REVIEW

Temperate forest health in an era of emerging megadisturbance

Constance I. Millar[1]* and Nathan L. Stephenson[2]

Although disturbances such as fire and native insects can contribute to natural dynamics of forest health, exceptional droughts, directly and in combination with other disturbance factors, are pushing some temperate forests beyond thresholds of sustainability. Interactions from increasing temperatures, drought, native insects and pathogens, and uncharacteristically severe wildfire are resulting in forest mortality beyond the levels of 20th-century experience. Additional anthropogenic stressors, such as atmospheric pollution and invasive species, further weaken trees in some regions. Although continuing climate change will likely drive many areas of temperate forest toward large-scale transformations, management actions can help ease transitions and minimize losses of socially valued ecosystem services.

Forests not only are essential components of the natural environment but also offer profound spiritual and material benefits to humanity. After centuries of exploitation, there is much to celebrate in the resilience (ability to rebound after perturbation) of temperate forests. Broad swaths of forest that were cut in recent centuries continue to regrow vigorously, absorbing a substantial proportion of anthropogenic carbon-dioxide emissions (*1*). Despite deeply concerning declines of ancient trees in forests worldwide (*2*), large trees are increasingly abundant in areas of temperate forests that are regrowing after logging (*3*). In other regions, air-quality regulations have reduced acidic deposition and other air-pollution effects on forests, providing improved conditions for forest growth and sustainability (*4*).

Despite some encouraging trends, 21st-century forests still face grave threats. For millennia, the main threat to forests was overexploitation, but recent research has identified a range of emerging challenges to forest persistence and health. We focus on emerging "megadisturbances" that are capable of driving abrupt tree mortality of a spatial extent, severity, and frequency surpassing that recorded during recent human history. Where these occur, effects to ecosystems and society follow. Thus, while acknowledging the resilience of many forests, we highlight here the nature and consequences of changing environmental conditions that increasingly threaten widespread regions of temperate forest. In particular, we describe the rise of an especially potent threat to forest health that has only recently begun to receive broad attention, that is, persistent and recurring drought combined with high temperatures (see Fig. 1).

Forest health, thresholds, and megadisturbance

Concepts of temperate forest health have changed substantially over the past several decades (*5*, *6*). Early definitions (*7*) described healthy forests as those with trees growing at their optimal capacity, free from serious effects from insects, disease, or wildfire. Fires were suppressed, and insects and pathogens controlled. Through the mid to late 20th century, evolving understanding of ecological dynamics, as well as increasing focus on forests as including organisms beyond the trees, led to recognition that natural disturbances—including fires, insects, and diseases—were essential ingredients of ecosystem functioning (*8*). Combined opinion shifted to a recognition that disturbance was inherent to forest dynamics and contributes to healthy forest functioning and resilience.

Most recently, however, researchers are seeking to understand how much disturbance can be tolerated before forest health and persistence are threatened. This concern emerges from several trends: increasing frequency, extent, and severity of disturbances; growing recognition of the profound effects of anthropogenic climate change; presence of novel anthropogenic stressors; and a burgeoning global human population that imposes escalating demands on forests (*9*). The focus of forest health has shifted toward evaluating forest conditions relative to supporting human needs—that is, the capacity of forests to sustainably provide ecosystem services. These services include provisioning (e.g., water), regulating (e.g., carbon sequestration), supporting (e.g., biogeochemical cycling), and cultural (e.g., recreational) benefits (*10*). To the complexity of ecological dynamics affecting forest health are thereby added the many ways in which humans use and value forests (*9*).

Recent forest research has thus focused on the role of thresholds and ecological conversions (changes in ecological state) (*11*–*14*). Whereas in recent decades, promoting resilience has been a widespread goal of forest management, the increasing pressure of chronic and acute disturbances is pushing many temperate forests toward and over resilience thresholds. The consequences of heat waves, extreme droughts, massive wildfire, and widespread insect outbreaks demonstrate to the public and scientists alike that resilience can be exhausted and that major ecological transformations can result. Serious thresholds are crossed when forests convert to vegetation types without trees and, as a result, lose valued forest ecosystem services.

