

## REVIEW SUMMARY

## FOREST ECOLOGY

## Pervasive shifts in forest dynamics in a changing world

Nate G. McDowell\*, Craig D. Allen, Kristina Anderson-Teixeira, Brian H. Aukema, Ben Bond-Lamberty, Louise Chini, James S. Clark, Michael Dietze, Charlotte Grossiord, Adam Hanbury-Brown, George C. Hurtt, Robert B. Jackson, Daniel J. Johnson, Lara Kueppers, Jeremy W. Lichstein, Kiona Ogle, Benjamin Poulter, Thomas A. M. Pugh, Rupert Seidl, Monica G. Turner, Maria Uriarte, Anthony P. Walker, Chonggang Xu

**BACKGROUND:** Forest dynamics arise from the interplay of chronic drivers and transient disturbances with the demographic processes of recruitment, growth, and mortality. The resulting trajectories of vegetation development drive the biomass and species composition of terrestrial ecosystems. Forest dynamics are changing because of anthropogenic-driven exacerbation of chronic drivers, such as rising temperature and CO<sub>2</sub>, and increasing transient disturbances, including wildfire, drought, windthrow, biotic attack, and land-use change. There are widespread observations of increasing tree mortality due to changing climate and land use, as well as observations of growth stimulation of younger forests due to CO<sub>2</sub> fertilization. These antagonistic processes are co-occurring globally, leaving the fate of future forests uncertain. We examine the implications of changing forest demography and its drivers for both future forest management and forecasting impacts of global climate forcing.

**ADVANCES:** We reviewed the literature of forest demographic responses to chronic drivers and transient disturbances to generate hy-

potheses on future trajectories of these factors and their subsequent impacts on vegetation dynamics, with a focus on forested ecosystems. We complemented this review with analyses of global land-use change and disturbance datasets to independently evaluate the implications of changing drivers and disturbances on global-scale tree demographics. Ongoing changes in environmental drivers and disturbance regimes are consistently increasing mortality and forcing forests toward shorter-statured and younger stands, reducing potential carbon storage. Acclimation, adaptation, and migration may partially mitigate these effects. These increased forest impacts are due to natural disturbances (e.g., wildfire, drought, windthrow, insect or pathogen outbreaks) and land-use change, both of which are predicted to increase in magnitude in the future. Atmospherically derived estimates of the terrestrial carbon sink and remote sensing data indicate that tree growth and potentially recruitment may have increased globally in the 20th century, but the growth of this carbon sink has slowed. Variability in growth stimulation due to CO<sub>2</sub> fertilization is evident globally, with observations

and experiments suggesting that forests benefit from CO<sub>2</sub> primarily in early stages of secondary succession. Furthermore, increased tree growth typically requires sufficient water and nutrients to take advantage of rising CO<sub>2</sub>. Collectively, the evidence reveals that it is highly likely that tree mortality rates will continue to increase, whereas recruitment and growth will respond to changing drivers in a spatially and temporally variable manner. The net impact will be a reduction in forest canopy cover and biomass.

**OUTLOOK:** Pervasive shifts in forest vegetation dynamics are already occurring and are likely to accelerate under future global changes, with consequences for biodiversity and climate forcing. This conclusion is robust with respect to the abundant literature evidence and our global assessment of historical demographic changes, but it also forms the basis for hypotheses

