Regional vegetation die-off in response to global-change-type drought

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Future drought is projected to occur under warmer temperature conditions as climate change progresses, referred to here as global-change-type drought, yet quantitative assessments of the triggers and potential extent of drought-induced vegetation die-off remain pivotal uncertainties in assessing climate-change impacts. Of particular concern is regional-scale mortality of overstory trees, which rapidly alters ecosystem type, associated ecosystem properties, and land surface conditions for decades. Here, we quantify regional-scale vegetation die-off across southwestern North American woodlands in 2002–2003 in response to drought and associated bark beetle infestations. At an intensively studied site within the region, we quantified that after 15 months of depleted soil water content, >90% of the dominant, overstory tree species (*Pinus edulis*, a piñon) died. The die-off was reflected in changes in a remotely sensed index of vegetation greenness (Normalized Difference Vegetation Index), not only at the intensively studied site but also across the region, extending over 12,000 km² or more; aerial and field surveys confirmed the general extent of the die-off. Notably, the recent drought was warmer than the previous subcontinental drought of the 1950s. The limited, available observations suggest that die-off from the recent drought was more extensive than that from the previous drought, extending into wetter sites within the tree species' distribution. Our results quantify a trigger leading to rapid, drought-induced die-off of overstory woody plants at subcontinental scale and highlight the potential for such die-off to be more severe and extensive for future global-change-type drought under warmer conditions.

tree mortality | vegetation dynamics | climate change impacts | woodlands | *Pinus edulis*

Global climate change is projected to yield increases in frequency and intensity of drought occurring under warming temperatures (1–3), referred to here as global-change-type drought. Protracted, subcontinental drought in the midlatitudes is a complex response driven in part by anomalies associated with oscillations in sea surface temperature (2–4), which can include oscillations over periods of decades or longer, such as those associated with the Atlantic Multidecadal Oscillation and the Pacific Decadal Oscillation (4), and shorter periods spanning several years, such as those associated with the El Niño Southern Oscillation (3). Greenhouse gas forcings are expected to alter these oceanic effects on drought patterns (1–3). Indeed, the most recent protracted drought in southwestern North America, spanning the beginning of the 2000 millennium, exhibited anomalous sea surface temperature patterns consistent with projections of global change response (3). Protracted drought can trigger large-scale landscape changes through vegetation mortality from water stress (5, 6), sometimes associated with bark beetle infestations (5), but the potential for regional to subcontinental scale vegetation die-off under global-change-type drought remains a pivotal uncertainty in projections of climate change impacts (1, 7, 8). Of particular concern is regional-scale mortality of overstory trees, which rapidly alters ecosystem type, associated ecosystem properties, and land surface conditions for decades. The potential for this response is highlighted by a rapid shift of a forest ecotone caused by *Pinus ponderosa* mortality in response to the 1950s drought (5). The effects of drought accompanied by warmer temperatures resulting from greenhouse forcings might be expected to produce even greater effects on vegetation change than those of periodic, protracted drought alone (5). Yet few, if any, studies quantify rapid, regional-scale vegetation die-off in response to drought, key environmental conditions triggering tree mortality, such as prior soil moisture conditions, or how anomalously high temperatures might alter such vegetation responses. Such relationships urgently need to be quantified to improve climate change assessments (9).

We evaluated the impacts of the recent drought on regional-scale mortality of piñon pine (*Pinus edulis*), which is sensitive to climate variation and dominates piñon-juniper woodlands, one of the most extensive vegetation types in the western North America (10–12). Specifically, we evaluated the impacts of the recent drought on regional-scale mortality in the context of the potential impacts of global-change-type drought, and (*i*) demonstrated that the recent drought is not as dry as the previous drought but is warmer in numerous respects, thereby providing a case study for global-change-type drought; (*ii*) quantified site-specific conditions in soil water content and local vegetation response (percentage of tree mortality, and a remotely sensed vegetation index related to photosynthetic activity and associated greenness, Normalized Difference Vegetation Index, NDVI) to precipitation and temperature dynamics; and (*iii*) estimated and verified regional-scale stress and mortality responses in vegetation to drought by using weekly NDVI data back to 1989 and supplemental aerial surveys and field inventories.

