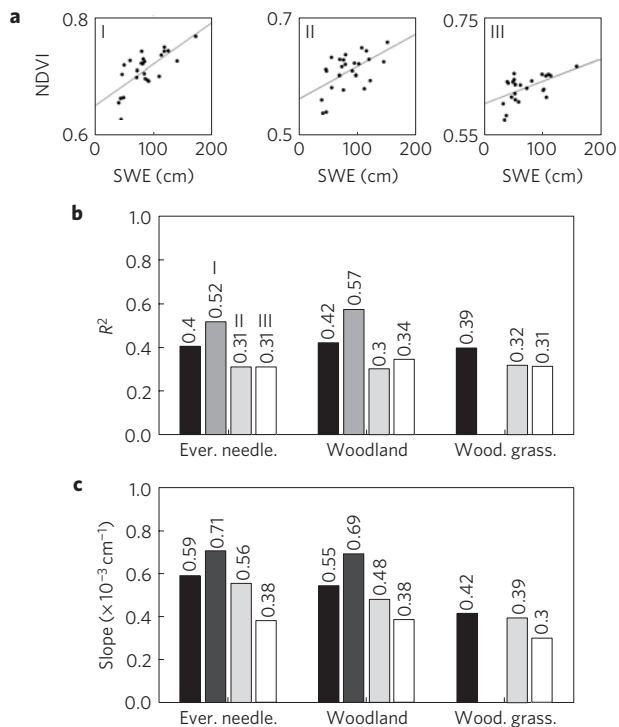


Figure 2 | Relationships between forest greenness and maximum snow accumulation on a regional basis. **a**, Relationship between the time series of annual mean peak NDVI and mean peak SWE for evergreen needleleaf forests in the northern (I), central (II) and southern (III) Sierra Nevada. The northern Sierra Nevada shows the highest R^2 value and highest sensitivity to changes in snowpack peak accumulation, whereas the weakest relationships and lowest sensitivity are observed in the southern Sierra Nevada. **b,c**, R^2 values ($p < 0.01$) (**b**) and slopes (**c**) of the relationships between mean peak NDVI and mean peak SWE for the three main cover types, and for the entire study region (black bars) and subregions (from dark grey to white for the northern to southern Sierra Nevada, respectively). Ever. needle., evergreen needleleaf forest; Wood. grass., wooded grassland.

off at the lowest elevations (region I, Fig. 3b). The sensitivity of forest greenness to maximum snowpack accumulation (for example, slopes of regression lines, Fig. 3a) peaked at elevations between 1,800 and 2,100 m (region II, Fig. 3c). At elevations above this range water limitation is depressed owing to greater snow accumulation and temperatures become a limiting factor for vegetation activity. At elevations below this range, ecological dynamics are less sensitive to snowmelt¹⁸ as a greater proportion of precipitation falls as rain versus snowfall. These elevational thresholds match those from modelling studies that suggest transpiration rates at lower elevation are relatively insensitive to snowmelt^{11,12}. At middle elevations energy limitations are suppressed and variability in snowmelt is highly correlated with vegetation greenness. Interestingly, this zone of maximum sensitivity coincides with elevation zones where increases in forest fire frequency peaked after the mid-1980s as a result of increases in temperature, earlier snowmelt and longer dry seasons¹.

Here it should be noted that several other processes will affect photosynthetic activity in these forest ecosystems, which together with uncertainties associated with the data sets, are responsible for the portion of the variability in peak vegetation greenness not explained by the interannual variations in maximum snow accumulation; see Supplementary Information and Supplementary Figs S1–S7 for an evaluation of issues associated with the data sets used. Discrimination between the effects of the understory and the overstory in the NDVI signal is not possible, a characteristic inherent of any pixel-based satellite product.

