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Comment on "Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum Elevations"

Nathan L. Stephenson* and Adrian J. Das

Crimmins *et al*. (Reports, 21 January 2011, p. 324) attributed an apparent downward elevational shift of California plant species to a precipitation-induced decline in climatic water deficit. We show that the authors miscalculated deficit, that the apparent decline in species' elevations is likely a consequence of geographic biases, and that unlike temperature changes, precipitation changes should not be expected to cause coordinated directional shifts in species' elevations.

Certain climatic water balance parameters summarize the seasonal interactions of energy (heat and solar radiation) and water in biologically interpretable ways (*1*, *2*). Actual evapotranspiration (AET) is an index of the simultaneous availability of biologically usable energy and water in the environment and therefore is positively correlated with net primary productivity. Climatic water deficit, defined as PET-AET (where PET is potential evapotranspiration), is an index of evaporative demand that is not met by available water (i.e., drought). Deficit is therefore related to heat stress that plants cannot regulate through transpiration, metabolic costs that cannot be met by active photosynthesis, and potential for xylem hydraulic failure. Finally, surplus is an index of biologically unusable water—excess water that leaves a site, through runoff or subsurface flow, without being evaporated or transpired.

Crimmins *et al*. (*3*) attributed an apparent downward elevational shift of several northern California plant species over a 70-year period to a precipitation-induced decline in annual PET-P (where P is precipitation), which they incorrectly called "climatic water deficit." Unlike annual AET, deficit, and surplus, annual PET-P does not reflect soil water dynamics, snow dynamics, or the seasonal interactions of energy and water, and therefore has no biological meaning (*1*, *2*). For example, in the summer-dry, winter-wet environment of California, extra precipitation arriving in summer would reduce annual deficit and increase annual AET, with corresponding biological effects, whereas the same amount of precipitation arriving in winter would mostly leave a site as unusable surplus. For these sharply contrasting cases, however, the associated changes in annual PET-P would be identical.

We used a modified Thornthwaite approach (*4*) to calculate water-balance parameters for the 33 weather stations and two time periods (1920 to 1949 and 1976 to 2005) that Crimmins *et al*. used to demonstrate declining PET-P and to calculate their expected consequent change in species' elevations. Our approach accounts for soil water dynamics and temperature effects on snow dynamics. (We assumed a soil water-holding capacity of 200 mm; greater and lesser values gave similar results.) Annual deficit declined by an average of 7 mm between the two time periods, although the decline was not significant (P = 0.17, t test) (Fig. 1). AET increased by 21 mm ($P < 0.0001$, t test). However, because most of the 119-mm increase in annual precipitation arrived in winter, a majority of it became surplus (average 98 mm; $P < 0.0001$, t test) (Fig. 1). Changes in surplus and –(PET-P) were statistically indistinguishable ($P = 0.17$, t test) (Fig. 1). Thus, the increased temperature and precipitation of the contemporary period had relatively little effect on biologically meaningful aspects of the water balance (AET and deficit), and the change that Crimmins *et al*. found in PET-P largely reflects surplus water that was unusable to plants.

The historical and contemporary vegetation data sets compared by Crimmins *et al*. were geographically biased relative to one another [figure S2 in (*3*)], suggesting that the observed species' elevational differences could reflect differences in space, not in time. For example, the median latitude of the contemporary plots was 1.3° (~140 km)

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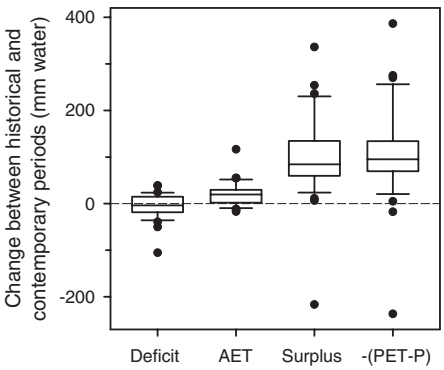

Fig. 1. Changes in annual climatic water balance parameters for the 33 weather stations between the historical (1920 to 1949) and contemporary (1976 to 2005) periods compared by Crimmins *et al*. (*3*). We changed the sign on Crimmins *et al*.'s index (PET-P) to facilitate comparisons. Boxes encompass the 25th through 75th percentiles; the other horizontal lines indicate the 10th, 50th (median), and 90th percentiles. A majority of the extra precipitation in the contemporary period became biologically unusable surplus, and the change in Crimmins *et al*.'s index is mostly a reflection of this.