Methods

We obtained monthly climate data for all meteorological stations in Arizona, New Mexico, Colorado, and Utah that were listed with the Western Regional Climate Center (www.wrcc.dri.edu; Western U.S. Climate Historical Summaries, September 1,

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Abbreviations: NDVI, Normalized Difference Vegetation Index; GAP, Gap Analysis Program.

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2004–Decmber 14, 2004) and determined annual values for total precipitation, mean minimum temperature, and mean maximum temperature. We then identified 22 of those stations associated with piñon-juniper woodlands based on two criteria. First, stations were within 1,000 m of the piñon-juniper vegetation type where *P. edulis* was either the dominant or codominant plant species, as defined by the United States Geological Survey Gap Analysis Program (GAP) distribution map of dominant vegetation (scale of 1:100,000; www.gap.uidaho.edu). The GAP map is derived from satellite imagery combined with existing data, air and field study, and expert knowledge. Our second criterion was that the record of monthly precipitation and temperature for the drought intervals of interest, defined below, was relatively complete: ≤2 months missing for any year of interest, except for two stations (Moab and El Vado) that were missing up to 4 months of data for one of the years. We compared the recent drought with that of the 1950s by focusing on the four driest consecutive years for each: 2000–2003 and 1953–1956, respectively. We tested for differences in total precipitation, mean minimum temperature, and mean maximum temperature between the two drought intervals by using *t* tests paired by station; we applied sequential Bonferroni adjustment to determine tablewide significance for the three *t* tests (13). We categorized anomalously dry or warm years as in the extreme 10 percentiles.

We evaluated synoptic vegetation changes by using the NDVI (1 km^2 = 1 pixel), calculated by using near–IR and visible reflectance values collected by the advanced very high-resolution radiometer located on several National Oceanic and Atmospheric Administration satellite platforms (14). NDVI has been widely used to estimate landscape patterns of primary production (14) and is correlated with foliar water content and water potential for *P. edulis* needles over a wide range of conditions, including recently deceased trees (15). Weekly values of NDVI from 1989 to 2003 were extracted by using the GAP-delineated piñon-juniper distribution of the four states. Before extraction, the NDVI data were corrected by using biweekly maximum value compositing to remove most cloud contamination and were corrected to reduce effects of atmospheric haze and ozone. These data were also detrended to account for artificial value drift by examining temporal signatures from invariant targets (16). The detrending provides a conservatively large adjustment that could mask some of the NDVI dynamics, and hence we present NDVI dynamics as a range bounded by nondetrended and detrended estimates. For each year, mean regional NDVI was calculated from the corrected images for late May through June (Julian weeks 22–26), a period when understory greenness was observed to have minimal effect, allowing overstory effects of die-off to be most apparent.

We used measurements from an intensively studied site located within the region, Mesita del Buey near Los Alamos, NM (17, 18), to document changes in (*i*) precipitation, temperature, and soil water content before and during the recent drought, and (*ii*) the associated responses in site NDVI and tree mortality. Soil water content was measured by using neutron attenuation at a 20-cm depth at 11 locations spaced at ≈10-m intervals; measurements were calibrated for local soils and generally obtained once or more per month. Mortality at Mesita del Buey was estimated through field surveys in 2002 and 2003 and was compared against baseline data. Weekly NDVI values for the Mesita del Buey site were estimated for a 3-×-3-pixel window (after comparing results with window sizes ranging from 1 × 1 to 9 × 9 pixels) to jointly mitigate spatial registration issues and land cover heterogeneity effects. For each year mean NDVI values for Mesita del Buey were calculated for late May through June (weeks 22–26) for intervals representing baseline (1989–1999) and drought after extensive die-off (2002–2003).

