Mountain runoff vulnerability to increased evapotranspiration with vegetation expansion

Michael L. Goulden[a,1] **and Roger C. Bales**[b,c]

[a]Department of Earth System Science, University of California, Irvine, CA 92697-3100; and [b]School of Engineering and [c]Sierra Nevada Research Institute, University of California, Merced, CA 95343

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Climate change has the potential to reduce surface-water supply by expanding the activity, density, or coverage of upland vegetation, although the likelihood and severity of this effect are poorly known. We quantified the extent to which vegetation and evapotranspiration (ET) are presently cold-limited in California's upper Kings River basin and used a space-for-time substitution to calculate the sensitivity of riverflow to vegetation expansion. We found that runoff is highly sensitive to vegetation migration; warming projected for 2100 could increase average basin-wide ET by 28% and decrease riverflow by 26%. Kings River basin ET currently peaks at midelevation and declines at higher elevation, creating a cold-limited zone above 2,400 m that is disproportionately important for runoff generation. Climate projections for 2085–2100 indicate as much as 4.1 °C warming in California's Sierra Nevada, which would expand high rates of ET 700-m upslope if vegetation maintains its current correlation with temperature. Moreover, we observed that the relationship between basin-wide ET and temperature is similar across the entire western slope of California's Sierra Nevada, implying that the risk of increasing montane ET with warming is widespread.

water resources | plant migration

Roughly 4 billion people globally and 20 million people in the state of California rely on mountain runoff for freshwater, and there is growing concern these water resources will prove vulnerable to climate change (1–6). River flow (Q) is a function of precipitation (P) minus evapotranspiration (ET) (P−ET); increased montane ET with warming, either because of the direct effect of temperature on evaporative demand or the indirect effect of warming on vegetation density and distribution, would reduce Q (5, 7–9). However, hydrologic model projections for California's Sierra Nevada have discounted this possibility, indicating little or no effect of warming on annual ET (10–13). This result appears linked to two model assumptions: (*i*) models have often assumed the properties of montane vegetation will remain static, and (*ii*) models have often implicitly assumed that current annual montane ET is almost entirely limited by water availability and that warming will simply hasten the beginning and end of the growing season.

Recent evidence calls both of these assumptions into question. Widespread increases in subalpine tree growth, tree-line altitude, and species distribution with elevation have been reported with recent climate trends in California and elsewhere, implying that rapid vegetation shifts are possible (14–16). Time series of Sierra Nevada forest greenness indicate a transition from water limitation at low elevation to cold limitation at high altitude, implying that upper elevation ET is sensitive to warming (17). Nonetheless, the extent to which annual montane ET is currently temperature-limited, as well as the sensitivity of large-scale ET to vegetation redistribution, remain largely unquantified.

We used the upper Kings River basin in California's Sierra Nevada as a case study of the sensitivity of montane runoff to increased ET with warming. The Kings River is one of ∼11 major rivers draining the western slope of the Sierra Nevada. The upper Kings River basin extends from the Pine Flat Reservoir to the Sierra crest and drains 3,998 km^2, with a mean elevation of 2,332 m and an estimated average precipitation of ∼1,000 mm yr^{-1}. The Kings River is particularly important for hydroelectric generation and as a source of water for agriculture: the Kings River service area was home to ∼750,000 people and generated gross agricultural revenues of ∼US$3 billion in 2003 (13, 18).

Results

The Sierra Nevada experiences a montane Mediterranean climate with more than 90% of annual precipitation falling in the local winter and spring. Large climate and vegetation gradients occur with elevation in the Kings River basin: precipitation increases with elevation to ∼500 m, where it begins to level off (19, 20); leaf area, canopy height, and biomass peak at midelevation and are reduced at upper and lower elevations. We installed four eddy covariance towers at ∼800-m elevation intervals in and around the basin, and combined these observations with remote sensing imagery to determine the current relationships between elevation, climate, and ET (21) (Figs. S1–S3).