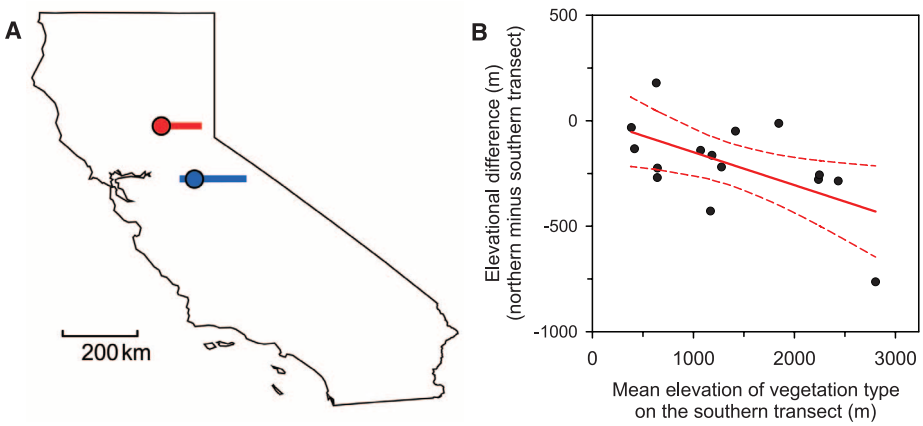

Fig. 2. Geographic bias and its consequences. (**A**) The median location in California of vegetation plots in Crimmins *et al*.'s historical (blue dot) and contemporary (red dot) data sets. The blue and red lines through the points represent, respectively, the southern and northern transects. (**B**) Contemporary vegetation types are found at significantly lower elevation on the northern than the southern transect, and the difference increases with elevation. Points are based on mean elevations of the 15 dominant native vegetation types on the two transects (*5*); the solid line is the linear regression, with its 95% confidence interval shown as dashed lines [compare with figure 4 in (*3*)].

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farther north than that of the historical plots (Fig. 2A) [not including the 27% of contemporary plots with unknown locations (*3*)]. To illustrate the potential effects of this magnitude of geographic difference, we defined 18-km-wide transects centered on each of these median latitudes, running from the foothills to the crest of the Sierra Nevada (Fig. 2A). Contemporary vegetation types (*5*) are found at significantly lower elevations on the northern than the southern transect (mean = –205 m, $P = 0.002$, *t* test), in rough agreement with the generalization that a poleward shift of 100 km in the temperate zone is accompanied by a ~100-m decline in species' elevations (*6*). For a number of possible reasons beyond the scope of this comment [including latitudinal differences in temperature lapse rates (*7*), land use effects, and truncation of species' ranges at highest and lowest elevations], the elevational differences in vegetation distributions between transects increased with elevation ($P = 0.025$) (Fig. 2B), a purely geographic effect that closely resembles Crimmins *et al*.'s purported temporal changes [figure 4 in (*3*)]. Thus, geographic bias alone could account for the species' elevational differences reported by Crimmins *et al*. If, after geographic biases are removed, some elevational differences persist, then altered fire regimes, logging, and other land use changes should be rigorously assessed as possible causes (*8*).

Even if Crimmins *et al*. failed to demonstrate a precipitation-driven decline in plant species' elevations, should we expect to see, as the authors contend, predominantly downward species shifts when future increases in precipitation outpace increases in evaporative demand? On both theoretical and empirical grounds, the answer is no. Crimmins *et al*. assumed that the interactions of energy and water can be adequately represented by a single metric (PET-P), with the effects of increasing precipitation counteracting the effects of temperature-driven increases in evaporative demand (PET). Yet the effects of changing evaporative demand and water availability on a site's water balance must be represented in two dimensions and are nearly orthogonal (*2*) (Fig. 3). Increasing evaporative demand is expected to drive species upward (Fig. 3B); for example, this is why species are usually found at higher elevations on sunward slopes than on shaded slopes (*2*, *9*). In sharp contrast, in summer-dry regions like California, increasing water availability (assuming its timing and amount are sufficient to substantially alter AET and deficit) will shift species along gradients of soil water-holding capacity or proximity to water without causing coordinated directional changes in elevation (Fig. 3C). Empirical support for this expectation comes from within Crimmins *et al*.'s study area, where certain forest types dominate on deep soils within a regional rainshadow (*2*, *10*). In the zone of nearly doubled precipitation outside of the rainshadow, rather than being found at much lower elevations the forest types are found on shallow soils but with no apparent elevational differences (*2*, *10*).