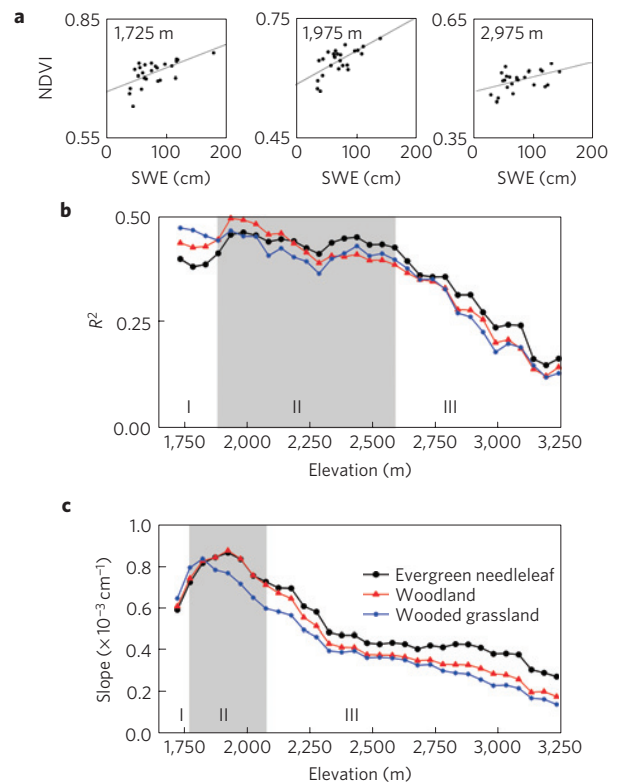


Figure 3 | Relationships between forest greenness and maximum snow accumulation across elevations. **a**, Relationship between the time series of annual mean peak forest greenness (NDVI) and mean peak SWE for evergreen needleleaf forests for three elevation zones; note the strong relationship and steeper slope of the linear trend at the mid-elevations. **b,c**, R^2 values ($p < 0.05$) (**b**) and slopes (**c**) of the relationships between mean peak forest greenness (NDVI) and mean peak SWE for elevation zones of 250 m displaced every 50 m to determine variations in the strength of the relationships with elevation. The points in the plots correspond to the mid-mark for each of the intervals; note the significant decline in the R^2 values and slopes of the trend lines at higher elevations. R^2 values above 3,100 m were not statistically significant ($p > 0.05$). Elevation regions marked as I, II and III are used to emphasize the drop-offs in R^2 values in **b**, and the range with the highest slopes in **c**.

Despite these aforementioned uncertainties, *in situ* measurements along an elevational transect in the southern Sierra Nevada support the conclusion that environments at the lower and middle elevations are water limited and the higher elevations are energy limited. Observations from flux towers at 2,015 and 2,700 m include GEE and SWE for the period WY 2009–2011. The 2,015 m site is within the elevation region that the analyses above indicate is the most sensitive to variations in maximum snow accumulation. The 2,700 m site is just above the elevation threshold where we observe a decrease in the correlations between peak NDVI and peak SWE. GEE at the lower elevation site (2,015 m) continued year-round (Fig. 4a), with a decline from October to March caused by reduced light and by photosynthetic shutdown on unusually cold days, a pattern consistent with weak co-limitation by water and winter cold. GEE at the higher elevation site (2,700 m) peaked in summer and early fall (June–October), and vegetation was dormant during winter and early spring (Fig. 4b), a pattern consistent with strong cold limitation. At the 2,015 m site, years with greater snow accumulation also had higher summer rates of gross photosynthesis (Fig. 4a). Peak summer rates of GEE at the 2,015 m site increased from 65.9 kg C ha⁻¹ d⁻¹ in 2009 to 76.4 kg C ha⁻¹ d⁻¹ in 2010 to 86 kg C ha⁻¹ d⁻¹ in 2011, and mean

