Response to Comments on “Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species’ Optimum Elevations”

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Wolf and Anderegg, Hijmans, and Stephenson and Das suggest that our findings of changes in climatic water balance driving downhill shifts in plant species distributions are flawed. We demonstrate that the conclusions these authors make are subject to the selection of methods they apply and do not provide sufficient evidence to reject our original findings.

We recently reported that changes in climatic water balance across much of the state of California have led to downhill shifts in plant species’ distributions (1). Wolf and Anderegg (2), Hijmans (3), and Stephenson and Das (4) contend that our analysis was flawed. We address their comments here.

Wolf and Anderegg (2) state that our results are narrowly applicable because of the limited number of species examined. We agree that overstating the scope of inference in scientific studies should be avoided and did not claim that our results were representative of all species in our study area. We simply stated that downhill shifts of plant species have occurred as reported elsewhere (5) and, under certain circumstances, may continue to occur. Wolf and Anderegg (2) note that the Wieslander surveys were not strictly presence-absence surveys. Although true for rare and herbaceous species, for the prominent woody species examined in (1), the Wieslander Vegetation Type Map (VTM) data set effectively contains the same level of detail as any presence-absence data set. For example, many plots in the VTM data set contain occurrence records for >12 woody species, suggesting that species need not be dominant over the entire plot to be recorded. This level of detail has previously led to the use of the VTM data for presence-absence modeling of woody species (6, 7). Wolf and Anderegg conclude by noting the lack of strong correlation between the magnitude of shifts in optimum deficit and optimum elevation as evidence against our hypothesis of niche tracking of water balance. However, under perfect niche tracking of water balance, we would expect no change in species optimums of water balance through time and hence no correlation between these variables.

The Technical Comment authors state that latitudinal bias in our data sets may invalidate our conclusions. Wolf and Anderegg (2) claim that the central Sierra Nevada and Central Coast regions were unsampled in the contemporary data set. This is false, as these two areas contained >1100 and >2300 vegetation plots, respectively. Hijmans (3) uses a linear regression between latitudinal bias and shifts in optimum elevation to suggest that latitudinal bias can account for our findings. We note that his critique omits critical details necessary for interpretation, such as a measure of fit and a simple plot. Consequently, we emulated his analysis and found that his regression model had low predictive power ($r^2 = 0.11$) and was sensitive to three outliers (species) that exert excessive leverage on the regression, as is apparent from a simple examination of Fig. 1A and corroborated using Cook’s distance and hat ($H$) value metrics (Fig. 1A; see caption for further detail). Further, *Juniperus occidentalis*, the species Hijmans presents in figure 1 of (3) as a graphical example of the influence of latitudinal bias, is identified as an outlier here. When these outliers are removed from our original data set, the purported relationship between latitudinal bias and shift in optimum elevation disappears ($r^2 = 0.02, P = 0.26$) (Fig. 1B) and our finding of significant downhill shifts is unchanged ($-77$ m, $P = 0.02, n = 61$). Although latitudinal bias did exist between our two data sets, Fig. 1B demonstrates that it had a nominal effect on the reported changes in species optimum elevations. The basis for the criticism leveled by the Technical Comment authors is the supposition that the greater sample density at higher latitudes in the modern data translates to a downward shift in the measure of central tendency of the distribution of the sample gradient (elevation). Indeed, this would be the case if we used means or medians. Instead, we use Gaussian optimums that use presence and absence data and are insensitive to sample effort along a gradient (8, 9), given that increased sample effort should leave the ratio of presence to absence (prevalence) unaffected. To confirm this, we compared species prevalence between the two data sets (historical and modern) within the northwestern and Cascade ecoregions (10), the area identified as the principle source of geographic bias by the technical comment authors. We found no discernible difference in species prevalence between the historical and modern data set for these ecoregions (paired t test, $P = 0.14, n = 61$).

