Brusca, R.C., W.M. Meyer, J. Overpeck, K. Franklin, J.F. Wiens, J. Eble, and W. Moore. 2014. Reply to C. David Bertelsen: Review of plant elevation changes in Arizona. Phytoneuron 2014-111: 1-4. Published11 December 2014. ISSN 2153 733X

REPLY TO C. DAVID BERTELSEN: REVIEW OF PLANT ELEVATION CHANGES IN ARIZONA

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David Bertelsen recently published an essay (Bertelsen 2014) discussing some methodological aspects of plant ecology. The methods he addressed have long been debated in the ecological literature and there is no need to comment on them here. However, his essay also critiqued our recent paper on plant distributions and climate change in the Santa Catalina Mountains (Brusca et al. 2014) and, incidentally, also the work of Robert Whittaker and William Niering (Whittaker & Niering 1964; Whittaker 1967). We feel that Mr. Bertelsen's summary of our paper was inaccurate and misleading, and we take this opportunity to correct his misunderstanding of our work.

Much of Bertelsen's essay faults us for giving evidence of plant elevational range distributions in the Santa Catalina Mountains that he feels are inaccurate for that mountain range. We are well aware of Bertelsen's many years of hiking Finger Rock Trail in the Santa Catalinas, recording changes in plant phenology across multiple habitats. However, his observational approach has little to do with our own, which was strictly to test a specific hypothesis. Our objective was to empirically test patterns predicted by models that suggest that upslope movements of plants are already underway. Because our questions and hypotheses focused solely on species elevation ranges, as do the models and Whittaker and Niering's publications upon which we are basing our comparisons, we do not require, as Bertelsen states, an understanding of where core and peripheral

populations reside. Our statistical analyses clearly support the dominate patterns in species range changes over the past 5 decades along this transect, which are (1) upslope shifts in their lower elevation range and (2) contracted elevational ranges. While this does not apply to all the species we studied, the majority of the species whose range differed from Whittaker and Niering (1964; hereafter W&N) showed upslope shifts in their lower elevation range (52%) and range contractions (59%). Compare this to only three species (11%) that had range expansions, two of which increased their elevational range, a pattern consistent with increasing temperatures at higher elevations.

Thus our goal was not to describe plant diversity in this mountain range. Our study was designed to repeat a single transect line, the 1963 W&N "Catalina Highway Transect." We made no claims that this transect should be viewed as representative of the entirety of the Santa Catalina Mountains. It is obvious that plant elevational ranges differ by location throughout the range, depending on many factors. To claim that we introduced "significant sampling bias" by not sampling riparian/wet canyon sites is to completely miss the point of our study. We attempted to find the best possible way to compare the admittedly poorly documented W&N data to current-day plant distributions, and thus we chose to use only the best W&N dataset, upland sites along their well-known Catalina Highway Transect. Of course, as Bertelsen notes, diversity in riparian habitats is often greater than in upland sites, but that was simply not the focus of our study. Bertelsen's observation that other researchers have reported alligator juniper from other elevations (e.g., Sabino Canyon) than those reported in our paper are irrelevant, because those were not from the W&N transect line. Alligator juniper has been reported by many other workers throughout the Catalina Mountains (e.g., Niering & Lowe 1984, from 3500 ft), but these other records were not from upland sites along the Catalina Highway Transect and so they have no bearing on our study.

Recently, Brian Enquist (University of Arizona) produced an interactive niche-model-based tree distribution predictor (Enquist 2014) that allows users to graphically visualize the effects of differ climate change scenarios on nearly a hundred tree species over time. We recommend this visual tool for those interested in climate effects on Southwestern montane ecosystems. A click on alligator juniper under different climate change scenarios is quite revealing.

The criticism that our plots were "near the heavily traveled [Catalina] Highway" and that this could have led to effects on plant distributions ignores the methodological protocols we used and described in our paper. Our plots were all 0.25 - 0.75 km from the highway, in rugged, steep terrain. We saw no evidence whatsoever of significant human impact in these areas, nor were they accessible to vehicles or road crews, etc., as Bertelsen claims Further, this was the same highway transect line used by W&N in 1963, and that was the sole source of our comparison.

