

## REVIEW

# Forest health and global change

S. Trumbore,<sup>1,2\*</sup> P. Brando,<sup>3,4</sup> H. Hartmann<sup>1</sup>

Humans rely on healthy forests to supply energy, building materials, and food and to provide services such as storing carbon, hosting biodiversity, and regulating climate. Defining forest health integrates utilitarian and ecosystem measures of forest condition and function, implemented across a range of spatial scales. Although native forests are adapted to some level of disturbance, all forests now face novel stresses in the form of climate change, air pollution, and invasive pests. Detecting how intensification of these stresses will affect the trajectory of forests is a major scientific challenge that requires developing systems to assess the health of global forests. It is particularly critical to identify thresholds for rapid forest decline, because it can take many decades for forests to restore the services that they provide.

Forests have evolved while experiencing disturbances such as drought, windthrow (when trees are uprooted or overthrown by wind), insect and disease outbreaks, and fire. However, forests worldwide increasingly must also cope with human-related intensification of stressors that affect forest condition, either directly through logging and clearing or indirectly through climate change, air pollution, and invasive species. These novel disturbances alter forest communities and environmental conditions outside the ranges in which current forests evolved and occur too fast for evolutionary adaptation processes to keep pace. Thus, the future of global forests will be determined by the trajectory of complex forest system responses to multiple stressors that span local to global scales.

The papers in this special section describe ongoing changes in tropical (1), temperate (2), boreal (3), and managed (4) forests as they respond to shifts in land use, climate, biodiversity, the frequency and intensity of extreme events, and disturbance regimes. These papers document how humans have fundamentally altered forests across the globe and warn of potential broad-scale future declines in forest health, given increased demand for land and forest products combined with rapid climate change. This review focuses on overarching questions common to all forests: How do we define forest health and detect when it is declining? How can we attribute observed broad-scale declines to interactions among the varied stresses that affect forests today? What are the time scales and trajectories of recovery for unhealthy forests, and can we identify dangerous levels of change in global forest health?

We argue that approaches to monitoring global forest health need to combine detection of changes in forest condition with observations that enable the attribution of observed changes to combinations of human, climatic, and biotic drivers. Further, mechanistic understanding based on experiments and long-term observations is required to identify trajectories leading to recovery or to rapid decline

of forest functions. Such approaches need to be undertaken at scales that span current gaps and link remote sensing and plot-level data.

## How do we measure forest condition and assess forest health?

Health as a concept applied to forests shares common problems with its application to human populations. At the scale of an individual, health can be defined as the absence of disease (Fig. 1). However, as the unit of scale of monitoring shifts from trees to entire forest stands or biomes, indicators of forest health become more difficult to assess. In forestry, for example, one common measure of forest condition at the stand level is productivity. Although this is a good proxy for timber production, it neglects important attributes of forest ecosystems such as

species assemblage, vegetation structure, biomass, and nutrient cycling. This shortcoming necessitates the definition of more holistic but often less easily quantified measures, and for decades researchers have struggled with operational definitions of ecosystem health (5).

Existing measures of forest health range from strictly utilitarian and related to local human needs, to more ecological definitions related to the persistence of forests or stands within a given landscape (Fig. 1) (6). The Food and Agriculture Organization of the United Nations (FAO) combines these perspectives by defining “forest health and vitality” based on the combined presence of abiotic (e.g., drought, heat, and pollution) and biotic (e.g., disease and pests) stresses and how they affect tree growth and survival; the yield and quality of wood and nonwood forest products; wildlife habitat; and recreation, scenic, or cultural value. Edmonds *et al.* (7) enumerate eight conditions of a healthy forest: (i) an ecosystem in which abiotic and biotic factors do not threaten current and future management objectives; (ii) a fully functional community of plants and animals and their physical environment; and (iii) an ecosystem in balance that (iv) sustains its complexity while providing for human needs, (v) is resilient to change and (vi) is able to recover from natural and human stressors while (vii) maintaining and sustaining functions and processes, and (viii) is free of “distress” symptoms such as reduced primary productivity, loss of nutrient capital, loss of biodiversity, or widespread incidence of disease or potentially tree-killing insects.

## Utilitarian indicators

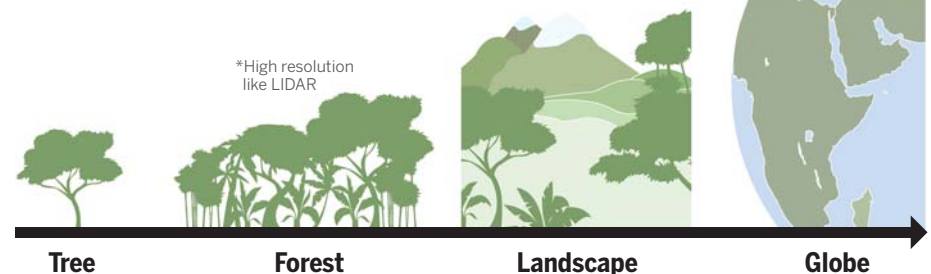
Disease	Wood yield	Water quality	Carbon storage
Damage	Pest infestation	Wood supply	Energy fluxes
Growth	Leaf area	Esthetics	Element fluxes