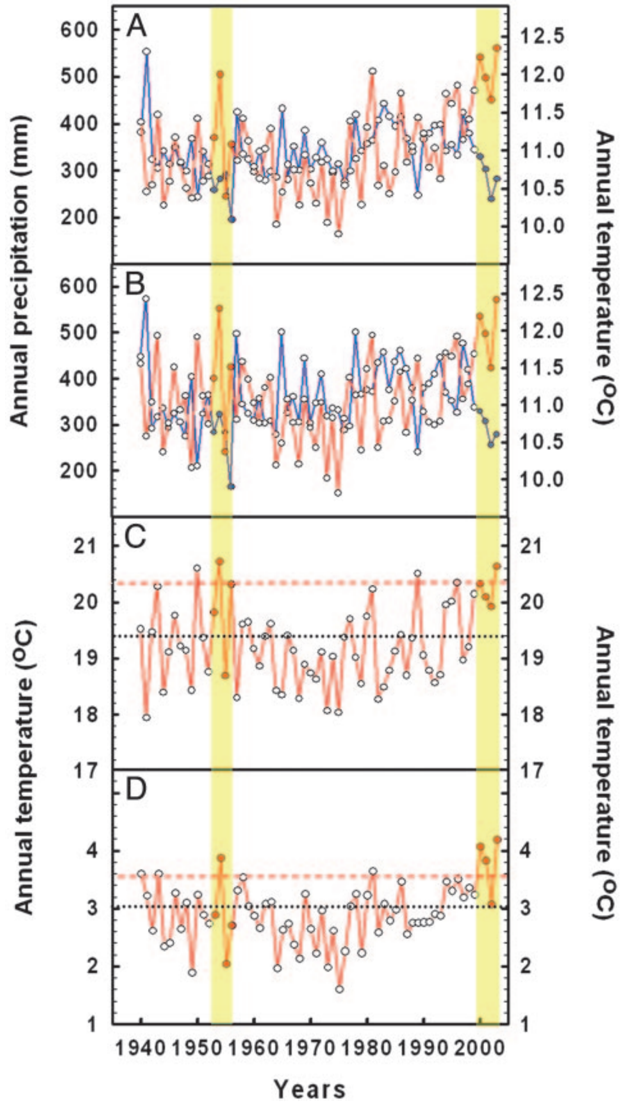

Fig. 1. Southwestern North American climate. (*A* and *B*) Annual mean precipitation (mm) and average of maximum and minimum temperatures (°C) for all stations in the four-state region (*A*) and only stations in or near piñon-juniper woodlands within that region (*B*) are shown. (*C* and *D*) Associated maximum (*C*) and minimum (*D*) temperatures for piñon-juniper woodlands (black line: long-term mean; red line: 10th or 90th percentile, differentiating driest or hottest years) are shown. Shaded bands indicate the four consecutive driest years of the 1950s drought (1953–1956) and the recent drought (2000–2003). Compared with the 1950s drought, the recent drought was wetter ($P < 0.05$) but warmer for maximum ($P < 0.05$) and especially minimum temperature ($P < 0.001$).

To confirm that regional NDVI changes within the GAP-delineated area were associated with tree mortality, we obtained data from aerial surveys conducted by the U.S. Department of Agriculture Forest Service and distributed by the Forest Health Technology Enterprise Team (19), which covered ≈60% of the piñon-juniper woodland distribution in the four states during 2002 and 2003. The surveys were flown 300–400 m above ground, and areas of noticeable stand-level mortality from drought and associated bark beetle infestation were sketch-mapped at the 1:100,000 scale. We also estimated *P. edulis* mortality for nonseedling trees (≥1-m height) at a verification site in each of the four states, based on either documented changes in inventories that were conducted before mortality event (Arizona, Colorado, New Mexico) or for which recent