Hijmans (3) presents results from a new bias correction approach. Unfortunately, he does not provide a minimum level of information neces-

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**Fig. 1.** Scatter plots of latitudinal bias versus shift in optimum elevation for entire data set (A) and with three statistical outliers removed (B). Solid red lines are from linear models (dashed lines represent 95% confidence intervals). Species identified as outliers in (A) are highlighted in red (*Juniperus occidentalis*, *Rhamnus crocea*, and *Symphoricarpos mollis*). These species were identified to exert excessive leverage on the regression analysis based on the Cook’s distance metric (22) and $H$ values (23). Cook’s distance values for the three species were 1.35, 1.2, and 0.98 (conservative cutoff for identifying an outlier is 1), whereas $H$ values were 0.074, 0.130, and 0.066 (cutoff for identifying outlier is 0.063), respectively. *Juniperus occidentalis* is represented by the point in the lower-right corner of (A).
sary for interpreting his results. For instance, he does not report the number of plots retained after his bias correction step, the sample size in terms of the number of species represented, or the ratio of species shifting their optima. We emulated the plot-pairing method described in (3) and found that robust statistical inferences were unfeasible with the small sample sizes retained. For example, using his methodology with the stated 1-km threshold left us with 600 plots and \( n = 9 \) species. Our original analysis yielded a sample density of about one plot per 20 km\(^2\), whereas the approach suggested by Hijmans (3) yields a sample density of one plot per 80 km\(^2\) at the 5-km threshold and one plot per 320 km\(^2\) at the 1-km threshold, a data reduction of 75 to 90\%. Thus, the small sample size used in Hijman’s analysis limits the validity of his conclusions. Likewise, Stephenson and Das (4) do not use our species presence-absence data but instead use arbitrarily defined vegetation communities to illustrate the potential effects of latitudinal bias on elevation means. This implicitly equates satellite-mapped vegetation alliances sampled along two transects to the species-specific data used in our analysis, and it assumes that Gaussian optima will be in a similar manner to means when faced with sampling bias.

Hijmans (3) states that the concept of “optimal elevation” should be avoided. We agree, which is why we also present results for changes in optima of water balance and temperature. The arguments presented by the Technical Comment authors cannot explain why we failed to detect species-level changes in optima for water balance (PET-P) between time periods (1). The latitudinal bias described by these authors would necessitate an apparent increase in water availability if species distributions remained static between time periods due to both geographic position and increased precipitation during the study period [see (11) for further details]. This is consistent with the middecadal drought in the 1920s and 1930s and the north-south gradient in moisture across the study area. Because we did not detect species-level changes in optima for water balance (\( J \)), it is not likely that species distributions remained static or that latitudinal bias can explain the entirety of our results.

Stephenson and Das (4) contend that we misrepresent the definition of climatic deficit and suggest that increased precipitation in the latter study period had little effect on the biologically meaningful components of water balance. We concede that our use of the term “deficit” to describe the metric of potential evapotranspiration—precipitation (PET – P) is not consistent with its more common usage in the literature. Stephenson and Das (4) also raise a valid point of contention regarding whether or not the increase in precipitation relative to the first 30-year period constitutes biologically usable water. To address their concerns, we emulated their analysis using a climatic water-balance model (12) similar to the one these authors present that accounts for soil water storage and drawdown (assuming a fixed storage of 200 mm) and includes the effect of temperature on snow hydrology. Our approach diverges from that of Stephenson and Das in that we use the Penman-Monteith equation (PM) (13) to estimate PET, whereas they use the Thornthwaite (TW) equation. We updated our previous estimation of PET (1) by incorporating revised data estimates (14) that are critical inputs to the PM equation. We demonstrate (Fig. 2A) that greater precipitation during the latter 30 years of the study period result in an increase in actual evapotranspiration (AET) of 21 mm (\( P = 0.01, t \) test) and a decrease in deficit of 32 mm (\( P = 0.006, t \) test), results that are consistent in sign with the results presented by Stephenson and Das (4) (Fig. 2B). Additionally, contrary to Stephenson and Das’s findings, we found that AET and deficit were sensitive to soil storage assumptions (e.g., deficit was –40 mm assuming 250 mm soil storage). These results are counter to their contention that increases in precipitation have had little influence on the “biologically meaningful” components of the water balance, because both AET and deficit show significant changes toward mesic conditions. Further, for the 33 meteorological stations used in our report (1), our original metric (PET-P) is highly correlated with annual deficit (\( r = 0.80, P < 0.0001 \)) and AET (\( r = -0.7, P < 0.0001 \)) as calculated using our revised model, suggesting that our original inferences were robust.