## Ecosystem indicators

Dead wood	Habitat quality	Seral diversity	Persistence
Disease resistance	Community structure	Connectivity	Invasion
Genetic variability	Soil fertility	Patchiness	Extinction

## Assessment tools

Inventory cruise	Inventory plots	Inventory plots	Remote sensing
Inventory plots	Remote sensing*	Remote sensing	Monitoring networks



**Fig. 1. Examples of forest-health indicators for utilitarian and ecosystem-centered perspectives.**

The common criteria spanning all of the spatial scales shown are (utilitarian) continued supply of forest products and services and (ecosystem) resistance and resilience to stress and disturbance. Some indicators cannot be directly measured or occur on spatial or temporal scales beyond human perception.

<sup>1</sup>Max Planck Institute for Biogeochemistry, 07745 Jena, Germany. <sup>2</sup>University of California–Irvine, Irvine, CA 92697, USA. <sup>3</sup>Instituto de Pesquisa Ambiental da Amazônia, Belém, Pará 66035-170, Brazil. <sup>4</sup>Woods Hole Research Center, Falmouth, MA 02450, USA.

\*Corresponding author. E-mail: trumbore@bgc-jena.mpg.de

However, even such a detailed set of attributes cannot completely capture forest health if spatial and temporal scales of forest ecosystems are not considered. Forests contain trees subjected to periodic stresses (e.g., drought stress) that affect the resilience of individuals and, if very intense or often repeated, can lead to mortality. We distinguish such stresses from disturbances that can kill healthy as well as unhealthy trees (e.g., windthrow, fire, and logging). Both can produce a dying patch of forest that might be considered in itself unhealthy but can facilitate a whole suite of essential ecological processes such as regeneration, nutrient cycling, or habitat creation at broader spatial scales. Thus, a healthy forest is one that encompasses a mosaic of successional patches representing all stages of the natural range of disturbance and recovery (7, 8). Such forests promote a diversity of nutrient dynamics, cover types, and stand structures, and they create a range of habitat niches for endemic fauna (9). The challenge is determining when the frequency, spatial extent, and strength of stresses and disturbances exceed the natural range of variability and affect the trajectory of vegetation recovery at the landscape to regional scale.

### What is the legacy of declines in forest health?

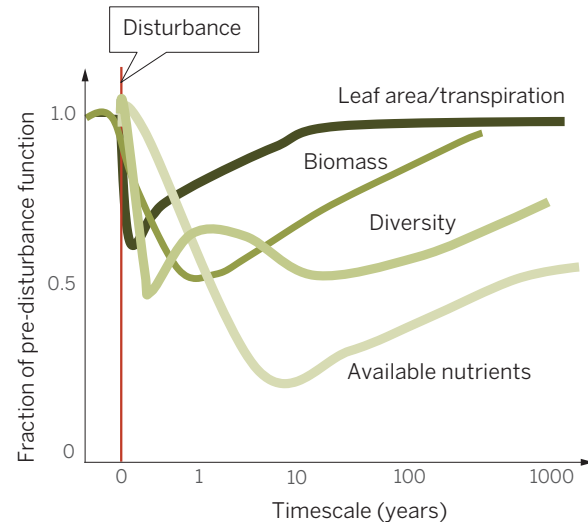
One of the key attributes of a healthy forest system is its ability to recover from disturbance. The accompanying papers in this issue provide accounts of specific instances where declines in forest health have been documented. These declines differ in each forest type and are driven by increased physiological stress [e.g., hot droughts (2)], susceptibility to pathogens (3, 4), increased disturbance-related mortality from fire (3), and tropical forest degradation by processes such as defaunation and selective logging (1). Most of these examples rely on observations of increased tree mortality, which is perhaps the most obvious symptom of an unhealthy forest.

Trees are long-lived organisms, and although an individual tree can die quickly, it can take decades to centuries to be replaced. Thus, the legacy of increased tree mortality can persist for a long time, which lends urgency to identifying and detecting potentially dangerous thresholds of forest health decline. Even if the affected forests eventually recover, more information is needed about how long the legacy of broad-scale forest dieback will affect important forest services and functions.

The various functions associated with forests recover over different time scales after major disturbances (Fig. 2). For example, even in severely damaged forests, new leaf cover can obscure open canopy areas in as little as a few months (10). As leaf area recovers, so do rates of photosynthesis and transpiration (11), key forest climate and water regulation services. These fluxes can approach predisturbance levels within years to a decade in selectively logged tropical forests (12) or forests recovering from fire. However, many other forest functions take much longer to regain predisturbance levels. Biomass and the associated carbon storage functions of forests recover

more slowly than fluxes, taking decades to centuries to replace losses (13, 14).