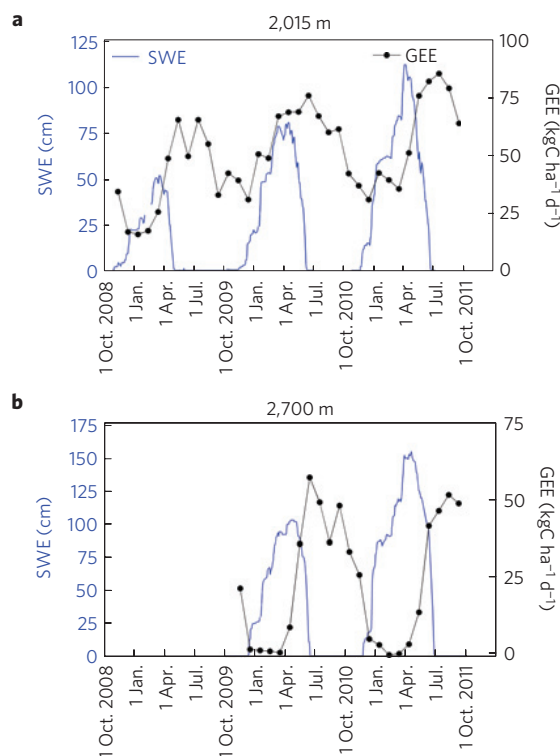


Figure 4 | *In situ* measurements of GEE and snow accumulation in the southern Sierra Nevada Mountains. **a**, SWE and GEE as indicators of the whole ecosystem photosynthesis at the lower elevation site for the period WY 2009–2011. **b**, SWE and GEE at the higher elevation site for the period WY 2010–2011. SWE data were obtained from snow pillow stations near the sites and at comparable elevations.

summer rates (June–September) increased from $51 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2009 to $66.5 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2010 to $78.1 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2011. These increases coincide with a progressive increase in winter SWE accumulation. On the other hand, at the 2,700 m site, the year with greater snow accumulation did not have markedly higher summer rates of gross photosynthesis (Fig. 4b). Peak summer rates of GEE at the 2,700 m site slightly decrease from $57.1 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2010 to $51.4 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2011, and mean summer rates also show a slight decrease from $47.5 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2010 to $46.9 \text{ kg C ha}^{-1} \text{ d}^{-1}$ in 2011. Such decreases occur despite an increase in maximum snow accumulation from 2010 to 2011. These observations establish: a correlation between land–atmosphere carbon exchange and SWE, and confirm the positive effect of snow accumulation on photosynthetic activity at middle elevations; and a reduction in the correspondence between land–atmosphere carbon exchange and SWE at the higher elevations. Both of these results provide direct observational evidence of the transition from a water-limited ecosystem at the lower elevations to energy-limited ecosystems at the higher elevations.

Freezing elevations during late winter storms are a primary indicator of forest ecotone elevation¹⁶. Species diversity and richness across elevational gradients often exhibit a humped pattern, with maximum diversity and richness at intermediate elevations conditioned to climatic factors such as temperature, rainfall and snow, depending on each species particular adaptation^{19,20}. For example, some plant and animal species groups depend on high and constant moisture, whereas others are restricted by specific winter temperatures²¹. The results presented here are evidence of similar controls on forest ecosystems' photosynthetic activity. Future increases in temperature will probably reduce the amount of precipitation that falls as snow and shift snowmelt earlier in

spring, particularly at the lower and middle elevations²². The results presented here indicate significant ecological sensitivity to these hydrologic changes associated with elevation. Although the magnitude of these effects is uncertain, future changes in mid-elevation forest productivity and composition should be expected as a result of changes in snow accumulation and melt.

Methods

This study focuses on the Sierra Nevada region, including areas above an elevation of 1,500 m. The extent of the Sierra Nevada study area is $35,783 \text{ km}^2$, separated into northern ($11,251 \text{ km}^2$), central ($13,170 \text{ km}^2$) and southern ($11,362 \text{ km}^2$) regions. Land cover information at a 1-km resolution was obtained from the global land cover classification collection of the Department of Geography of the University of Maryland^{23,24}. This product, generated from imagery from the Advanced Very High Resolution Radiometer (AVHRR) satellites acquired between 1982 and 1994, was analysed to distinguish 14 land cover classes. See Supplementary Information for a description of the predominant land cover types.