Annual ET based on eddy covariance was greatest at 1,160 and 2,015 m, and 44% lower at 405 m and 49% lower at 2,700 m (Fig. 1*A*). Remotely sensed ET followed a similar pattern, with a midelevation maximum and declines at lower and upper elevation. P based on the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (20) and P−ET both increased with elevation. P−ET integrated across the entire watershed agreed with both the absolute magnitude and interannual variability of Kings River discharge (21) (Fig. S3). The patterns of P and ET create a zone at 2,400–3,600 m that is disproportionately important for runoff generation, accounting for 50% of watershed area and 68% of P−ET (Fig. 1*B*).

Significance

Climate change has the potential to reduce the supply of surface water by accelerating mountain vegetation growth and evapotranspiration (ET), though the likelihood and severity of this effect are poorly known. We used the upper Kings River basin in California's Sierra Nevada as a case study of the sensitivity of runoff to increased ET with warming. We found that Kings River flow is highly sensitive to vegetation expansion; warming projected for 2100 could increase ET across the Kings River watershed by 28% and decrease riverflow by 26%. Moreover, we found a consistent relationship between watershed ET and temperature across the Sierra Nevada; this consistency implies a potential widespread reduction in water supply with warming, with important implications for California's economy and environment.

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[1]To whom correspondence should be addressed. Email: mgoulden@uci.edu.

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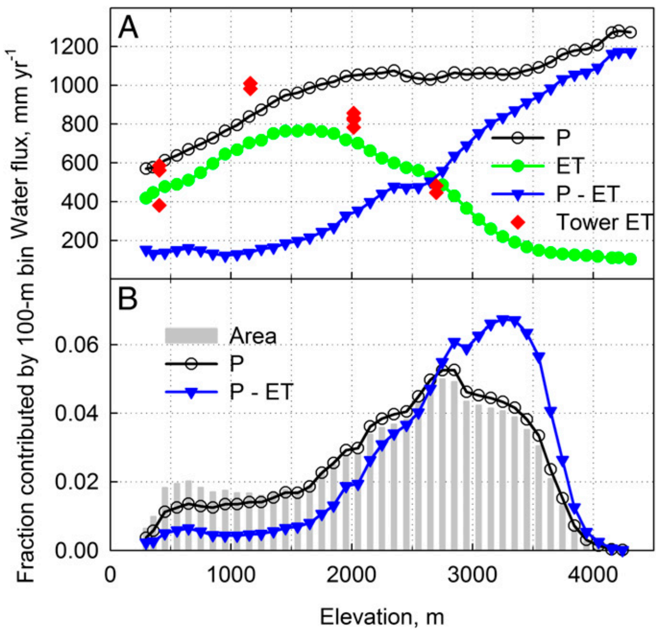

Fig. 1. (*A*) Relationships between elevation (meters above sea level) and ET by eddy covariance (filled red diamonds show individual water years), ET from NDVI (lines connect filled green circles), precipitation (P; lines connect open circles; 1981–2010 PRISM normal), and P−ET (lines connect blue inverted filled triangles; calculated by difference). (*B*) Fraction of total Kings River basin P (lines connect open circles), P−ET (lines connect blue inverted triangles); and area (gray bars) in each 100-m elevation bin.

The P−ET increase at high altitude is mainly (~80%) attributable to reduced ET (Fig. 1*A*). We quantified the limitations imposed by cold and moisture stress on eddy covariance gross primary production (GPP) (21) by analyzing the seasonal patterns of CO_2 uptake. GPP at 405 m was limited strongly by summer moisture stress; GPP at 1,160 and 2,015 m was limited by neither moisture stress nor cold; GPP at 2,700 m was limited strongly by winter cold (Fig. 2*A*). ET is well correlated with GPP across the elevation gradient (21), and the two fluxes are mechanistically linked through leaf gas exchange and plant phenology, implying that the same processes determine the altitudinal patterns ET. An analysis of the spatial correlation between remotely sensed ET and climate yielded a similar result. ET was systematically lower at locations with colder temperatures and less precipitation (Fig. S4); the combined effect of temperature and precipitation explained 66% of the ET variation across the basin (Figs. S2 and S5). The temperature and precipitation regressions were used to further partition the controls on ET with elevation. Moisture stress limitation decreased with increasing elevation to ~1,000 m; the midelevation zone was relatively unlimited by moisture or cold; cold limitation increased with elevation above ~2,000 m (17) (Fig. 2B and Fig. S6).