Other forest functions, such as biodiversity, can take even longer to recover, because they depend on the presence of individual species (Fig. 2). Although gap formation in forests can sustain biodiversity at the landscape or regional level (15), very broad-scale disturbances such as deforestation and firestorms dramatically reduce diversity. In such cases, the recovery of biodiversity requires replacement of the full range of tree species as well as of the fauna they host. For example, dead wood is an important carbon store and provides habitat for specific fauna; if the dead-wood pool is destroyed by harvesting or burning, it can take centuries to recover (14). Soil-derived nutrients are resupplied slowly by atmospheric dust or mineral weathering. Thus, nutrient depletion associated with disturbance may ultimately limit the rate and degree of recovery of other functions. The difficulty is to determine which of these functions are required to recover a healthy forest condition.



**Fig. 2. Time scales of recovery for different forest functions after a disturbance.** Disturbances, such as deforestation or fire, are followed by erosion and forest regrowth. Whereas functions associated with leaf area, such as photosynthesis and transpiration, recover within a decade, biomass (and therefore carbon storage) recovers more slowly, with mineral nutrients recovering most slowly of all.

Although we have concentrated on ecosystem properties, the definition of forest recovery also has implications for the utilitarian perspective. Forests that do not fully achieve predisturbance levels of diversity or nutrient status can almost fully regain wood production or carbon storage services, given sufficient time. A single large event such as a drought may remove the most susceptible species and leave behind more drought-resistant trees (16), potentially reducing tree mortality in successive droughts. However, if selective mortality occurs over a large enough area, the carbon storage and diversity services that were offered by the drought-sensitive species will take decades to centuries to recover. Thus, broad-scale and persistent degradation

of forests will have lasting consequences, even if the forests themselves eventually recover. Given how long we may live with the consequent loss of function, it is important to develop methods to evaluate the risks of broad-scale forest decline, especially given the novel combinations of stresses and disturbances expected to affect forests in the coming century.

### How much disturbance or stress is too much?

Healthy forests maintain their overall services over areas large enough to encompass the spatial scale of natural disturbance and recovery. Levels of disturbance that fall within the range of “background” variability to which forests are adapted (green area in Fig. 3) tend to produce a healthy mix of forest patches and to maintain water balance, biomass, and diversity at landscape scales. At very high levels of stress or disturbance and low levels of forest health (red area in Fig. 3), risks such as net loss of soil nutrients through erosion or loss of seed bank or seed dispersal vectors mean that the

forest has lost many of its intrinsic characteristics, which may delay or prevent recovery. In such extreme cases, a shift to a new vegetation state is possible. The real concern is how to define where the transition between “normal” and “too much” stress takes place (orange area in Fig. 3) and how to determine whether this transition is an abrupt threshold or a linear decline.

Whereas deforestation fundamentally changes the ability of forests to perform basic functions, changes in forest structure and diversity linked to other forms of disturbance are less obvious and harder to quantify. Increased disturbance intensity, disturbance frequency, or even the introduction of new kinds of disturbances can trigger abrupt nonlinear declines in the ability of forests to perform intrinsic functions (17–19). Increasingly, forests are subjected to climatic or biotic stresses and to stochastic disturbances, some of which fall outside the range of normal back-

ground levels (Fig. 4) (20–22). Of particular concern is the coupling of direct, local, human-related disturbances with ongoing, more diffuse changes in climate and atmospheric composition. Although not all global changes are likely to cause declines in forest health [e.g., increased atmospheric CO<sub>2</sub> may stimulate productivity (23)], overall levels of tree stress and forest disturbances are mostly expected to increase individually beyond their historic values in the next century (Fig. 4) (24).

Disturbances and stresses also do not act independently. For example, the interactions among extreme weather events, logging, and human-ignited forest fires have caused widespread tree mortality and degradation in tropical forest ecosystems (25). Broad-scale deforestation reinforces

such processes by expanding areas of forest edges, thereby increasing vulnerability to further disturbances (26). A second example is the relationship between warmer temperatures and accelerated insect life cycles, which allows pest species to cause greater damage during the growing season (27). Interactions with climate stressors such as drought can further increase mortality rates in weakened or insect-damaged trees (28). Although both of these examples probably cause mortality in excess of background conditions, the larger question is whether they are novel and severe enough to change the trajectory and rate of subsequent forest recovery (Fig. 3). In both examples, deciphering the causes of increased mortality required intensive studies at the plot scale, as well as controlled experiments to under-

proxies for forest condition globally (e.g., canopy cover, photosynthesis, and phenology) (29), it remains unclear how trends detected from space correspond to other aspects such as tree mortality, diversity, and function (30). Other measures, such as the fraction of trees in a stand infested by insects, are highly informative but require repeated measurements of individual trees in forest plots. Thus, most assessments of forest health at the continental-to-global scale rely on more easily measured indicators of selected processes or key attributes (e.g., tree cover), but they may miss other indicators of declines in health, such as increased mortality or the loss of key fauna that serve as pollinators or seed vectors.