Forest health can be considered in the context of disturbance effects. Four patterns of 21st-century forest response to cumulative disturbance range from resilient (healthy) to collapse (unhealthy) states, as megadisturbances increase in frequency and extent (Fig. 2). Thresholds can

Fig. 1. Drought- and bark-beetle–induced mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests, northern Warner Mountains (Drake Peak), Oregon. [Photo by C. I. Millar]

[1]U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station, Albany, CA 94710, USA. [2]U.S. Geological Survey, Western Ecological Research Center, Three Rivers, CA 93271, USA.
*Corresponding author. E-mail: cmillar@fs.fed.us

occur within and between classes; ecological functions of forests change; and capacities to deliver ecosystem services are altered. This framework helps to distinguish a healthy amount of disturbance from profound transformations that affect society in undesired ways.

Rise of the "hotter drought"

For millennia, drought has been a key disturbance agent in temperate forests. Over the past few decades, however, rising global temperatures have contributed to droughts of a severity that is unprecedented in the last century or more (*12*, *15–18*). These exceptional droughts have been variously called "global-change-type droughts" (*19*), "hot droughts" (*20*), or "hotter droughts" (*14*); we use the last term because it best contrasts these recent droughts with the generally cooler droughts of earlier in the last century. Hotter droughts have emerged as particularly powerful drivers of temperate forest mortality (*14*).

Hotter droughts affect forests both directly and indirectly (*14*). Directly, higher temperatures increase tree water stress by increasing the atmosphere's evaporative demand for water (*21*). Such temperature-induced increases in evaporative demand have transformed what would otherwise be typical droughts (in terms of low precipitation) into droughts of historically unprecedented severity (*15*, *17*, *18*). Additionally, with warming temperatures, precipitation that formerly fell as snow increasingly falls as rain (*22*, *23*). In historically snow-dominated forests, the diminished snowpacks melt earlier and are thus unable to replenish soil moisture during the driest parts of the year (*23–25*), further increasing water stress on trees. Finally, the direct effects of tree water stress can be exacerbated by detrimental physiological effects of high temperatures (*12*). Hotter droughts can also affect forests indirectly by making them more vulnerable to attacks by insects and pathogens (described in the next section). Both the direct and indirect effects of hotter drought can yield abrupt and threshold responses in forest condition and process (Fig. 2) (*14*).

The historically unprecedented severity of some recent hotter droughts has, in turn, driven unprecedented temperate forest mortality (*15*, *26*, *27*) (Fig. 3). Although the most severe examples come from semi-arid forests, as global temperatures continue to rise most temperate forests may experience elevated forest mortality during hotter droughts (*28*). Importantly, in addition to the acute effects of hotter drought, increasing temperatures can also result in long-term chronic increases in drought stress even when precipitation remains average or increases (*29*). Such chronic temperature-induced increases in drought stress in the absence of declining precipitation have been implicated in long-term increases in background (noncatastrophic) tree mortality rates, such as in western North America (*30*).

Compound stressors

Hotter droughts are emerging as novel drivers of forest megadisturbance, but they do not act in isolation, and their effects are often compounded