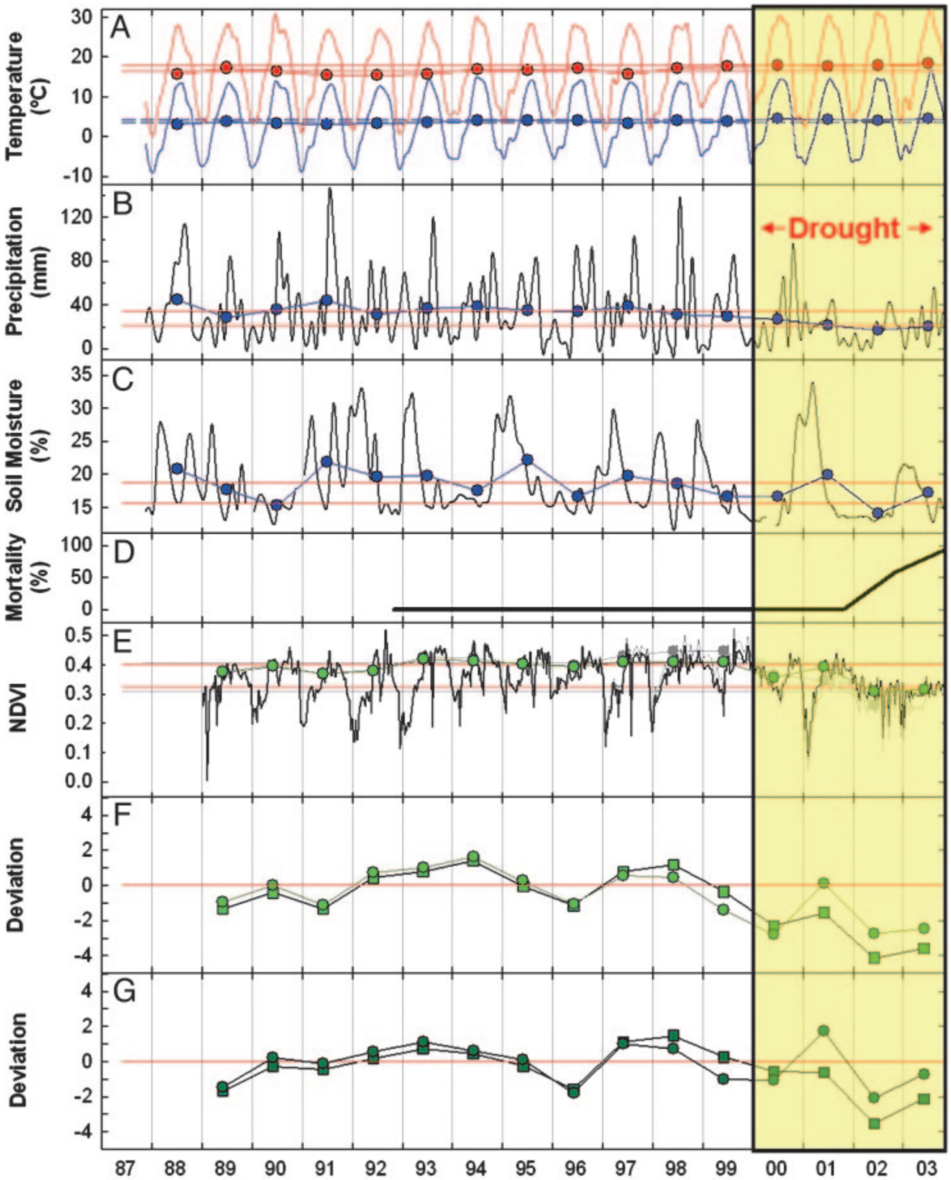

Fig. 2. Drought-induced mortality at Mesita del Buey, northern New Mexico. Shown for predrought and drought periods are: minimum (blue) and maximum (red) temperature (°C) (*A*), precipitation (mm) (*B*), volumetric soil water content at 20 cm (%) (*C*), *P. edulis* mortality (*D*), weekly NDVI at Mesita del Buey (*E*), and NDVI for late May-June for Mesita del Buey (*F*) and the region encompassing *P. edulis* (*G*). For *A*–*E*, circles indicate means (annual for *A*–*C* and late May-June for *E*–*G*); horizontal lines indicate predrought and drought means, with the latter being warmer, wetter, or lower in NDVI. For *E*, gray lines are nondetrended estimates; for *F*–*G*, squares are nondetrended and circles are detrended estimates.