We reproduced the results of Stephenson and Das (Fig. 2B) using our water-balance model and the TW algorithm to estimate PET and find that the difference between our estimates can be traced to the use of different PET equations. We chose to use the PM method because (i) The TW approach predetermines PET to track temperature, given that it relies solely on temperature as a dynamic component. In contrast, the PM approach includes additional relevant factors such as vapor pressure deficit (VPD) and incident radiation. (ii) The TW method has been repeatedly shown to result in substantial biases in PET estimates in regions with arid summer conditions (e.g., our study area) (15). (iii) The TW equation has been shown to produce PET trend estimates of the wrong sign when compared with more sophisticated methods and observations of pan-evaporation (16, 17). Indeed, contrary to the PET trend data we present in our original report (1), our updated PET estimates (calculated with PM) decreased 11 mm (\( P < 0.01, t \) test), despite warmer temperatures during the latter 30-year record. These results are consistent with the sign of pan-evaporation trend measurements made over the past 50 years in our study area [figure 2 in (17)], which is effectively the only empirical data we can bring to bear on this problem. In our case, the estimated change in PET calculated with PM is a consequence of asymmetric changes in maximum, minimum, and dew-point temperature that resulted in an estimate 0.019 kPa decrease in regional VPD between 1920 to 1949 and 1976 to 2005.

Stephenson and Das (4) conclude with a theoretical model that suggests changes in available water will not result in coordinated directional changes in species elevation shifts. Although the implications of their model are intriguing, a full vetting of its assumptions and merits is beyond the scope of this response. However, we do highlight several issues related to the present discussion. First, if we assume that their model is correct, then the lower PET estimates over the latter study period suggest a downshift of elevation. Second, mapping geographic variables like elevation (which covaries with many drivers of PET in a nonlinear manner) or edaphic gradients in water availability (which can negatively covary with elevation due to soil depth) onto the environmental space defined by AET and deficit is not easily resolved because these relationships are not inherently linear or monotonic, as portrayed (4). Last, given that the empirical data presented in support of their model assumes a space-for-time substitution, their model does not yet account for the influence of temperature change on PET.

Fig. 2. Changes in annual water-balance parameters between historical (1920 to 1949) and contemporary (1976 to 2005) periods for 33 weather stations used in (1). Values are derived from a modified climatic water-balance model (12) with fixed soil storage of 200 mm using estimates of PET derived from the Penman-Monteith method (A) and Thornthwaite method (B).
not lend itself readily to identifying mechanisms that would actually drive distributional shifts. We present one hypothesis here: At local scales, soil depth tends to increase with decreasing elevation in convergent environments. Thus, increases in precipitation are more likely to be realized as increases in AET and decreases in deficit in these lower elevation sites. Survival rates of seedlings and saplings have been shown to increase with increasing relative growth rates and water availability (i.e., higher AET) (18, 19). Thus, site differences in seedling/sapling survivorship could account for the observed downward shifts, ameliorating restricted opportunities for regeneration brought on by protracted drought conditions in the study area during the 1920s and 1930s.

In summary, we thank the Technical Comment authors for critically reviewing our work and highlighting many of the issues that must be considered when examining historical data. Although we do not agree with many of the criticisms these authors have raised, we do feel that their scrutiny has highlighted both the strengths and weaknesses of our original report and has identified profitable areas for further research.

References and Notes

11. Using data from 33 cooperative observer program (COOP) stations within the study region and published values (20), we derived the following lapse rates for the study area: (i) $\frac{d(\text{temp})}{d\text{elev}} = -0.5^\circ\text{C}/100\text{m}$; $\frac{d(\text{temp})}{d\text{lat}} = -0.6^\circ\text{C}/100\text{km}$; (ii) $\frac{d(\text{precip})}{d\text{lat}} = 80\text{mm}/100\text{km}$; $\frac{d(\text{precip})}{d\text{elev}} = 25\text{mm}/100\text{m}$; (iii) $\frac{d(\text{PET})}{d\text{lat}} = -25\text{mm}/100\text{km}$; $\frac{d(\text{PET})}{d\text{elev}} = -14.5\text{mm}/100\text{m}$. Using these values and an assumption of static species distributions, a difference in latitude of 104 km N and 125 m downhill in elevation (due to the latitudinal bias for species described by Hijmans (3)) would result in an apparent decrease in PET-P of 49 mm, irrespective of changes in climate. When accounting for this and the decrease in PET-P during the study period [130 mm (2)], the Technical Comment authors’ claim would necessitate an average decrease in species optima for water balance (PET-P) of ~119 mm.
14. The additional data sources include (i) bias-corrected monthly average downward shortwave radiation flux from the geostationary operational environmental satellite (GOES), (ii) monthly average wind velocities from the North American Regional Reanalysis (21), and (iii) monthly average dew-point temperature derived from the parameter-elevation regressions on independent slopes model (PRISM). Due to a lack of long-term data for (i) and (ii), we fixed these as being constant across time; however, our approach accounts for changes in maximum temperature, minimum temperature, and dew-point temperature.

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