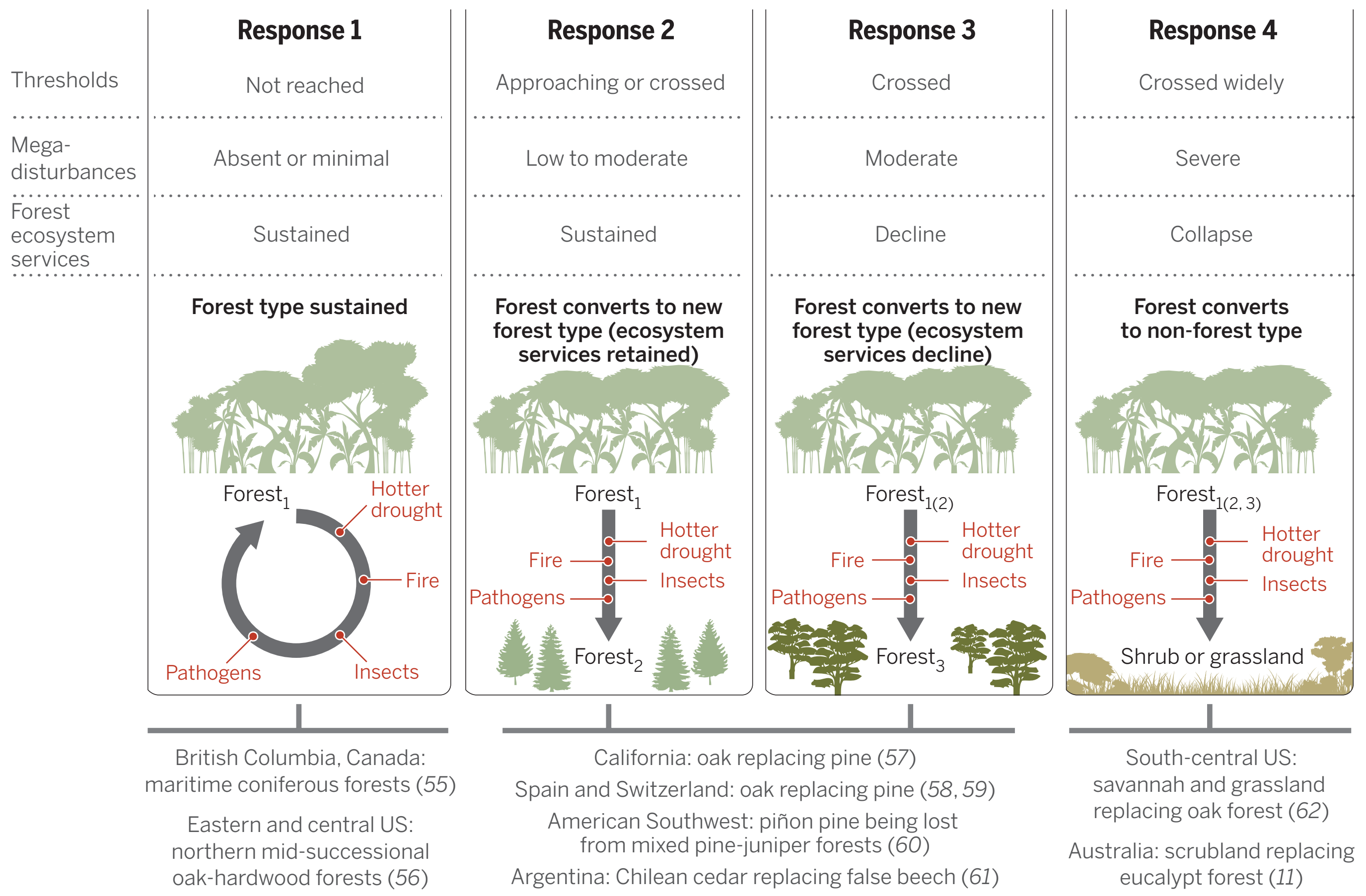

Fig. 2. Temperate forest responses to 21st-century disturbances. (**Response 1**) Existing forests are resilient and capable of sustaining structure, composition, function, and forest ecosystem services. (**Response 2**) As a result of disturbances that affect species composition, forests convert to new forest types but retain primary ecosystem functions and services. The transition results from changes in species abundances or the loss of one or more minor species. (**Response 3**) Existing forests convert to new forest types, and the changes are substantial enough that ecologic functions change and forest ecosystem services decline. Major structural changes may have occurred, or one or more dominant tree species are lost and may or may not be replaced by species not formerly present or present in minor amounts. (**Response 4**) Existing forests transform to nonforest types, such as shrublands or grasslands, losing forest structure, composition, and function; forest ecosystem services severely decline. Thresholds can occur both within classes and between classes. [Examples from (*55–62*)]