We examined output from the ensemble runs of the Community Climate System Model version 4 (CCSM-4) prepared using the representative concentration pathways (RCP) and historic experiments in the Coupled Model Intercomparison Project Phase 5 (CMIP-5). The mean 2085–2100 temperature increase in the atmosphere's lower 4 km above central California ranged from 1.3 °C for RCP 2.6 to 4.1 °C for RCP 8.5 (Fig. S7).

We used the ET regressions against temperature and precipitation (Fig. S4) to estimate the effect of 2085–2100 warming (Figs. S7–S9) on basin water balance. ET below ~2,000 m was unaffected by warming alone; ET above ~2,000 m increased in proportion to warming (Fig. 3). The low emission RCP 2.6 expanded ET 200-m upslope, which increased basin ET by 10% (Fig. 4*A*). The high emission RCP 8.5 expanded ET 700-m upslope, which increased basin ET by 28%. RCP 2.6 with constant P decreased P−ET by 9%; RCP 8.5 with constant P decreased P−ET by 26%.

Precipitation projections for 2100 remain uncertain, with considerable model-to-model and run-to-run variability. Previous analyses have indicated future drying in the southwestern United States (6), but some of the CCSM-4 CMIP-5 ensemble runs indicate a wetter Sierran climate. A recent hydrologic assessment estimated an ~5% mean precipitation decline for the region (22), and we adopted this value for comparison. A 5% P reduction alone decreased total-basin P−ET by 8% (Fig. 4*A*). A 5% P decrease and RCP 2.6 warming decreased P−ET by 17%. A 5% P decrease and RCP 8.5 warming decreased P−ET by 33%.

We tested our analysis by comparing the ET for 11 major rivers on the western slope of the Sierra Nevada against the corresponding mean temperature. ET was estimated for 1981–2010 by subtracting the observed full natural river flow (Q) for each basin from the corresponding spatially integrated P. The basin mean elevations ranged from 1,210 to 2,330 m, and mean daily maximum temperatures from 18.7 °C to 12.8 °C. Basin $P - Q$ was well correlated with temperature (Fig. 4*B*) ($R^2 = 0.716$), with a sensitivity of 44.6 mm $°C^{-1}$; this sensitivity is consistent with that derived in a completely independent way for the Kings River basin (Fig. 4*A*) (31.8 mm $°C^{-1}$).

Discussion and Conclusions

We draw three conclusions. First, Sierran ET peaks at midelevation and declines above ~2,000 m; this result is supported by the eddy covariance and remote-sensing observations (Fig. 1*A*), and also by $P - Q$ comparisons within (19, 23) and between river basins (Fig. 4*B*). Second, reduced ET at higher elevation

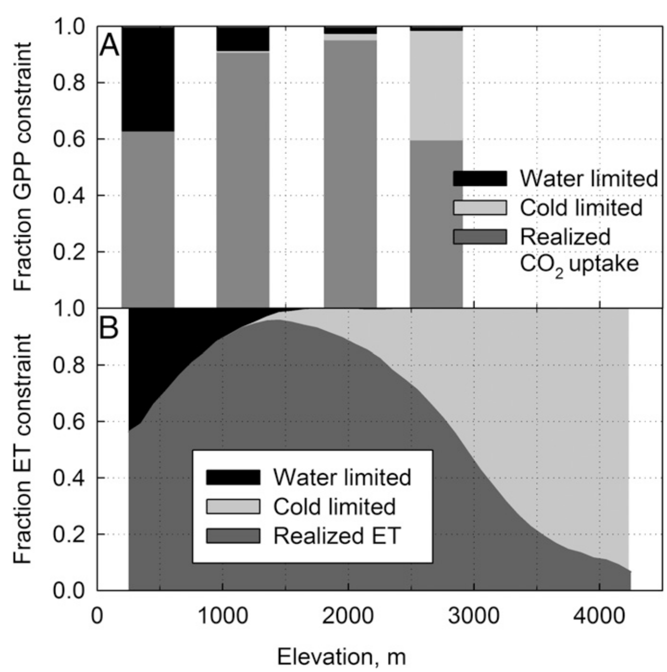

Fig. 2. (*A*) Relationship between elevation and the relative importance of water and cold limitation on eddy covariance-determined GPP (the annual gross CO_2 uptake). (*B*) Relationship between elevation and the relative importance of water and cold limitation on NDVI-based ET. The black area in both plots indicates the fractional loss attributed to water limitation in summer; the light gray area indicates loss attributed to cold limitation in winter; the intermediate gray area indicates the fraction of possible GPP or ET realized.