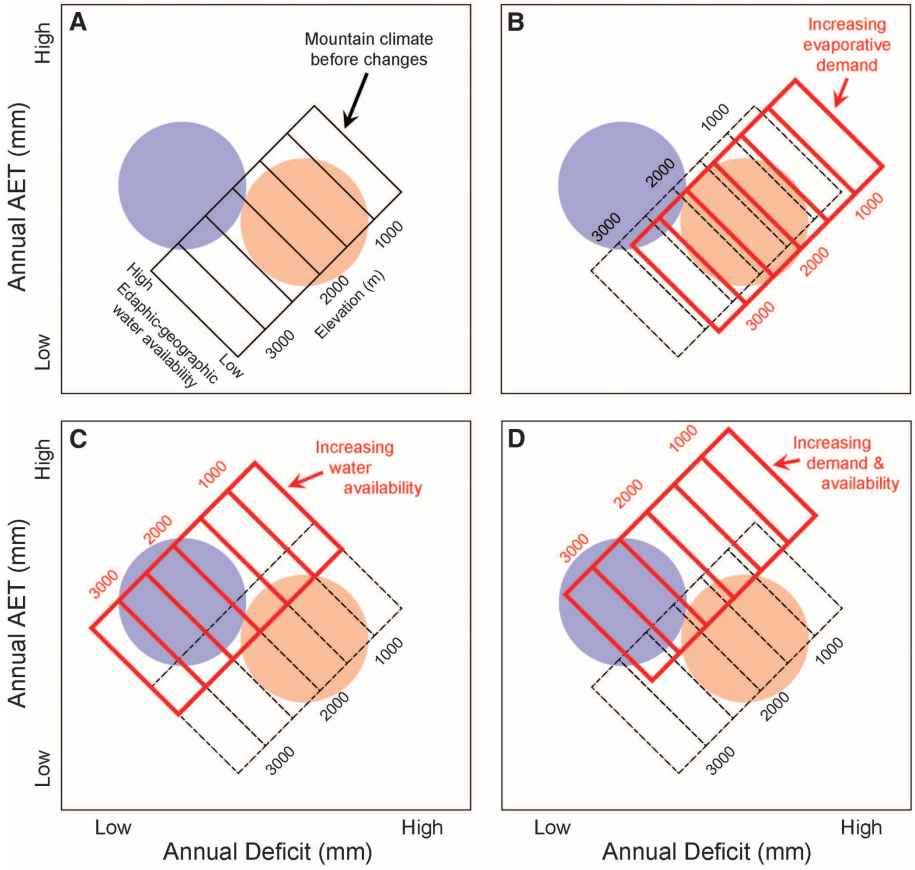

Fig. 3. Schematic illustration of the differing effects of changing evaporative demand and water availability on the climatic water balance and species' distributions [see (*2*) for background and supporting information]. The blue and orange circles represent two species' climatic niches, which are fixed relative to AET and deficit. (**A**) The black rectangle delimits a mountain's climatic space. Because AET + deficit = PET, the diagonal lines of slope –1 represent constant PET and thus constant elevation (*2*); for simplicity, we assume that all sites share similar aspect [emphasizing different aspects would shift the location of the rectangle (*2*) but would not affect any of the results or conclusions that follow]. PET declines and elevation increases from upper right to lower left. At a given elevation (constant PET), local water availability (as determined by soil water-holding capacity, distance from water, and the like) increases from lower right to upper left (*2*). (**B**) With regional warming (but unchanging precipitation), PET will increase at all elevations, which must increase AET, deficit, or both (*2*). The mountain's new climatic space (red rectangle) therefore has shifted relative to the species' fixed climatic niches, and the species' niches are now found at higher elevations. (**C**) Increasing water availability (assuming unchanging temperature and thus unchanging PET) drives climatic changes that are nearly orthogonal to those of (B). Because AET + deficit = PET, and PET remains unchanged, increasing water availability can only cause declines in deficit offset by identical increases in AET (*2*). The new climatic space has shifted along the water availability gradient; for example, the blue species is no longer limited to the wettest sites (such as riparian zones or deep soils) at a given elevation. The potential elevational range of the blue species has expanded while that of the orange species has contracted. Notably, however, mean species' elevations are unchanged. (**D**) With increasing evaporative demand and water availability, AET increases but deficit can either increase or decrease, depending on the magnitude of increase in demand relative to availability. Regardless of the direction of deficit changes (slightly decreasing is shown), species' niches will be found at higher, not lower, elevations. Certain other hypothetical niche shapes and orientations (not shown) can sometimes cause individual species to behave in unexpected ways (such as shifting downward despite increasing evaporative demand, or shifting upward or downward in response to precipitation changes). However, observed distributions of vegetation types along climatic gradients confirm that, averaged over many species, the patterns described above are expected to dominate (*2*, *10*).

Finally, the combined effects of increasing evaporative demand and available water—even if the extra water substantially reduces deficit—should drive species upward, not downward in elevation (Fig. 3D). Although many species undoubtedly will exhibit unexpected responses to future climatic changes (*11*, *12*), our general expectation for a warming climate is that most plant species will shift upward in elevation, regardless of changes in precipitation.

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