through interactions with other stressors. In recent decades, outbreaks of insects and pathogens have resulted in millions of hectares of forest defoliation, canopy dieback, declines in growth, and forest mortality in western North America and Europe (*31*–*34*). In many cases, climate was a direct or indirect trigger for these other agents of megadisturbance or influenced the severity and extent of outbreaks. In temperate forests, warming temperatures can trigger population increases in many insect species, which serve as catalysts for widespread outbreaks. Indirectly, drought can weaken trees to a point where insects and pathogens are able to overwhelm tree defenses, further catalyzing widespread outbreaks and epidemics. In some cases, insect outbreaks are not directly related to climatic events, and causes pertain instead to vagaries of regional context and forest type (*34*, *35*). Independently or in combination with other stressors, insect and pathogen disturbances can lead to changes in forest condition similar in magnitude to climate effects (*36*).

Hotter droughts interacting with other stressors are also catalyzing major changes in fire regimes (*37*, *38*), and the term "mega" is most often applied to fires (*11*, *39*). Of overriding concern is the increasing frequency of uncharacteristically severe and large fires and longer fire seasons in temperate forests globally (*37*, *38*). Megafires are more likely where conditions favor build-up of dry fuel, either standing or on the forest floor. Droughts directly affect fuel flammability and structure through lowering moisture contents and increasing tree mortality, and indirectly through cumulative effects from insect epidemics and diseases that alter forest conditions. As with insects and disease, megafires often occur in atypically dense forest stands (often the legacy of past management actions, including fire suppression), homogeneous forest structure, and where large fires occurred previously (*39*, *40*). To the extent that these large fires increase in the future, the potential for shifts to new forest types and nonforest vegetation will accelerate (Fig. 2).

Other anthropogenic environmental changes affect forest health, although not all detrimentally. In some cases, nitrogen and carbon dioxide as atmospheric pollutants can act as fertilizers, improving tree growth, although effects are highly varied and often transient (*4*, *41*, *42*). At chronically high concentrations, and in combination with climate-change effects, air pollutants can defoliate and weaken trees, reduce forest growth, and contribute to forest mortality (*4*, *43*, *44*). Similarly, many nonnative invasive species—including insects, pathogens, plants, and mammals—interact with heat and drought to impair forest health (*32*, *33*). In North America, for instance, alien pathogens widely transformed chestnut and elm forests and increasingly threaten high-elevation pine ecosystems (*32*, *33*). After wildfires in the Great Basin woodlands of western North America, invasion by nonnative cheatgrass (*Bromus tectorum*) can alter fire regimes to the extent that they favor persistence of invasive