mortality was inferred (Utah); verification sites varied from 4 to 49 in number of plot or belt transects and 0.2–4.9 hectares for total area surveyed. The New Mexico site spanned the more intensively studied Mesita del Buey site and included wider coverage.

Results

The recent drought spanning southwestern North America was anomalously dry, similar to the subcontinental drought of the 1950s, but contrasted with that drought in having anomalously high temperatures for the entire region (Fig. 1*A*) and for locations only within the distributional range of *P. edulis* (Fig. 1*B*). Within the distributional range of *P. edulis*, total precipitation during the 4-year interval for the recent drought (2000–2003) was slightly greater than that for the 1950s drought (Fig. 1*B*; $P < 0.05$). Yet the recent drought was warmer than the 1950s drought with respect to maximum annual temperature (Fig. 1*C*; $P < 0.05$) and particularly with respect to minimum annual temperature (Fig. 1*D*; $P < 0.001$) and average summer maximum temperature (June and July; $P < 0.001$). At the intensively studied site within the region located in northern New Mexico (Mesita del Buey), mean minimum and mean maximum temperatures were warmer during than before the recent drought (Fig. 2*A*), a period of reduced annual precipitation spanning 2000–2003 (Fig. 2*B*). The timing and amount of the reductions in precipitation in conjunction with simultaneous warmer temperatures resulted in 10 consecutive months (October 1999–August 2000) of dry soil water conditions (<15% volumetric water content, associated with a soil water potential of less than −2.5 MPa; ref. 18), which was later followed by an additional 15 consecutive months of dry soil water conditions (August 2001–October 2002; Fig. 2*C*). Bark beetle (*Ips confusus*) infestation and change in foliar water and spectral conditions were observed subsequently during 2002 and 2003 (15). Resulting *P. edulis* mortality at Mesita del Buey exceeded 90% (Fig. 2*D*). The tree mortality at this site is reflected in a >20% decrease in NDVI, highlighted by the reduced NDVI values for 2002 and 2003 that persisted once the *P. edulis* mortality began (Fig. 2 *E* and *F*). Premortality effects of the drought are evident in the depressed values of site NDVI for 2000, a very dry year, and then are partially offset by increased NDVI in 2001, because of a relatively wet 2000–2001 winter and associated herbaceous response. The site-specific changes in NDVI are roughly parallel with regional-scale changes in NDVI (Fig. 2*G*), which also dropped off substantially in 2002 and to a lesser extent in 2003. The site-specific mortality at Mesita del Buey proceeded into 2003, despite a pulse of soil moisture during the 2002–2003 winter (Fig. 2*F*), with NDVI remaining depressed through 2003. Conversely, at the regional scale where mortality was less complete, the winter 2002–2003 pulse of soil moisture appears to have resulted in an increased herbaceous response that partially masks the effect of the tree die-off (Fig. 2*G*). Nonetheless, even using the conservatively detrended estimate, NDVI-depressed values at the regional scale remain substantial. Indeed, reductions in NDVI of similar magnitude to those linked directly to tree mortality at Mesita del Buey covered much of the *P. edulis* distribution, indicating the spatial extent and variation of drought-induced mortality (Fig. 3*A*). Regional aerial surveys conducted by the U.S. Forest Service for a subset of the area within the study region confirm that there was widespread mortality for >12,000 km^2 (Fig. 3*B*), as reflected in our estimates of NDVI changes. Additional field plot inventories provide further confirmation of widespread *P. edulis* mortality, with mortality from the drought and associated infestations of the bark beetle *I. confusus* at the four verification areas ranging from 40% to 80% (Fig. 3*B*).