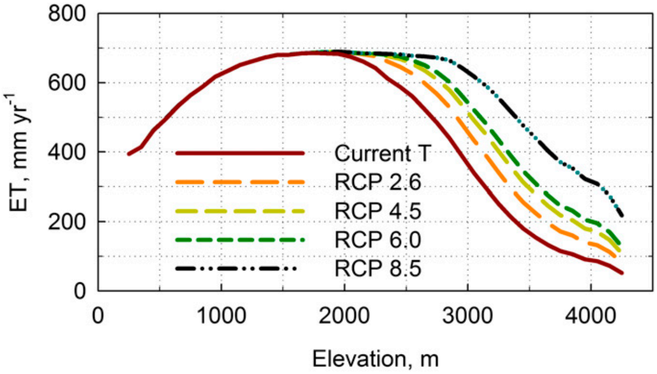

Fig. 3. Relationships between elevation (meters above sea level) and mean ET for warming projected for 2085–2100 with the four RCP. ET under current conditions was calculated using the climate regressions applied to the 1981–2010 PRISM Normals. ET under a warmer climate was calculated using the climate regressions and the elevation dependent warming predicted for each RCP. Precipitation was held constant at the 1981–2010 PRISM normal.

reflects cold limitation; this result is supported by shifts at higher elevation to winter dormancy (Fig. 2*A*) (21), denser canopies on southern aspects (Fig. S6), and denser canopies during lighter snowpack years (17). Third, the sensitivity of basin-wide ET to temperature is ∼30 mm °C^{-1}; this finding is based on the analysis of ET within the Kings River basin (Fig. 4*A*) and P − *Q* between river basins (Fig. 4*B*).

In concert, these findings imply that increased ET with warming and vegetation expansion would have a large effect on Kings River discharge. The annual average, ground-based lapse around the Kings River basin was −5.3° km^{-1} in 2011 (21), and warming by 2100 could move vegetation as much as 700-m upslope, assuming distribution is controlled exclusively by temperature. Warming at the 2,700-m site would decrease cold limitation and expand the growing season. Ultimately, the vegetation at 2,700 m may thicken and resemble that currently found at 2,015 m, with a concomitant local ET increase of up to 80%. A similar phenomenon could play out across the higher basin, decreasing basin-wide P−ET by as much as 26%.

A decline in ET at lower elevation with warming appears unlikely; we do not expect a simple uphill ET translation, with a compensatory lower-elevation ET decrease that quantitatively offsets the upper-elevation increase. This is not to say warming will not impact the lower-elevation zone; phenology shifts, increasing moisture stress, plant mortality, fire risk, biomass loss, and upslope species redistribution are possible (24–26). However, P−ET in this belt is already comparatively low, and it appears annual ET in this zone will continue to be constrained by water input and will neither increase nor decrease with warming. Our regression approach did not consider the possible effect of warming on midelevation ET, where annual ET is limited by neither winter cold nor summer water availability. The 1,060-m site has a higher annual ET than the 2,015-m site (Fig. 1*A*), despite large differences in snowpack duration; it is possible that warming will accelerate midmontane ET in ways that are not captured by our analysis.

The possibility of a large Sierran ET increase with warming conflicts with previous hydrologic assessments (10–13). This discrepancy is attributable to two phenomena that have received little research attention in the Sierra Nevada and that hydrologic models are struggling to represent (5, 8, 9). The first issue is obvious: models have assumed the distribution of vegetation type and density will remain static (10–13), whereas there is consensus in the ecological literature that upslope redistribution is likely and may have already begun (4, 15, 16, 26, 27).