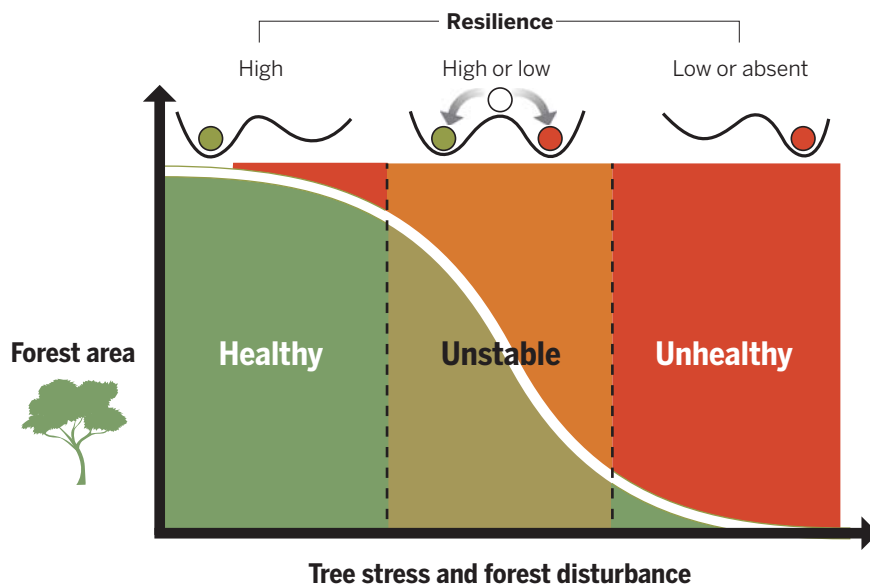
The only systematic global assessment of forest health is the FAO Global Forest Resource

remote sensing data on changes in forest distribution and land use. Because there are no standard protocols for data collection, methods are highly variable, and information on insect pests and diseases, fires, and biotic and abiotic disturbances is sparse, sporadic, or even unavailable for many countries. In particular, spatial and temporal patterns of stressor occurrence may be difficult to identify without a more standardized approach. Nonetheless, the FAO assessment currently provides the best-available information on areas of forest subjected to different kinds of disturbances.

Another initiative that would benefit from better quantification of changes in forest conditions is the United Nations program for Reducing Emissions from Deforestation and Forest Degradation (REDD; [www.un-redd.org](http://www.un-redd.org)). This is an economic instrument for rewarding tropical nations that avoid carbon emissions to the atmosphere or that regain carbon by reforestation. To be successful, REDD requires spatial and temporal monitoring of changes in carbon stocks due to deforestation and forest degradation, the latter of which usually results from selective logging, forest fragmentation, and surface fires. Although efforts are being made to make processes across nations more comparable (33), REDD is being implemented largely at the country and sub-country level.

Given the global importance of forests, the projections of increased future disturbances, and the need to inform conservation mechanisms, it is vital to design an approach that can identify the transition from healthy to unhealthy forests as well as characterize the underlying causes. This includes developing a strong enough understanding of the background levels of forest disturbance to identify events that could alter recovery trajectories. Systematic identification and attribution of individual tree-mortality events based on field plots have proven effective in this respect, but they are too costly to be performed at global scales. Progress has also been made toward mapping broad-scale forest degradation caused by selective logging (34), mortality events associated with hurricanes (35) or strong winds (36, 37), and disturbances including fires (38–41). Over the decades for which they are available, Landsat data can be used to help define background levels of disturbance. However, the spatial resolution (one pixel, usually about 30 × 30 m) of these multidecadal records is not sufficient to document smaller-scale mortality (e.g., a few trees or less within a pixel). Lack of information at this scale limits our ability to track changes in forest condition globally, because it is the scale at which the most tree mortality can occur (36, 42).

We currently have no way to assess the importance of observed occurrences of drought- and heat-induced tree mortality and associated declines in global forest health. Allen *et al.* (43) indicate the need for establishing a global network for monitoring broad-scale tree mortality and its ecological consequences (44). Global trends in mortality rates might be one of the most robust indicators of global forest health; monitoring these trends would also yield valuable information



**Fig. 3. Schematic representation of changes in forest health as a function of tree stress and forest disturbances.** Resilience (top) is indicated by the tendency of a system to stay in its current vegetation state (high resilience) or to switch to another state (low resilience); states are indicated by “wells,” with the system more likely to move to the deeper well once some threshold has been crossed. The green area indicates forests experiencing background levels of stress and disturbance that are relatively weak, affect mostly small areas, and cause no fundamental changes in forest functioning. Such forests tend to be resilient at a broad range of spatial scales (i.e., they tend to stay in their current state, as indicated by the circle in the deeper well above). This background level of tree stress and disturbance is difficult to measure using current remote sensing techniques; it is usually estimated using plot-based inventories. As unprecedented levels of tree stress and disturbances are reached, the area experiencing complete breakdown of basic functions and resilience is expected to substantially increase, creating positive feedbacks with climate that could cross a threshold and lead to a novel (nonforest) ecosystem. This shift in forest condition is detectable from space using high-resolution images. Our main questions have to do with the orange area: How can we determine whether the transition from healthy to unhealthy is an abrupt threshold, and (if so) how can we detect early signs that an abrupt threshold is about to be crossed?