Discussion

Our results are notable in documenting rapid, regional-scale mortality of a dominant tree species in response to subcontinental drought accompanied by anomalously high temperatures. Although the proximal cause of mortality for most of the trees was apparently infestation by bark beetles, such outbreaks are tightly tied to drought-induced water stress (5, 20). The soil water content in the months preceding tree mortality was sufficiently low to have produced high plant water stress and cessation of transpiration and photosynthesis in *P. edulis* (18). Importantly, there was high mortality of as much as 90% or more at studied high elevation sites, such as Mesita del Buey, Mesa Verde in Colorado, and near Flagstaff, AZ, which are near the upper limit of *P. edulis* distribution and where precipitation and water availability are generally greater than at many other locations where this species occurs. In contrast, mortality in response to the 1950s drought in the same landscape as Mesita del Buey in northern New Mexico was documented predominantly on drier, mostly lower elevation sites, based on the presence or absence of standing or downed dead piñon wood (21). Most of the patchy mortality in the 1950s was associated with trees >100 years old, whereas nearly complete tree mortality across many size and age classes was observed in response to the recent drought (ref. 22 and data for Figs. 2*D* and 3*B*). Collectively, these observations suggest that the mortality response to the recent drought was greater in magnitude and extent than the mortality response to the 1950s drought. The warmer temperatures associated with the recent drought would have increased the energy load and water stress demands on the trees and may account for the apparently greater resulting mortality. The effects of water and temperature stress during the recent drought could have been further exacerbated by (*i*) anomalously high precipitation in the southwestern North America from about 1978–1995 that allowed rapid tree growth and increased stand densities, resulting in potentially greater intraspecific competition for drought-limited water and greater susceptibility to drought, beetle infestation, and associated pathogens (22) and/or (*ii*) amplifying effects of warmer temperatures and longer growing seasons on beetle growth rates and population dynamics (23). Nonetheless, previous studies of drought-induced die-off have highlighted the underlying importance of water stress in triggering die-off (5, 20).