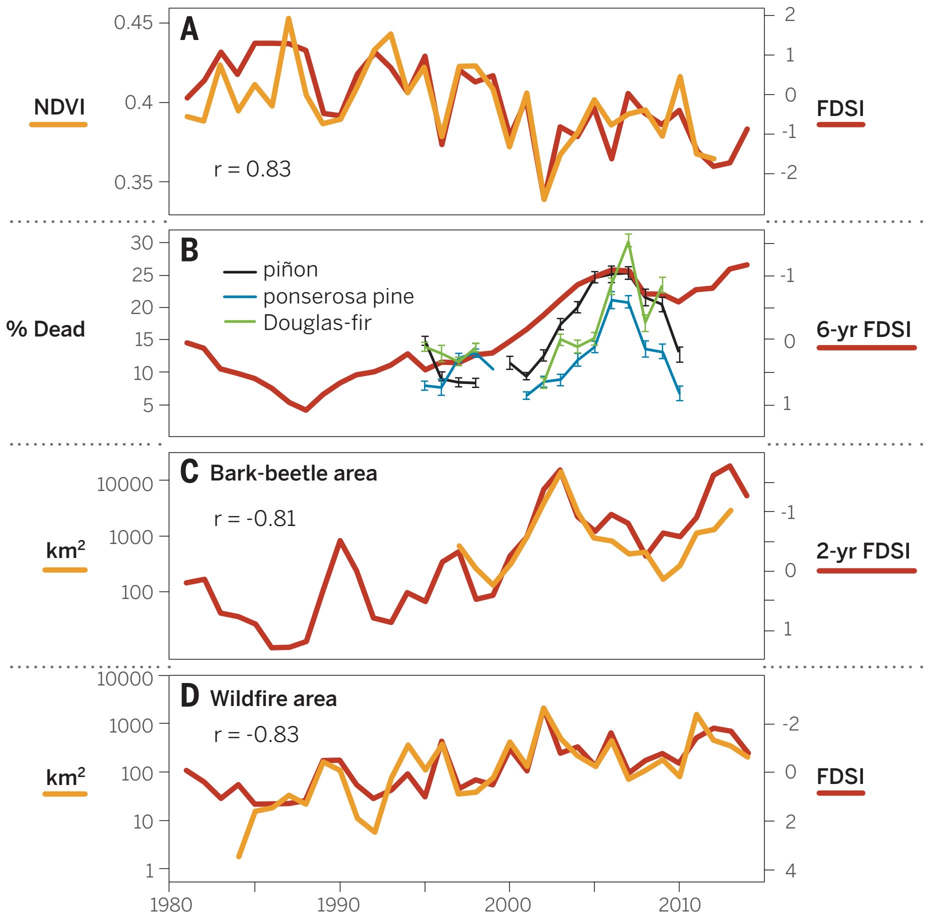

Fig. 3. Effects of hotter drought in the American Southwest. The forest drought-stress index (FDSI) integrates the effects of warm-season water deficit (controlled mostly by high temperature) and cold-season precipitation. Declining values of FDSI correspond to increasing drought. In the Southwest, increasing drought has been accompanied by (**A**) declining vegetation greenness [normalized difference vegetation index (NDVI)], a remotely sensed index of greenness; (**B**) increasing mortality of the three most common conifers; (**C**) increasing area affected by bark-beetle outbreaks; and (**D**) increasing area affected by wildfires. [Adapted by A. P. Williams (July 2015) with permission from Macmillan Publishers Ltd. (*15*)]

grassland and exclude restoration of native tree species (*45*).

Effects on forest ecosystem services

The effects on ecosystem services resulting from hotter droughts and compounding stresses vary, based on how the ecological functions of forests are affected and on the regional demands and needs of society (*9*). Extensive forest mortality can impair water quantity and quality, forest products, cultural and spiritual values, and recreation, with concomitant effects on rural and urban economies (*33*, *46*). Forest fires, in particular, have profound effects on human life, property, and economies. While megafires represent a small fraction of total wildfires, they account for a disproportionately large percentage of suppression costs, private property losses, natural resource damages, and fatalities, representing some of the worst civil disasters on record (*11*, *39*, *47*).

Forests play a particularly critical role in the global carbon cycle, mediating climatic changes by providing feedback to atmospheric carbon dioxide concentrations. Over at least the past several decades, temperate forests have provided a valuable ecosystem service by acting as a net sink of atmospheric carbon dioxide (*1*), partly offsetting anthropogenic emissions. As megadisturbances increase in frequency, extent, and severity, this service is likely to diminish. At the extreme, temperate forests could become net sources rather than sinks of atmospheric carbon dioxide (*9*, *48*).

Forests of the future: Easing transitions

What do these changes portend for temperate forests through the 21st century? In the short term, some forests will likely continue to absorb or rebound from disturbances, sustain a diversity of ecological functions, and deliver ecosystem services similar to those of past decades (Fig. 2). Over the longer term, however, most temperate forests are likely to change in condition (*49*), with megadisturbances frequently catalyzing these effects (*14*). The changes could range from minor shifts in forest structure (e.g., tree density and ages) and species compositions to major transformation of vegetation types, some resulting in novel ecosystems relative to recent centuries. In many cases,