The second issue is less obvious and involves the effects of moisture stress on phenology. Previous analyses of Sierran ET have often assumed montane tree roots are restricted to the shallow surface soil and forests have a short growing season constrained by moisture access in summer (28). This assumption has led to predictions that warming will hasten both the onset of high rates of ET in spring and the depletion of soil moisture and decline of ET in summer, leading to a quantitative phenological offset that minimizes the effect of warming on annual ET (2, 10, 12). More recently, the importance of deep montane rooting and access to moisture in the underlying fractured bedrock has been recognized; this deep rooting buffers trees from seasonal shifts in precipitation and evaporative demand and leads to a year-round growing season at mid elevation (e.g., refs. 21, 29, and 30). In turn, forest access to large stores of belowground moisture leads to the conclusion that declining summer ET is unlikely to offset increasing winter and spring ET, and forms the basis for our focus on the annual, rather than seasonal, effects of warming on ET.

In fact, we see both of these scenarios playing out along the elevation gradient. At lower elevation, where water availability is currently limiting, we expect a phenological offset that quantitatively offsets accelerated winter ET by decreased summer ET (Figs. 2 and 3). At upper elevation, where ample P and deep rooting allow year-round moisture access, we do not expect a compensatory summer ET decline, but rather increased annual ET. The effect of warming on basin-wide ET is expected to be dominated by the higher elevations, where high P and deep

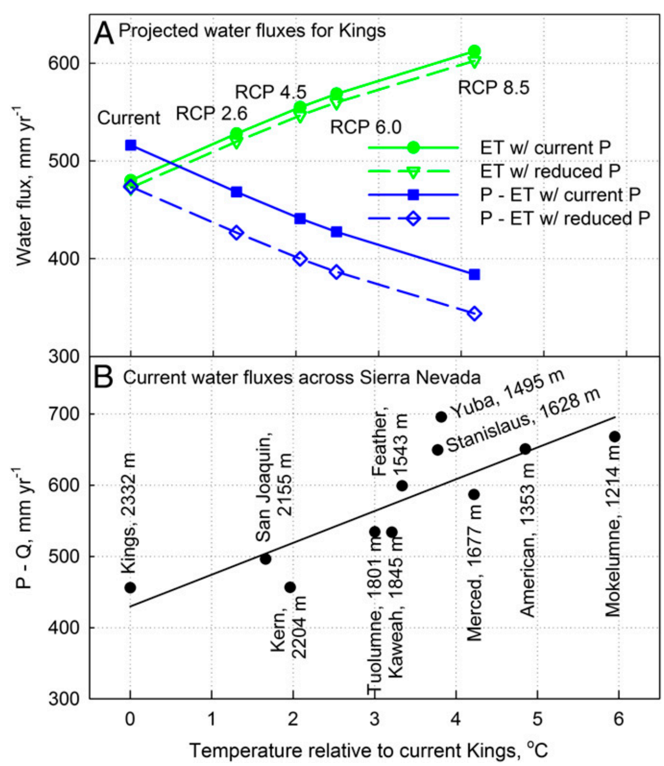

Fig. 4. (*A*) Effect of warming and P reduction on Kings River basin-average ET (mm yr^{-1}; lines connect green circles and inverted triangles) and P−ET (mm yr^{-1}; lines connect blue squares and diamonds). Basin-wide ET was calculated for all combinations of current conditions (1981–2010 PRISM normals), 2085–2100 elevation-dependent warming with the four RCP, and 5% P reduction. The ET sensitivity to warming under current P was 31.8 mm °C^{-1}. (*B*) The observed 1981–2010 relationship between basin-wide mean *T* and P − *Q* across 11 large river basins on the western Sierra Nevada slope. The P − *Q* sensitivity to temperature was 44.6 mm °C^{-1} [P − *Q* (mm yr^{-1}) = 44.64 × Δ*T* (°C) + 430.0; R^2 = 0.716].

rooting reduces the likelihood of a phenological offset, leading to increased annual ET. Rooting depth and deep moisture access will therefore play central roles in mediating the impact of climate change on the Sierra Nevada, and further work is needed to improve the representation of rooting depth in models of Sierran hydrology and ecology.