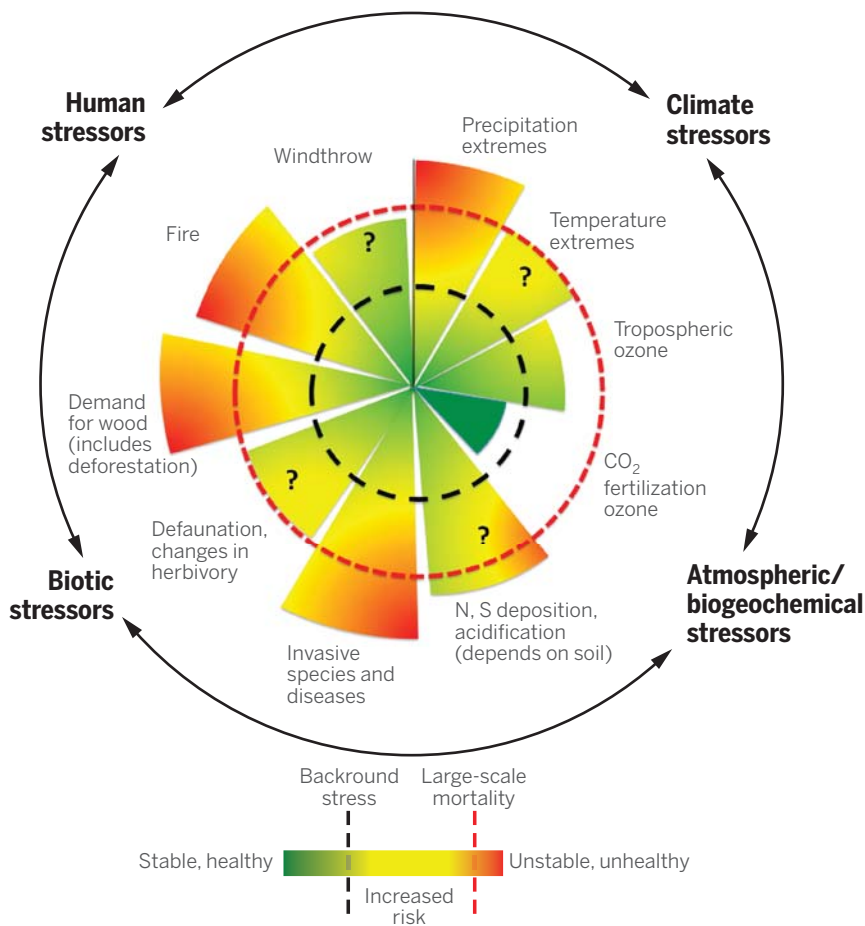
stand how individual and combined factors lead to tree mortality.

#### How can we monitor declines in forest condition at global scales?

The tools currently applied to measure forest condition leave large gaps in coverage and cannot supply all the information needed to systematically assess changes in global forest health. Although remote sensing techniques provide some useful

Assessment (31, 32). This report evaluates “forest health and vitality” based on individual countries’ reporting of areas of forest affected by various stresses (fire, insects, disease, physical damage by animals, weather extremes, and invasive species). Although the FAO assessment represents an ecosystem approach and is therefore less affected by stakeholder interests than are utilitarian assessments, the reporting framework relies on submissions by individual countries, complemented by





**Fig. 4. Examples of different stresses and disturbances affecting forests and how they are expected to change in the future, compared with preindustrial background levels.** We have adopted the approach and style used for planetary boundaries (50). Stressors can be broadly placed in categories such as “climate,” “biotic,” and “human,” but there are many connections among them. For example, stressors, even those set by humans, are more severe and more likely to cause mortality during extreme drought and humidity events. Similarly, a tree stressed by drought may have fewer reserves and succumb more easily to insect or disease outbreak. Although some global changes are probably making forests more resilient (e.g., elevated CO<sub>2</sub> or possibly increased deposition of limiting nutrients from pollution or dust), many others that may negatively affect forests have increased in severity and/or frequency over the past decades and are predicted to increase further in the future. Question marks signify processes for which uncertainties are large, either in terms of how current levels exceed background conditions or how effects may increase or decrease resilience (e.g., nutrient deposition).

about the role of forest disturbance and recovery in the global carbon cycle (14, 38, 42) and provide test models and remote sensing products that could be used to scale up results from plots. Understanding the trajectory of complex forest-system responses to multiple stressors from local to global scales requires three steps: (i) detection of acute and long-term changes in forest condition and attribution of the causes, (ii) identification of mechanistic relationships between forest-health decline and multiple stressors, and (iii) long-term monitoring of forest recovery after decline and of the natural range of variability in forest condition.