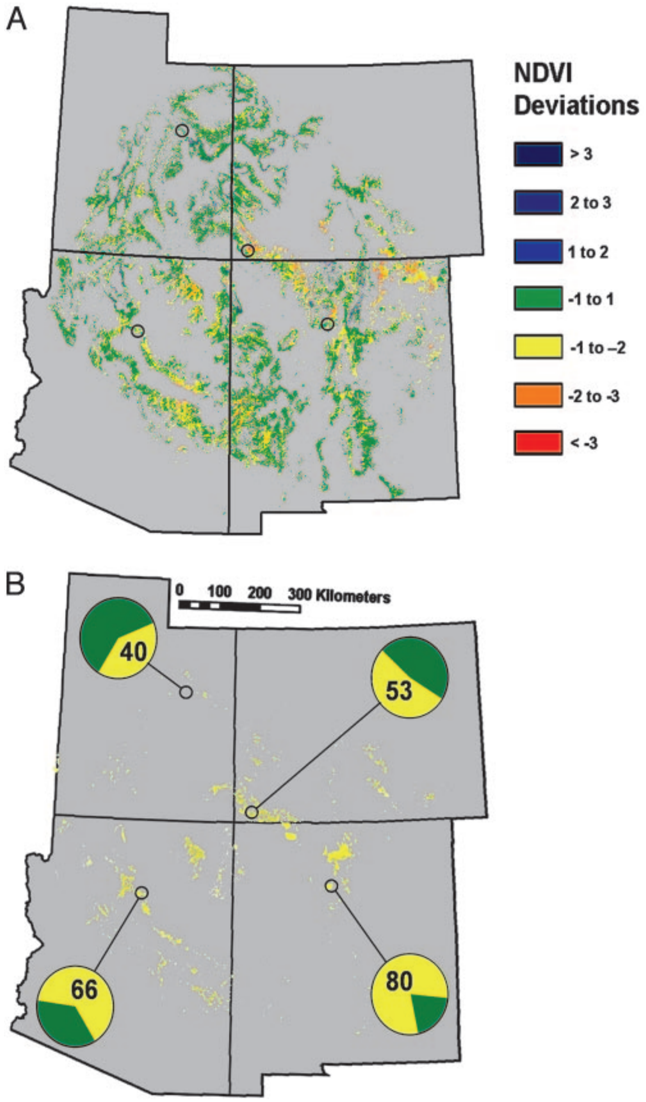

Fig. 3. Regional drought-induced vegetation changes. (*A*) Change map for NDVI for the region encompassing *P. edulis* distribution within Arizona, New Mexico, Colorado, and Utah, based on deviation from 2002–2003 relative to the predrought mean (1989–1999) during the period late-May to June. (*B*) Aerial survey map of piñon-juniper woodlands, delineating areas that experienced noticeable levels of tree mortality (including larger, older trees), conducted by the U.S. Forest Service (19) in four study areas throughout the region, corroborates the NDVI and aerial survey maps and documents stand-level estimates of mortality that range from 40% to 80% of nonseedling trees.

The rapid, extensive regional changes in vegetation cover through tree die-off that we have quantified for southwestern North America have a number of important, interrelated ecological implications (12, 24), including potentially large changes in carbon stores and dynamics, of concern for carbon-related polices and management (9). Other interrelated implications include large changes in near-ground solar radiation (25), runoff

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and erosion (5), genetic structure of the dominant tree species on the landscape (26), and land surface microclimate feedbacks to the atmosphere (27). Additionally, future production of piñon nuts, an important food source for several species of birds and small mammals and for local people (28), is expected to be greatly reduced over an extensive area. Persistence of the recent drought could lead to further mortality of *P. edulis* and other plant species within its distribution. Notably, a dominant herbaceous species within piñon-juniper woodlands, *Boutelua gracilis*, underwent a >50% reduction in live basal cover between 1999 and 2003 near the Mesita del Buey site. Even codominant, woody species of *Juniperus monosperma*, which are much more drought tolerant than *P. edulis* (18), are undergoing mortality in response to the drought, ranging from 2% to 26% at our four field verification sites.

The cessation of drought conditions may be insufficient for reestablishment of *P. edulis* and associated plant species, as documented for landscape response of *Pinus ponderosa* after the 1950s drought (5). Such rapid shifts in vegetation may represent abrupt, rapid, and persistent shifts in not only ecotones, but also in dominant vegetation cover and associated ecosystem process (5, 7–8). At a minimum, the spatially extensive die-off will need to be considered in regional environmental assessments and management decisions over the next several decades, the shortest interval required for a *P. edulis*-dominated overstory structure to reestablish. More generally, an improved predictive capability to forecast ecological responses to climate at regional scales is needed to effectively deal with the consequences of large-scale, long-term climate forcings (2, 8). Our results highlight how drought-induced die-off can span across the range of a vegetation type and challenges the current paradigm for climate-induced vegetation dynamics, which focuses largely on changes at the margins of a species' range and the ecotone boundaries within that range (1, 5, 6). Additionally, if temperatures continue to warm, vegetation die-off in response to future drought may be further amplified (5, 8, 9, 12). This recent drought episode in southwestern North America may be a harbinger of future global-change-type drought throughout much of North America and elsewhere, in which increased temperature in concert with multidecadal drought patterns associated with oceanic sea surface oscillations can drive extensive and rapid changes in vegetation and associated land surface properties.