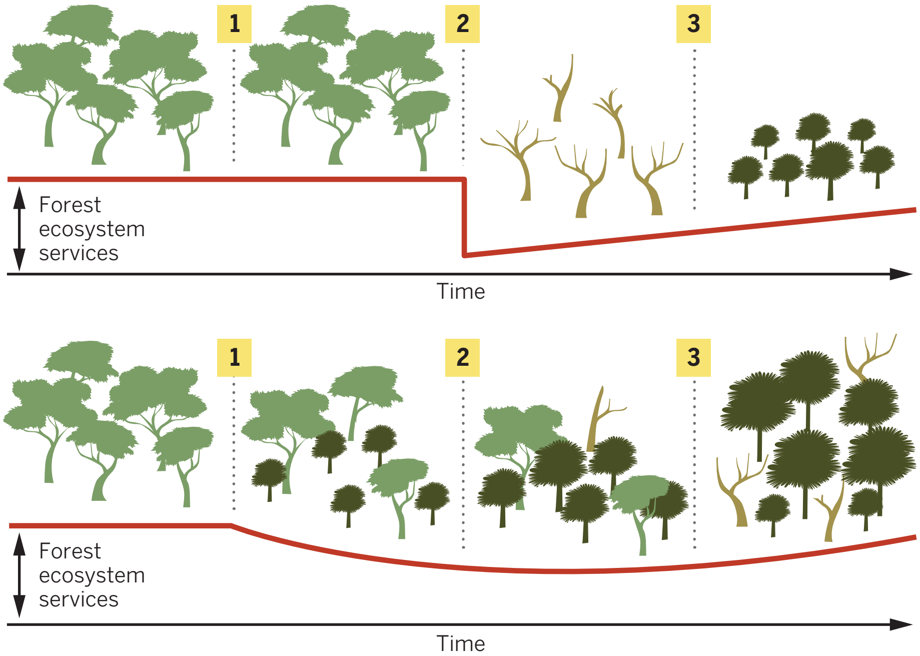

Fig. 4. Management practices can influence the nature of transitions between forest types. Numbers represent forest transitions through time. (**Top**) (**1**) Despite rapid directional environmental changes, managers strive to maintain forests within historical ranges of conditions and may initially succeed. (**2**) The forest may be inherently unstable in the new environment and, once a threshold is exceeded, substantial mortality occurs, with an abrupt loss of most forest ecosystem services. (**3**) After the die-back, recovery of forest ecosystem services is slow. (**Bottom**) (**1**) Managers anticipate an impending forest transition and facilitate it by reducing the probability of sudden die-back (e.g., by thinning the forest to reduce competition for water) and by assisting establishment of species better adapted to future conditions. (**2**) The transition is gradual rather than abrupt, and ecosystem services are maintained at a higher (although reduced) level. (**3**) Forest ecosystem services more rapidly approach their original levels. Although some forest ecosystem services are eventually lost in both cases, active management might facilitate a gradual rather than abrupt transition.

drought-hardy species, species with physiological plasticity capable of coping with compound stresses, and species with shorter statures might outcompete current species (*50*, *51*). Native insects and pathogens may effectively act as invasive exotics as they move beyond their historic ranges (*52*).

Minimizing the effects to society from these transitions is emerging as a primary goal for forest management today (Fig. 4). A challenge to research will be to develop tools to assess the sensitivity of forests to thresholds from cumulative disturbances and evaluate their vulnerability to transformation. If we can identify in advance the most vulnerable forests, in some cases management intervention might be able to ease the transition to new and better-adapted forest states, minimizing losses of ecosystem services. Because the scope of the challenge is vast, triage exercises will almost certainly be necessary to identify the highest-priority forests and those where management action might have the greatest effect.

Success will depend on far more integrated and coordinated efforts by institutions, agencies, and governments than presently exists (*53*). Distributed monitoring systems that observe changes on multiple scales of forest health are essential; these will become increasingly reliant on remote methods. Climate adaptation will likely move from compartmentalized to comprehensive strategies, with attention to proactive methods (*54*). Although thresholds are likely to be approached in the future, and changes are inevitable, the actions we take now in temperate forests can ease and guide transitions, diminishing effects to forest ecosystems and human societies.