Monitoring allows rapid identification of where and when unusual forest decline is occurring. Monitoring deforestation and severe forest degradation, as well as broad-scale climate-induced vegetation disturbance, is possible at the global level using remote sensing products with high

spatial and temporal resolution (42, 39, 45). However, it is more difficult to use these tools to attribute observed changes to specific causes, especially when the causes are combinations of human, biotic, and climatic stresses. For example, a large stand-killing fire may have a human ignition source, but its intensity could reflect drought conditions and fuel-load buildup from previous disturbance or management decisions.

Forest inventory assessments often measure indicators of tree and forest health (e.g., crown condition and disease occurrence) to evaluate forest condition in plots, which then must be aggregated to provide information at regional or national scales. Data at this intermediate scale that are needed for linking plots with remote sensing observations are largely missing for many regions [with some exceptions (12)], as they depend on an understanding of disturbance inten-

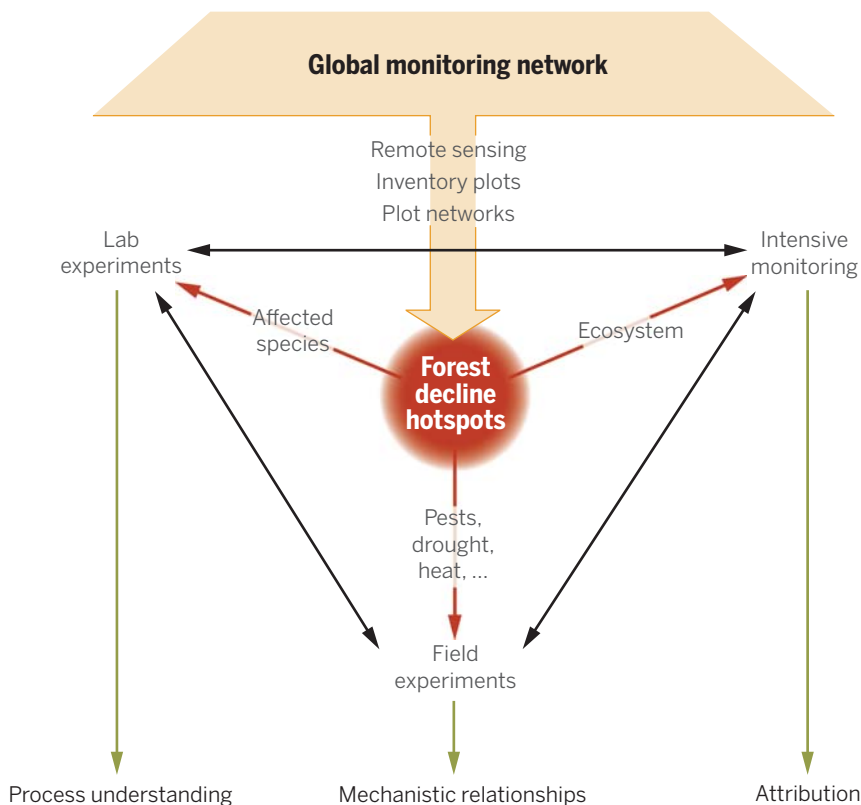
sity and frequency across large areas. Protocols for forestry inventory plots need to be as similar as possible, at least for assessments of key parameters such as pest infestation level and crown dieback. Only then can forest condition data can be compared across different legislative regions.

Information at the scales needed to link plot data to remote sensing pixels constitutes a major gap, especially with respect to detecting and attributing altered rates of tree mortality. Repeated aircraft surveys to detect changes in biomass over large regions using lidar and radar techniques can be useful at this intermediate scale (10, 12, 46). Efforts to evaluate tropical forest degradation (e.g., loss of biomass and diversity) using a combination of satellites have proven effective in identifying areas of future deforestation, but they may underestimate the area of degradation created by selective logging, fire, or windthrow (34). A recently approved European Space Agency satellite mission (Biomass) will, for the first time, enable repeated global surveys of forest structure and change (47).

Mechanistic relationships between the multiple and interacting stresses and disturbances and forest decline (orange area in Fig. 3) are not well characterized. Most ecological experiments are designed to test the effects of a single factor such as drought, elevated CO<sub>2</sub>, or changes in ozone (48), and those that attempt to test more than two factors quickly grow to an unmanageable size. New theoretical and experimental approaches, combined with long-term observations, are needed to link forest performance parameters to climatic, biogeochemical, and biotic stressors at multiple scales and to allow identification of stress thresholds. In particular, mortality functions in global dynamic vegetation models should be responsive to multiple stressors.