Both individual plants and entire ecosystems show strong functional convergence with climate, raising the possibility of widespread upward ET expansions with warming. For example, the inverse relationship between thermal and water limitation with elevation (Fig. 2) has been previously described in temperate semiarid regions (28); consistent relationships between elevation and properties, such as biodiversity, are widely recognized (31); and a similar relationship between temperature and ET holds across the entire western slope of the Sierra Nevada (Fig. 4*B*). However, this does not mean the discharge from all rivers will prove equally vulnerable to warming. The Kings River basin is comparatively cold as a result of a high mean altitude (Fig. 4*A*), and runoff from warmer basins, where the current mean ET is less limited by winter cold, may prove less sensitive to warming.

Our analysis relies on a simple empirical approach, whereas it is likely that models with much more mechanistic detail will ultimately provide the most reliable hydrologic forecasts, especially for novel conditions and locations. Nonetheless, our approach is well justified, given current understanding as well as inherent advantages offered by empirical strategies. Uncertainty over phenomenon, such as the effect of rooting depth on hydrology and montane plant phenology, currently limits the development of process-based models. Moreover, inputs at fine scales are often inadequate to drive detailed models of montane hydrology. Additionally, simple approaches may offer inherent advantages over mechanistic strategies. For example, emergent ecosystem properties associated with resource optimization (32) strengthen the correlation between remotely sensed indices and ET beyond that based solely on the biophysical controls on ET. Hence, our spatial extrapolation of annual ET was ultimately founded on both the effect of Leaf Area Index on ET, and the feedback of annual ET and GPP to Leaf Area Index (Fig. S1). This bidirectional relationship allowed estimates of ET that were superior to those based on a more explicit consideration of the unidirectional biophysical controls on ET (21). There is widespread agreement that mechanistic models will ultimately outperform simpler approaches, but there is little evidence that understanding of Sierran hydrology has reached the point where this is the case.

The simplicity of our approach allows us to clearly identify the underlying assumptions and limitations; several additional caveats require emphasis. Our study relied on a space-for-time approach, and assumed that climate is the main controller of the current ET distribution (Fig. S4). Our analysis will overstate the impact of climate on ET if nonclimatic factors that covary with elevation help explain the spatial patterns of ET. Additionally, we did not consider mechanisms that may mitigate vulnerability, including lags in vegetation and ecosystem-type migration (33), the effect of rising atmospheric CO_2 on hydrology (34), and the possible use of forest management to suppress ET (35). For example, upslope vegetation migration may be delayed by dispersal, establishment, or edaphic conditions (36). The lack of deeply weathered regolith at higher elevations may be especially important, possibly slowing or preventing the upward movement of vegetation with climate change and limiting the impact on river flow (37).

We view our analysis as a first step that establishes the vulnerability of montane ET and P−ET to upslope vegetation redistribution. The outstanding question is no longer whether warming has the potential to accelerate montane ET and reduce runoff, but how rapidly canopy density, plant species composition, and regolith porosity can redistribute with climate change. Further work is needed to better quantify the risk: prognostic models that couple biogeography, geomorphology, and hydrology will ultimately be needed to forecast the impact of climate change on montane hydrology.

Materials and Methods

Ground-Based Measurements. For ground-based measurements (Figs. 1*A* and 2*A*) we installed four eddy-covariance towers at ∼800 m altitude intervals in and around the upper Kings River basin (21). All sites were on granite and had vegetation that was typical for the elevation and that had not been disturbed recently. Observations from six additional towers in Southern California were used to establish a relationship between Normalized Difference Vegetation Index (NDVI) and annual ET (Fig. S1).

We analyzed the seasonal patterns of gross ecosystem exchange (GEE) to quantify the limitations imposed by summer moisture stress and winter cold. We divided each year into three elevation-dependent intervals based on meteorological conditions and fluxes. We used the GEE observations during the peak growing season to determine a best-fit rectangular hyperbola against light for periods that were neither cold nor water limited. We then ran the entire time series of observed light through the corresponding peak growing season rectangular hyperbola to calculate a time series of the GEE that would be expected in the absence of cold or moisture limitation (the unlimited GEE). We then summed unlimited GEE and also the observed GEE for the three intervals. Finally, we calculated the fractional reduction in GEE for each interval as the observed GEE divided by the unlimited GEE. We attributed the fractional GEE reduction in winter to cold limitation and the GEE reduction in late summer to water limitation.