REFERENCES AND NOTES

1. Y. Pan *et al.*, *Science* **333**, 988–993 (2011).
2. D. B. Lindenmayer, W. F. Laurance, J. F. Franklin, *Science* **338**, 1305–1306 (2012).
3. P. E. Kauppi *et al.*, *Biogeosciences* **12**, 855–862 (2015).
4. W. deVries, M. H. Dobbertin, S. Solberg, H. F. van Dubben, M. Schaub, *Plant Soil* **380**, 1–45 (2014).
5. W. A. Warren, *Soc. Nat. Resour.* **20**, 99–117 (2007).
6. A. Sulak, L. Huntsinger, *J. For.* **110**, 312–317 (2012).
7. T. E. Kolb, M. R. Wagner, W. W. Covington, *J. For.* **92**, 10–15 (1994).
8. K. F. Raffa *et al.*, *J. For.* **107**, 276–277 (2009).
9. D. Thom, R. Seidl, *Biol. Rev. Camb. Philos. Soc.* 10.1111/brv.12193 (2015).
10. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Synthesis* (Island Press, Washington, DC, 2005).
11. M. A. Adams, *For. Ecol. Manage.* **294**, 250–261 (2013).
12. R. Teskey *et al.*, *Plant Cell Environ.* **38**, 1699–1712 (2015).
13. C. P. O. Reyer *et al.*, *J. Ecol.* **103**, 5–15 (2015).
14. C. D. Allen, D. D. Breshears, N. G. McDowell, *Ecosphere* **6**, 129 (2015).
15. A. Park Williams *et al.*, *Nat. Clim. Change* **3**, 292–297 (2013).
16. M. Lindner *et al.*, *J. Environ. Manage.* **146**, 69–83 (2014).
17. S. M. Vicente-Serrano *et al.*, *Environ. Res. Lett.* **9**, 044001 (2014).
18. N. S. Diffenbaugh, D. L. Swain, D. Touma, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 3931–3936 (2015).
19. D. D. Breshears *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 15144–15148 (2005).
20. J. Overpeck, B. Udall, *Science* **328**, 1642–1643 (2010).
21. D. D. Breshears *et al.*, *Front. Plant Sci.* **4**, 266 (2013).
22. G. J. McCabe, D. M. Wolock, *Clim. Change* **99**, 141–153 (2010).
23. T. P. Barnett, J. C. Adam, D. P. Lettenmaier, *Nature* **438**, 303–309 (2005).
24. P. W. Mote, A. F. Hamlet, M. P. Clark, D. P. Lettenmaier, *Bull. Am. Meteorol. Soc.* **86**, 39–49 (2005).
25. I. T. Stewart, D. R. Cayan, M. D. Dettinger, *J. Clim.* **18**, 1136–1155 (2005).
26. J. Carnicer *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 1474–1478 (2011).
27. G. Matusick, K. X. Ruthrof, N. C. Brouwers, B. Dell, G. S. J. Hardy, *Eur. J. For. Res.* **132**, 497–510 (2013).
28. B. Choat *et al.*, *Nature* **491**, 752–755 (2012).
29. G. J. McCabe, D. M. Wolock, *Clim. Change* **2015**, 1–13 (2015).
30. P. J. van Mantgem *et al.*, *Science* **323**, 521–524 (2009).
31. B. J. Bentz *et al.*, *Bioscience* **60**, 602–613 (2010).
32. R. N. Sturrock *et al.*, *Plant Pathol.* **60**, 133–149 (2011).
33. A. S. Weed, M. P. Ayres, J. A. Hicke, *Ecol. Monogr.* **83**, 441–470 (2013).
34. A. Sallé, L.-M. Nageleisen, F. Lieutier, *For. Ecol. Manage.* **328**, 79–93 (2014).
35. W. R. Anderegg *et al.*, *New Phytol.* 10.1111/nph.13477 (2015).
36. C. E. Flower, M. A. Gonzalez-Meler, *Annu. Rev. Plant Biol.* **66**, 547–569 (2015).
37. M. Flannigan *et al.*, *For. Ecol. Manage.* **294**, 54–61 (2013).