The NDVI data set is the product of the Global Inventory Modelling and Mapping Studies of the University of Maryland^{25,26}. The data set is derived from AVHRR imagery and is available biweekly at 8-km spatial resolution for a 25-year period spanning from 1982 to 2006. Peak NDVI values were obtained for each WY (October–September) and for each pixel, similar to considering the NDVI values for each pixel as a time series. By performing the analysis this way, variations in the timing of the peak NDVI for a given year within the region are accounted for, as the peak NDVI value can occur at different times for each pixel. To avoid contamination of the NDVI signal by snow, imagery acquired during the snow cover period was not used to evaluate annual peak NDVI. In this regard, 61% of the peak NDVI values occur in the months of July and August, and 97% occur between the months of June and September. The 8-km NDVI grids were then intersected with the 1-km land cover grid, and the peak NDVI values were assigned to the cover types within each particular grid cell. See Supplementary Information and Supplementary Figs S1–S6 for detailed comparisons of the spatial and elevational patterns observed with the AVHRR Global Inventory Modelling and Mapping Studies and Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI (MOD13Q1), and an evaluation of the subpixel distribution of NDVI. Similar analyses have also demonstrated strong correspondence between AVHRR and MODIS NDVI (refs 27–29).

Daily SWE data were obtained from the network of snow pillow stations in the California region. The data set integrates stations from the Natural Resources Conservation Service SNOTEL network and snow sensors from the California Department of Water Resources. Peak SWE values were determined for each season for the period between WY 1982 and 2006, coincident with the NDVI period of record. A total of 107 stations were used, although for any given year, not all stations contain valid peak SWE values owing to discontinuity of the records. Yearly averages of peak SWE (WY 1982–2006) ranged between 39 and 157 cm for the entire study region, and between 42 and 172 cm for the northern Sierra Nevada, 39 and 150 cm for the central Sierra Nevada, and 33 and 157 cm in the southern Sierra Nevada. Average peak SWE values for the period WY 1982–2006 for the northern, central and southern Sierra Nevada were 86 cm, 84 cm and 70 cm, respectively; the total domain average peak SWE was 81 cm. An evaluation of the representativeness and consistency of the snow pillow data in the Sierra Nevada region is included in Supplementary Information and Supplementary Fig. S7.

Topographic information at a 1 arc-sec scale ($\sim 30\text{-m}$) obtained from the US Geological Survey National Map Seamless Server was used to generate a 1-km scale digital elevation model to match the grid of the land cover classification. The elevation-zone analyses consisted of selecting the area within a 250-m elevation window and comparing the mean peak NDVI for each land cover type within the elevation zone to the mean peak SWE for the stations within the same elevation zone. The limits of the zone are iteratively displaced every 50 m within the range of elevations in the entire study area.

In situ measurements of GEE at two locations in the southern Sierra Nevada were analysed for the period WY 2009–2011. The lower elevation site (2,015 m) is located within the Providence Creek watershed ($37^\circ 04' 04'' \text{ N}$, $119^\circ 11' 40'' \text{ W}$), in a mid-montane forest with a canopy of white fir and various pine species with 53% cover, a mean height of 13.5 m and a maximum height of 30.1 m. The higher elevation site (2,700 m) is located within the Shorthair Creek watershed ($37^\circ 04' 00'' \text{ N}$, $118^\circ 59' 19'' \text{ W}$), in an open subalpine forest of lodgepole pine with 31% cover, a mean height of 10.2 m and a maximum height of 22.4 m. Tower heights are 48 m at the 2,015 m site, and 33 m at the 2,700 m site. The infrared CO_2 gas analysers are closed path LI-7000 (LiCor). Methods for CO_2 uptake calculations are fully described in ref. 30.

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Author contributions

E.T. jointly conceived the study and designed the analyses with N.P.M. E.T. collected and performed the data analyses of NDVI and SWE. E.T. and N.P.M. carried out interpretation of results jointly, and E.T. prepared the initial manuscript. M.L.G., A.E.K. and R.C.B. provided the GEE data, and contributed with interpretations of the GEE and SWE measurements and the corresponding text. E.T. and N.P.M. edited the final version of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.T.

Competing financial interests

The authors declare no competing financial interests.