The dynamics of long-term forest recovery, and especially the time scales required to restore different utilitarian or ecosystem functions, are poorly understood for many ecosystems. Long-term monitoring of forest plots combined with chronosequences of disturbance and recovery (14, 15, 49) in multiple forest types are required. Understanding factors such as the role of plant (tree) diversity or herbivore abundance in the trajectory of recovery will be critical for supporting increased resilience of forests to more frequent, intense, or novel disturbances in the future.

A successful strategy for global monitoring of forest health, for attributing the causes of decline, and for developing a mechanistic understanding of the underlying processes should thus comprise (Fig. 5): (i) observations of naturally occurring forest conditions, especially improvements in detecting tree and forest mortality; (ii) in situ manipulations of the hypothesized causes of decline in vulnerable ecosystems to verify their attribution and to determine the parameters of mechanistic relationships; (iii) focused research on the underlying processes under controlled environmental conditions in lab facilities and greenhouses; and (iv) the integration of understanding with models that can span spatial and temporal scales. Such a structured approach will



## Modeling/prediction of future forest conditions

**Fig. 5. Proposed design for global assessment of forest health and prediction of future forest conditions.** A network of inventory and research plots combined with remote sensing information allows detection of hotspots of forest decline. In these locations, intensive monitoring and manipulations of environmental drivers allow attribution of the causes of decline and clarify mechanistic relationships between drivers and responses; in addition, investigations under controlled conditions (e.g., greenhouse studies) of physiological responses to environmental cues yield understanding of the underlying processes. Taken together, these approaches allow assessments of current forest health and provide the understanding of process-based mechanisms required for modeling future forest health.

generate understanding of the processes involved and provide the scientific mechanisms required for modeling future forest condition in a rapidly changing environment (Fig. 5).

### Are we facing a future without healthy forests?

This key question is not yet possible to answer, and no existing observing system can track ongoing changes in a way that enables confident attribution of causes, predictions of recovery trajectories versus further decline, or understanding of the consequences for the maintenance or loss of forest services. Given that many of the trees alive today will experience temperatures and CO<sub>2</sub> levels outside the range to which they are adapted, it is critical to improve efforts to monitor forests and especially tree mortality.

Forests have existed for far longer than humans and have already survived a wide range of past changes in climate conditions. Over the long term, forests will probably prove resilient to rapid anthropogenic changes in climate and environment, whether in their current form or in novel com-

munity assemblages. Human concerns about forest health mostly reflect our dependence on the continued availability of the products and services that forests provide. Our vulnerability to even temporary disruptions in their supply underlines our urgent need to detect, understand, and predict potential declines in global forest health.

### REFERENCES AND NOTES

- S. L. Lewis, D. P. Edwards, D. Galbraith, *Science* **349**, 827–832 (2015).
- C. I. Millar, N. L. Stephenson, *Science* **349**, 823–826 (2015).
- S. Gauthier, P. Bernier, T. Kuuluvainen, A. Z. Shvidenko, A. D. Schepaschenko, *Science* **349**, 819–822 (2015).
- M. J. Wingfield, E. G. Brockerhoff, B. D. Wingfield, B. Slippers, *Science* **349**, 832–836 (2015).
- R. Costanza, B. Norton, B. Haskell, in *Ecosystem Health: New Goals for Environmental Management*, R. Costanza, Ed. (Island Press, Washington, DC, 1992), pp. 239–256.
- T. E. Kolb, M. R. Wagner, W. W. Covington, *J. For.* **92**, 10–15 (1994).
- R. L. Edmonds, J. K. Agee, R. I. Gara, *Forest Health and Protection* (McGraw-Hill, New York, 2000).
- K. F. Raffa *et al.*, *J. For.* **5**, 276–277 (2009).
- T. Kolb, M. R. Wagner, W. W. Covington, in *Forest Health Through Silviculture: Proceedings of the 1995 National Silviculture Workshop*, L. G. Eskew, Ed. (General Technical Report RM-GTR-267, U.S. Forest Service, Fort Collins, CO, 1995), pp. 5–13.