Bertelsen claims that we compared our data to 34 of the W&N "plots," but that is incorrect. As we noted in our paper, we compared our data to the 30 plots shown in their Catalina Hwy transect diagram (Fig. 1, p. 10) that were upland (non-riparian/wet canyon) montane (3500-9000 ft elevation) sites. This figure is a graphical representation of the large W&N data table in the same paper, and the sites that were used for comparison are listed in the table (p. 15) as "elevation belts" III through VIII along the Catalina Highway, excluding "deeper ravines or canyons with flowing streams." To get the 34 points in this graph that Bertelsen apparently counted, one would need to include the 4 "Canyon Forest/Ravine" sites, which we specifically excluded (because we focused only on upland sites).

Bertelsen claims we did not include "non-occurrence" data, but this is incorrect. Complete lists of all plant species from every transect were cited (Moore et al. 2013), and these lists provide evidence of occurrence/non-occurrence for the 27 species we reported on.

Bertelsen faults us for not collecting voucher specimens. However, all 27 of the species we identified and counted are large well-known perennials, from trees to large shrubs that any competent naturalist could easily identify. And they were the most common plants in our plots. Nearly half of the species were conifers, oaks, and large perennial shrubs (well-tested field keys to southern Arizona conifers and oaks can be found at <http://rickbrusca.com/http___www.rickbrusca.com_index.html/ Research.html>). As we stated in our paper, "It is worth noting that even a casual observer could recognize the changes in plant elevation boundaries since the W&N surveys of 50 years ago — without so much as stopping the car as they drive up the Catalina Highway. Large and conspicuous plants such as alligator juniper, bracken fern, beargrass, and sotol simply do not begin to appear [along the highway] until much higher elevations than reported by W&N in 1964." Large, obvious and widely distributed species such as pines, firs, oaks, alligator juniper, bracken fern, and bear grass cannot be easily mistaken for anything else in the Santa Catalina Mountains. Furthermore, the lead botanist on our plot surveys was John F. Wiens, author/reviser of the standard botanical reference for Arizona (*Plants of Arizona, 2nd ed*).

Bertelsen criticizes the lack of georeferencing, specific elevations, and other associated data in the original W&N dataset. As we addressed in our paper, this is a challenging aspect of working with old datasets — the W&N fieldwork was done long before the advent of GPS or even desktop computers. But these data can also be rare goldmines of important information, and Whittaker's 50yr old Catalina Highway Transect has always been regarded as a pioneering cornerstone in American plant ecology. We compensated for lack of georeferenced and point-elevation data in the W&N dataset in numerous ways, including not recognizing an elevation shift unless our data fell entirely outside the 1000 ft elevation band used by W&N. This highly conservative approach potentially greatly underestimated elevation change in species since 1963. For example, if the W&N data recorded the lower elevation boundary for a species as 4000-5000 ft and our data record the lower elevation boundary of that species at 5100 ft, we recognize only a ± 100 ft elevation shift, even though the actual shift could be as much as 1100 ft. We also restricted our analysis to common species in order to avoid possible sampling errors with rare species. Furthermore, our sample plots were separated from one another (on average) by just 50 m in elevation, and species showing upslope movement of lower elevation had an average gain of nearly 160 m — more than three times our elevation sampling breaks — further indicating that our sampling effort was adequate.

Bertelsen points out that "correlation does not imply causation," which is of course true. However, we made no claim of specific causation in our study. We simply tested the hypothesis, based on modeling studies, that warming and drying climates are driving plant species up mountain slopes, and we found that on one transect line in one mountain range in Arizona that these factors (rising air temperatures, declining precipitation, and changing plant elevation ranges) were correlated, thereby supporting/not falsifying the prediction. The importance of this study lay in the 50-year old data set that was available from the historical work of Robert Whittaker — an historical record rarely available for field studies.

The last sentence of Bertelsen's essay is perhaps the most curious of all. It states that "With any degree of certainty, we can only say that short-term change in one response over a few decades is consistent with what we might expect with a changing climate." This is precisely the same conclusion drawn from our study.

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