Spatially Gridded P, ET, and P−ET. We extrapolated P, ET, and P-ET to the upper Kings River basin (21) (Figs. 1 and 2*B*). Elevation was taken from the Shuttle Radar Topography Mission (http://earthexplorer.usgs.gov). P was obtained for 1981–2010 (20) (http://prism.oregonstate.edu). ET was calculated from NDVI measured by the Moderate Resolution Imaging Spectroradiometer (MODIS MYD13Q1 Collection 5) Aqua satellite and averaged for snow- and cloud-free periods (http://daac.ornl.gov/MODIS). NDVI data were averaged for each water year, and ET was calculated based on a regression across 46 site years in 10 California ecosystems (Fig. S1). Gridded P−ET was calculated, and P, ET, and P−ET sorted into 100-m elevation bins and averaged.

We analyzed the current spatial relationships between the NDVI-based ETs and the corresponding 30-y climate normals (Fig. S4). We created a coregistered data stack of elevation, ET, and normal maximum air T (T_{max}) and P and analyzed the relationship between ET and T_{max} for all pixels that were not P-limited (pixels with $P < 900$ mm yr^{-1}), and between ET and P for all pixels that were not T-limited (pixels with $T_{max} > 12$ °C). We fit separate sigmoidal regressions between ET and T_{max} for the non–P-limited dataset (Fig. S4*A*), and between ET and P for the non–T-limited dataset (Fig. S4*B*).

We used the sigmoidal equations to separately calculate the ETs that would be expected for each pixel based on local P and T_{max} climatology. We then estimated the ET for each pixel as the minimum from the two sigmoidal equations (Fig. S5). We used the two regressions to flag each pixel as P-limited, T-limited, or unlimited, and to calculate the fractional ET limitation imposed by P or T. Finally, we binned all of the pixels at 100-m elevation intervals and averaged the fractional limitation imposed by P or T.

Climate Projections. For climate projections (Figs. 3 and 4*A*) we examined output from the CCSM-4 for the RCP and historic experiments in the CMIP-5. We downloaded monthly near-surface air temperature, air temperature, geopotential height, and precipitation for each of the five or six ensemble runs (www.earthsystemgrid.org/dataset/ucar.cgd.ccsm4.cmip5.output.html). We averaged temperature across 2085–2100 and 1950–2005. We output the projections for three grid cells immediately upwind (west) of our study region. We averaged across the ensemble runs (Fig. S7) and interpolated by altitude the 2085–2100 increase in air temperature over the historical mean for each 0.002083° resolution pixel in the Kings River basin. We also examined the RCP precipitation output for grid cells in the Sierra Nevada.

We combined the RCP temperature projections for each pixel in the Kings basin with the T- and P-based sigmoidal regressions (i.e., Fig. S4). We added the projected warming to the 1981–2010 PRISM temperature for each pixel, and calculated the ET that would be expected as the minimum of the two sigmoidal regressions. We calculated the P−ET for each pixel based on the 1981–2010 precipitation and also assuming a 5% P reduction. We binned the resulting ETs at 100-m elevation intervals and averaged, and also averaged across all pixels in the watershed.

Comparison Across River Basins. For comparison across river basins (Fig. 4*B*) we compared the water balance for 11 large river basins draining the western slope of the Sierra Nevada with mean basin temperature. The historic monthly full natural flow was downloaded for each river basin (http://cdec.water.ca.gov) and the annual flow summed and averaged for 1981–2010. The river basins were demarcated by the US Geologic Survey 8 Digit Watershed Boundary Dataset (http://datagateway.nrcs.usda.gov). The river basin boundaries were then combined with the PRISM 1981–2010 normals and the mean T_{max}, P, and elevation calculated. The observed riverflow (*Q*) and P were normalized by basin area and subtracted to estimate basin-average ET, which was compared with the mean basin elevation and T_{max}.

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