38. W. M. Jolly *et al.*, *Nat. Commun.* **6**, 7537 (2015).
39. S. L. Stephens *et al.*, *Front. Ecol. Environ* **12**, 115–122 (2014).
40. M. J. Jenkins, J. B. Runyon, C. J. Fettig, W. G. Page, B. J. Bentz, *For. Sci.* **60**, 489–501 (2014).
41. M. E. Fenn *et al.*, *Bioscience* **53**, 404–420 (2003).
42. S. Piao *et al.*, *Glob. Change Biol.* **21**, 1601–1609 (2015).
43. M. Lorenz *et al.*, in *Forest and Society: Responding to Global Drivers of Change*, G. Mery *et al.*, Eds. (IUFRO World Series, Vienna, International Union of Forest Research Organizations, 2010), pp. 55–74.
44. Y. Hoshika *et al.*, *Sci. Rep.* **5**, 9871 (2015).
45. W. D. Billings, in *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*, G. M. Woodell, Ed. (Cambridge Univ. Press, Cambridge, 1990), pp. 301–322.
46. I. L. Boyd, P. H. Freer-Smith, C. A. Gilligan, H. C. J. Godfray, *Science* **342**, 1235773 (2013).
47. J. Williams, *For. Ecol. Manage.* **294**, 4–10 (2013).
48. J. A. Hicke, A. J. H. Meddens, C. D. Allen, C. A. Kolden, *Environ. Res. Ltrs.* **8**, 035032 (2013).
49. P. Gonzalez, R. P. Neilson, J. M. Lenihan, R. J. Drapek, *Glob. Ecol. Biogeogr.* **19**, 755–768 (2010).
50. X. Jiang *et al.*, *J. Clim.* **26**, 3671–3687 (2013).
51. N. G. McDowell, C. D. Allen, *Nat. Clim. Change* **5**, 669–672 (2015).
52. A. J. Woods, *J. For. Sci.* **60**, 484–486 (2014).
53. B. E. Law, *Glob. Change Biol.* **20**, 3595–3599 (2014).
54. C. I. Millar, C. W. Swanston, D. L. Peterson, in *Climate Change and United States Forests*, D. L. Peterson, J. M. Vose, T. Patel-Weynand, Eds. (Springer, Berlin, 2014), pp. 183–222.
55. R. A. Hember *et al.*, *Glob. Change Biol.* **18**, 2026–2040 (2012).
56. M. C. Dietze, P. R. Moorcroft, *Glob. Change Biol.* **17**, 3312–3326 (2011).
57. P. J. McIntyre *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1458–1463 (2015).
58. A. Rigling *et al.*, *Glob. Change Biol.* **19**, 229–240 (2013).
59. J. Carnicer *et al.*, *Glob. Ecol. Biogeogr.* **23**, 371–384 (2014).
60. D. D. Breshears, L. López-Hoffman, L. J. Graumlich, *Ambio* **40**, 256–263 (2011).
61. M. Suarez, T. Kitzberger, *Can. J. For. Res.* **38**, 3002–3010 (2008).
62. D. P. Bendixsen, S. W. Hallgren, A. E. Frazier, *For. Ecol. Manage.* **347**, 40–48 (2015).

ACKNOWLEDGMENTS

We thank M. Dettinger (U.S. Geological Survey), C. J. Fettig (U.S. Forest Service), J. Hicke (University of Idaho), S. Stephens (University of California, Berkeley), and A. P. Williams (Lamont-Doherty Earth Observatory) for reviewing the draft manuscript; A. P. Williams for providing an update of FDSI trends for Fig. 3; and D. Delany (U.S. Forest Service) for help with figures. C.I.M. and N.L.S. are supported by the U.S. Forest Service and U.S. Geological Survey, respectively.

10.1126/science.aaa9933

Temperate forest health in an era of emerging megadisturbance
Constance I. Millar and Nathan L. Stephenson
Science **349**, 823 (2015);
DOI: 10.1126/science.aaa9933