

Vegetation synchronously leans upslope as climate warms

David D. Breshears^{*†‡§}, Travis E. Huxman^{*†¶}, Henry D. Adams[‡], Chris B. Zou^{*}, and Jennifer E. Davison^{*}

^{*}School of Natural Resources, [†]Institute for the Study of Planet Earth, [‡]Department of Ecology and Evolutionary Biology, and [¶]Biosphere 2/B2 Earthscience, University of Arizona, Tucson, AZ 85721

Ecologists have long sought to understand how vegetation relates to climate (1, 2). Such knowledge underlies effective mitigation and adaptation to contemporary climate change (3). Warming temperatures associated with anthropogenic increases in greenhouse gases have led ecologists to predict that vegetation gradients will “march” up the hill as climate envelopes shift with elevation, at a lag that scales with species’ generation times (4, 5). This prediction derives from the hypothesis that low-temperature constraints relax in association with warming climate, resulting in more favorable conditions for establishment and growth at the leading edge of a species’ range (e.g., the upper elevation boundary on a mountain) (6, 7). Because of competition and change in plant-available water, the trailing edge is expected to track the leading edge (5) with the central tendency expected to concurrently “march” upslope. This type of response has important implications for predicting and mitigating climate change impacts, particularly for vegetation spanning elevation gradients. If, rather than collectively moving with climate change, responses of dominant species assembled along an elevation gradient are highly individualistic, there is greater potential for more novel, nonanalog vegetation assemblages. Several types of plant distribution responses to contemporary changes in climate have been documented, such as truncation of species’ ranges at lower boundaries via tree mortality (8, 9), range-wide decreases in species abundance, either in response to extreme events (10) or due to increased background rates of mortality without increases in recruitment (11), and increases in the mean elevation in the distribution of species in a region (12). Yet no study to date has provided critically needed information on how distributions of dominant species along a gradient of vegetation communities change relative to one another, and how those changes relate to key ecosystem properties such as overall vegetation cover. In a new study in this issue of PNAS, Kelly and Goulden (13) address this knowledge gap, documenting how dominant plant species along an entire, contiguous valley–mountain gradient shift their distributions upslope synchronously with one another in response to anthropogenic warming.

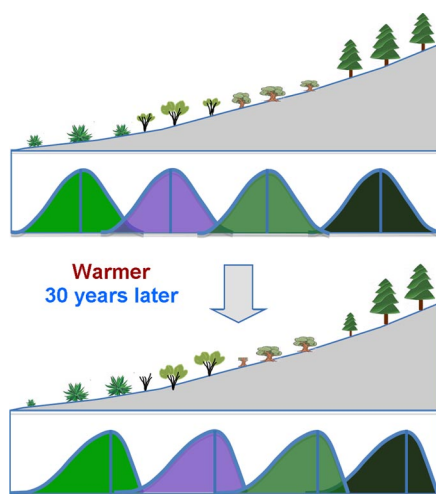


Fig. 1. Dominant plant species along an elevation gradient shifted synchronously with one another over a 30-year span that had a concurrent temperature increase, based on a new study by Kelly and Goulden (13). The ranges of the plant species’ distributions remained the same, resulting in an overall “leaning” of the vegetation gradient toward higher elevation.

Kelly and Goulden (13) document rapid changes in a vegetation gradient—spanning >2,000 m in elevation along the Santa Rosa Mountains in southern California—that occurred over a 30-year interval during which regional climate warmed. Over this period the central tendencies of the distributions of dominant plant species along the elevation gradient shifted synchronously upslope, in contrast to expectations based on population dynamics (5) and paleoecological studies (4) that vegetation responses should lag behind changes in climate. The range limits of each dominant species, however, remained unchanged. Consequently, in contrast to expectations of a “march” up the hill, the vegetation gradient essentially synchronously “leaned” upslope—the distribution shifted upslope within the existing range (Fig. 1). These synchronous species shifts arguably represent the net result of enhanced growth and new establishment at upper elevation sites and decline and mortality at the lower elevations. Interestingly, the functional characteristic of total ecosystem cover remained constant, suggesting that cover recessions of one species offset increases in the co-occurring lower elevation species, and resulted in the “lean-

ing” of plant distributions (i.e., more weighted toward the upslope direction). Rather astonishingly, the mean elevation increase in the vegetation distributions closely matched estimates based on local lapse rates and the corresponding temperature change over the 30-year interval.

Gradient analysis has been a powerful tool in ecology, from the development of the life-zone concept to testing of community ecology theory (1, 2, 14). Vegetation gradients have the potential to serve as powerful barometers of climate change (9), providing a more integrated assessment of responses to punctuated disturbance events that can trigger mortality driven by drought (8, 9), changes in fire regimes (15), or non-native species invasions (16). The new research by Kelly and Goulden (13) makes a critical step forward in detecting subtler but substantial changes across an entire gradient that are not the simple result of one process. Rather, these changes are the net result of establishment, growth, decline, and mortality—processes that are notoriously tuned to different temporal scales. The synchronous response across the gradient will be important for others to consider in assessing potential climate change impacts and mitigation options. Their findings for a relatively simple climate (i.e., Mediterranean, where the single seasonal pulse of precipitation is reduced by warmer temperature) also need to be evaluated for more complex regimes (e.g., bimodal precipitation).

The results add an important insight for those trying to answer the question, How will vegetation respond to climate change? The “lean” response contrasts with the previously mentioned “march” up the hill, or with that of a “crash” (Fig. 2). These response types are not mutually exclusive but rather could occur in combinations or in sequences in time associated with either trends and/or events in climate (17). Overall vegetation responses, rates of migration, and

Author contributions: D.D.B., T.E.H., H.D.A., C.B.Z., and J.E.D. wrote the paper.