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1. Intergovernmental Panel on Climate Change (2001) *Climate Change 2001: Synthesis Report, A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change*, eds. Watson, R. T. & Core Writing Team (Cambridge Univ. Press, New York).
2. Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R. & Mearns, L. O. (2000) *Science* **289,** 2068–2074.
3. Hoerling, M. & Kumar, A. (2004) *Science* **299,** 691–694.
4. McCabe, G. L., Palecki, M. A. & Betancourt, J. L. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 4136–4141.
5. Allen, C. D. & Breshears, D. D. (1998) *Proc. Natl. Acad. Sci. USA* **95,** 14839–14842.
6. Fensham, R. J. & Holman, J. E. (1999) *J. Appl. Ecol.* **36,** 1035–1050.
7. Intergovernmental Panel on Climate Change (1998) *The Regional Impacts of Climate Change: An Assessment of Vulnerability, A Special Report of Intergovernmental Panel on Climate Change Working Group II, Annex C*, eds. Watson, R. T., Zinyowera, M. C. & Moss, R. H. (Cambridge Univ. Press, New York).
8. Peters, D. P. C., Pielke, R. A., Sr., Bestelmeyer, B. T., Allen, C. D., Munson-McGee, S. & Havstad, K. M. (2004) *Proc. Natl. Acad. Sci. USA* **101,** 15130–15135.
9. Breshears, D. D. & Allen, C. D. (2002) *Global Ecol. Biogeog.* **11,** 1–5.
10. Ogle, K., Whitham, T. G. & Cobb, N. S. (2000) *Ecology* **81,** 3237–3243.
11. Trotter, T. R., Cobb, N. S. & Whitham, T. G. (2002) *Proc. Natl. Acad. Sci. USA* **99,** 10197–10202.
12. Brown, J. H., Whitham, T. G., Morgan Ernest, S. K. & Gehring C. A. (2001) *Science* **293,** 643–650.
13. Rice, W. R. (1989) *Evolution* **43,** 223–225.
14. Wang, J., Rich, P. M. & Price, K. P. (2003) *Int. J. Remote Sens.* **24,** 2345–2364.
15. Stimson, H. C., Breshears, D. D., Ustin, S. L. & Kefauver, S. C. (2005) *Remote Sens. Environ.* **96,** 108–118.
16. Kastens, J. H., Jakubauskas, M. E. & Lerner, D. E. (2003) *IEEE Trans. Geosci. Remote Sens.* **41,** 2590–2594.
17. Breshears, D. D., Rich, P. M., Barnes, F. J. & Campbell, K. (1997) *Ecol. Appl.* **7,** 1201–1215.
18. Breshears, D. D., Meyers, O. B., Johnson, S. R., Meyer, C. W. & Martens, S. N. (1997) *J. Ecol.* **85,** 289–299.
19. U.S. Forest Service (2003) *Forest Insect and Disease Conditions in the Southwestern Region, 2002* (USDA Forest Service, Southwestern Region, Forestry and Forest Health, Albuquerque, NM), Publication R3-03-01.
20. Waring, G. L. & Cobb, N. S. (1992) in *Plant-Insect Interactions*, ed. Bernays, E. A. (CRC, Boca Raton, FL), Vol. 4, pp. 167–226.
21. Allen, C. D. (1989) Ph.D. thesis (University of California, Berkeley).
22. Swetnam, T. W. & Betancourt, J. L. (1998) *J. Climate* **11,** 3128–3147.
23. Logan, J. A., Regniere, J. & Powell, J. A. (2003) *Front. Ecol. Environ.* **1,** 130–137.
24. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. (2001) *Nature* **413,** 591–596.
25. Martens, S. N., Breshears, D. D. & Meyer C. W. (2000) *Ecol. Model.* **126,** 79–93.
26. Mitton, J. B. & Duran, K. L. (2004) *Mol. Ecol.* **13,** 1259–1264.
27. Pitman, A. J., Narisma, G. T., Pielke, R. A. & Holbrook, N. J. (2004) *J. Geophys. Res. Atmos.* **109,** D18109.
28. Floyd, M. L., ed. (2003) *Ancient Piñon-Juniper Woodlands: A Natural History of Mesa Verde Country* (Univ. Press of Colorado, Boulder).