- G. P. Asner, M. Keller, J. N. M. Silva, *Glob. Change Biol.* **10**, 765–783 (2004).
- S. D. Miller *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 19431–19435 (2011).
- G. P. Asner *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 16738–16742 (2010).
- J. Q. Chambers *et al.*, *Oecologia* **141**, 596–611 (2004).
- J. E. Janisch, M. E. Harmon, *Tree Physiol.* **22**, 77–89 (2002).
- D. M. Marra *et al.*, *PLOS ONE* **9**, e103711 (2014).
- P. Meir *et al.*, in *Amazonia and Global Change*, M. Keller, M. Bustamante, J. Gash, P. Silva Dias, Eds. (AGU Geophysical Monograph Series vol. 186, American Geophysical Union, Washington, DC, 2009), pp. 429–449.
- C. A. Nobre, L. Borma, *Curr. Opin. Environ. Sustain.* **1**, 28–36 (2009).
- C. D. Allen *et al.*, *For. Ecol. Manage.* **259**, 660–684 (2010).
- P. M. Brando *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6347–6352 (2014).
- J. A. Marengo, J. Tomasella, W. R. Soares, L. M. Alves, C. A. Nobre, *Theor. Appl. Climatol.* **107**, 73–85 (2012).
- N. Diffenbach, M. Ashfach, *Geophys. Res. Lett.* **37**, 1–5 (2010).
- E. Litchman, K. F. Edwards, C. A. Klausmeier, *Front. Microbiol.* **6**, 254 (2015).
- R. J. Norby *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 18052–18056 (2005).
- Intergovernmental Panel on Climate Change, *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change*, C. B. Field *et al.*, Eds. (Cambridge Univ. Press, Cambridge, 2012).
- M. A. Cochrane *et al.*, *Science* **284**, 1832–1835 (1999).
- K. A. Harper *et al.*, *Conserv. Biol.* **19**, 768–782 (2005).
- J. A. Hicke *et al.*, *Glob. Change Biol.* **18**, 7–34 (2012).
- K. F. Raffa *et al.*, *Bioscience* **58**, 501–517 (2008).
- M. C. Hansen *et al.*, *Science* **342**, 850–853 (2013).
- S. J. Goetz, A. G. Bunn, G. J. Fiske, R. A. Houghton, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 13521–13525 (2005).
- FAO, *Global Forest Resources Assessment 2005* (FAO Forestry Paper 147, FAO, Rome, 2005).
- FAO, *Global Forest Resources Assessment 2010* (FAO Forestry Paper 163, FAO, Rome, 2010).
- UN Reducing Emissions from Deforestation and forest Degradation (UN-REDD+) Programme, *Emerging Approaches to Forest Reference Emission Levels and/or Forest Reference Levels for REDD+* (FAO, Rome, 2014).
- G. P. Asner *et al.*, *Science* **310**, 480–482 (2005).
- R. Negrón Juárez, D. B. Baker, H. Zeng, T. K. Henkel, J. Q. Chambers, *J. Geophys. Res. D Atmos.* **115**, G04030 (2010).
- J. Q. Chambers *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 3949–3954 (2013).
- F. D. B. Espírito-Santo *et al.*, *Nat. Commun.* **5**, 3434 (2014).
- D. J. Mildrexler, M. Zhao, F. A. Heinsch, S. W. Running, *Ecol. Appl.* **17**, 235–250 (2007).
- D. J. Mildrexler, M. Zhao, S. W. Running, *Remote Sens. Environ.* **113**, 2103–2117 (2009).
- M. Flannigan, B. Stocks, M. Turetsky, M. Wotton, *Glob. Change Biol.* **15**, 549–560 (2009).
- A. A. C. Alencar, P. M. Brando, G. P. Asner, F. E. Putz, *Ecol. Appl.* (2015).
- N. G. McDowell *et al.*, *Trends Plant Sci.* **20**, 114–123 (2015).
- C. D. Allen, D. D. Breshears, N. G. McDowell, *Ecosphere* (2015); [www.esajournals.org/doi/full/10.1890/ES15-00203.1](http://www.esajournals.org/doi/full/10.1890/ES15-00203.1)
- H. Hartmann, H. D. Adams, W. R. L. Anderegg, S. Jansen, M. J. B. Zeppel, *New Phytol.* **205**, 965–969 (2015).
- M. C. Hansen, S. V. Stehman, P. V. Potapov, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 8650–8655 (2010).
- S. R. Levick, G. P. Asner, *Biol. Conserv.* **157**, 121–127 (2013).
- K. Scipal *et al.*, in *Geoscience and Remote Sensing Symposium (IGARSS), 2010 IEEE International* (Institute of Electrical and Electronics Engineers, Piscataway, NJ, 2010), pp. 52–55.
- Z. E. Kayler *et al.*, *Front. Ecol. Environ.* **13**, 219–225 (2015).
- M. L. Goulden *et al.*, *Glob. Change Biol.* **12**, 2146–2162 (2006).
- W. Steffen *et al.*, *Science* **347**, 1259855–1259855 (2015).

### ACKNOWLEDGMENTS

P.B. received funding from NSF (DEB-1146206) and the Brazilian National Council for Scientific and Technological Development (Bolsa de Produtividade number 307084/2013-2). S.T. and H.H. thank C. Allen for sharing an early draft of his paper and the participants of the International Interdisciplinary Workshop on Tree Mortality, held in October 2014 in Jena, Germany.

10.1126/science.aac6759

---

*This copy is for your personal, non-commercial use only.*

---

**If you wish to distribute this article to others**, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

**Permission to republish or repurpose articles or portions of articles** can be obtained by following the guidelines [here](#).

**The following resources related to this article are available online at [www.sciencemag.org](http://www.sciencemag.org) (this information is current as of August 31, 2015 ):**

**Updated information and services**, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/349/6250/814.full.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/349/6250/814.full.html#related>

This article **cites 41 articles**, 17 of which can be accessed free:

<http://www.sciencemag.org/content/349/6250/814.full.html#ref-list-1>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>