The authors declare no conflict of interest.

See companion on page 11823.

[§]To whom correspondence should be addressed at: School of Natural Resources, University of Arizona, Tucson, AZ 85721. E-mail: daveb@email.arizona.edu.

© 2008 by The National Academy of Sciences of the USA

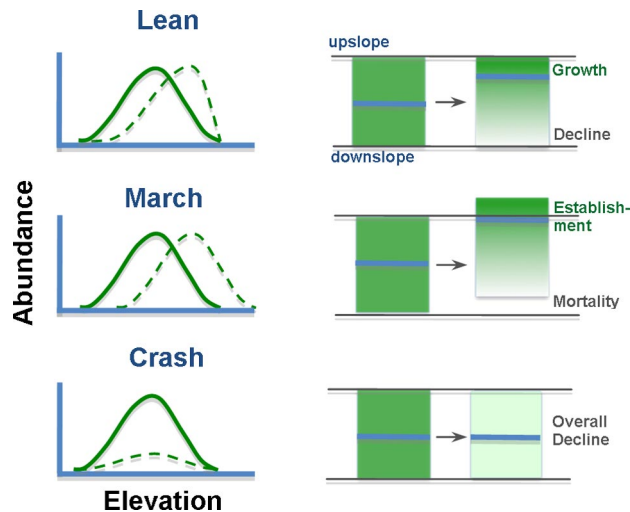


Fig. 2. Types of distributional change for species on an elevation gradient, resulting from changes in growth, establishment, decline, and/or mortality: “Lean,” where the range remains constant but the central tendency shifts, as highlighted in a new study (13); “March,” where the entire distribution and its range moves upslope (5); and “Crash,” where mortality is widespread across the range (10). These types are not mutually exclusive and could occur in various combinations or sequences to affect distribution range, central tendency, and/or skewness.

changes in ecosystem properties are likely all sensitive to these different types of responses. This sensitivity should be considered in assessments of vegetation change, whether approached by using simple climate envelopes or more mechanistic models (18). Novel communities (19) and complex ecosystem responses (8, 20) pose challenges

and are more probable if dominant plants along community gradients do not respond synchronously. In addition, the “lean” response could have biodiversity implications associated with the decrease in habitat area for a species that occurs moving upslope (5).

In short, the finding of Kelly and Goulden (13) is particularly significant

in that (i) it documents synchronous change among dominant species across an entire vegetation gradient; (ii) the change occurred relatively rapidly, rather than with a major lag as previously postulated; and (iii) the magnitude of elevation change corresponds directly to expectations associated with co-occurring temperature change. Their results also cut to the heart of early debate in community ecology (1), which focused on the degree to which species distributions are individual functions of abiotic gradients (Gleason) or resultant from high degrees of species interactions (as a “superorganism” – Clements). Whittaker (14) weighed in on this debate with classic research indicating that vegetation gradients were the product of highly individualistic responses of species to driving variables (especially temperature and precipitation). Now, the new research of Kelly and Goulden (13) highlights a synchronous response that spans across communities and will likely refocus attention on the role of individualistic versus synchronous responses of vegetation to climate change.

ACKNOWLEDGMENTS. We are supported by Biosphere 2/B2 Earthscience through the Philecology Foundation, U.S. Department of Energy National Institute for Climate Change Research Grant DE-FC02-06ER64159, National Science Foundation Drought-Induced Regional Response Network Grant DEB-0443526, and U.S. Department of Agriculture CSREES Fellowship Grants 2005-38420-15809 and 2007-38420-17775.

- McIntosh RP (1985) *The Background of Ecology: Concept and Theory* (Cambridge Univ Press, Cambridge, UK).
- Merriam CH (1898) *Life-Zones and Crop-Zones of the United States*, US Department of Agriculture, Division of Biological Survey Bulletin 10 (Government Printing Office, Washington, DC).
- Intergovernmental Panel on Climate Change (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the IPCC* (Cambridge Univ Press, Cambridge, UK).
- Davis MB (1989) Lags in vegetation response to greenhouse warming. *Climate Change* 15:75–82.
- Peters RL, Lovejoy TE, eds (1992) *Global Warming and Biological Diversity* (Yale Univ Press, New Haven, CT/London).
- Harte J, Shaw R (1995) Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. *Science* 267:876–880.
- Adams HD, Kolb TE (2005) Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *J Biogeogr* 32:1629–1640.
- Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proc Natl Acad Sci USA* 95:14839–14842.
- Gitlin AR, et al. (2006) Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conserv Biol* 20:1477–1486.
- Breshears DD, et al. (2005) Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144–15148.
- van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol Lett* 10:909–916.
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771.
- Kelly A, Goulden M (2008) Rapid shifts in plant distribution with recent climate change. *Proc Natl Acad Sci USA* 105:11823–11826.
- Whittaker RH (1967) Gradient analysis of vegetation. *Biol Rev Cambridge Philos Soc* 42:207–264.
- Bradley BA, Houghton RA, Mustard JF, Hamburg SP (2006) Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Global Change Biol* 12:1815–1822.
- D’Antonio RF, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87.
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: Events, not trends. *Front Ecol Environ* 5:365–374.
- Shugart, HH (1998) *Terrestrial Ecosystems in Changing Environments* (Cambridge Univ Press, Cambridge, UK).
- Williams JW, Jackson ST (2007) Novel climates, non-analog communities, and ecological surprises. *Front Ecol Environ* 5:475–482.
- Brown JH, Whitham TG, Ernest SKM, Gehring CA (2001) Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science* 27:643–650.