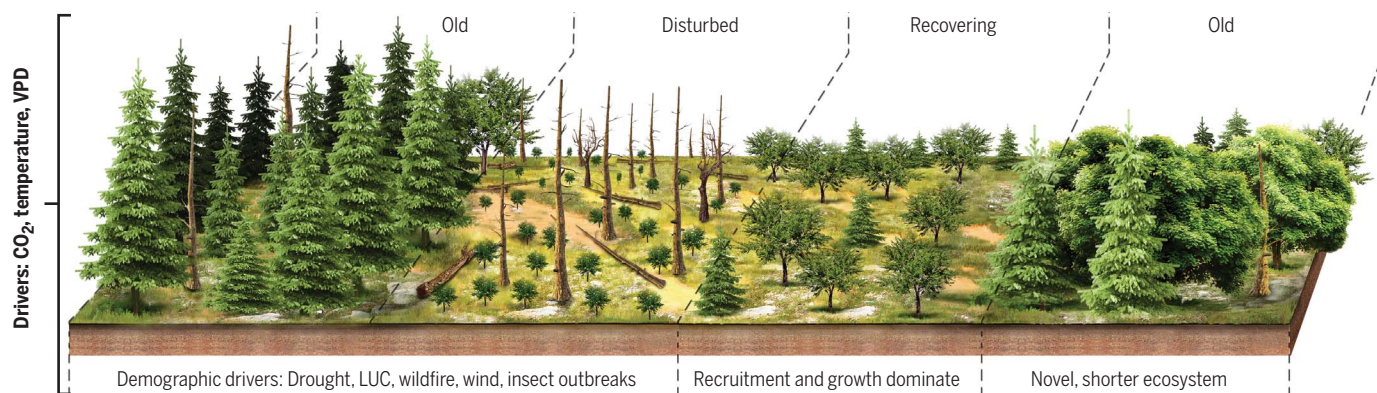
## ON OUR WEBSITE

Read the full article at <https://dx.doi.org/10.1126/science.aaz9463>

regarding the patterns and processes underlying the shifts in forest dynamics. These hypotheses will be directly testable using emerging terrestrial and satellite-based observation networks. The existing evidence and newly made observations provide a critical test of Earth system models that continue to improve in their ability to simulate forest dynamics and resulting climate forcing. Ultimately, forest managers and natural resource policies must confront the consequences of changing climate and disturbance regimes to ensure sustainable forests and accrue their associated benefits. ■

The list of author affiliations is available in the full article online.

\*Corresponding author. Email: [nate.mcdowell@pnsl.gov](mailto:nate.mcdowell@pnsl.gov)  
Cite this article as N. G. McDowell *et al.*, *Science* **368**, eaaz9463 (2020). DOI: 10.1126/science.aaz9463



**A conceptual diagram of the components of forest dynamics and the disturbances that drive them.** In the far-left panel, a mature ecosystem is responsive primarily to localized mortality, and the primary drivers of demography are chronically changing variables such as CO<sub>2</sub>, temperature, and vapor pressure deficit (VPD). In the next panel, the system is disturbed by fire, insect outbreak, or another large-scale perturbation that removes most of the overstory trees,

and species adapted to rapid postdisturbance recruitment become established. In the third panel, recruitment and growth dominate demographic processes, with mortality increasing over time as competition leads to self-thinning. In the last panel, a mature ecosystem is dominated by species that have replaced the original community in response to chronic environmental changes, leading to a novel ecosystem.

## REVIEW

## FOREST ECOLOGY

# Pervasive shifts in forest dynamics in a changing world

Nate G. McDowell<sup>1\*</sup>, Craig D. Allen<sup>2</sup>, Kristina Anderson-Teixeira<sup>3,4</sup>, Brian H. Aukema<sup>5</sup>, Ben Bond-Lamberty<sup>6</sup>, Louise Chini<sup>7</sup>, James S. Clark<sup>8</sup>, Michael Dietze<sup>9</sup>, Charlotte Grossiord<sup>10</sup>, Adam Hanbury-Brown<sup>11</sup>, George C. Hurtt<sup>7</sup>, Robert B. Jackson<sup>12</sup>, Daniel J. Johnson<sup>13</sup>, Lara Kueppers<sup>11,14</sup>, Jeremy W. Lichstein<sup>15</sup>, Kiona Ogle<sup>16</sup>, Benjamin Poulter<sup>17</sup>, Thomas A. M. Pugh<sup>18,19</sup>, Rupert Seidl<sup>20,21</sup>, Monica G. Turner<sup>22</sup>, Maria Uriarte<sup>23</sup>, Anthony P. Walker<sup>24</sup>, Chonggang Xu<sup>25</sup>

Forest dynamics arise from the interplay of environmental drivers and disturbances with the demographic processes of recruitment, growth, and mortality, subsequently driving biomass and species composition. However, forest disturbances and subsequent recovery are shifting with global changes in climate and land use, altering these dynamics. Changes in environmental drivers, land use, and disturbance regimes are forcing forests toward younger, shorter stands. Rising carbon dioxide, acclimation, adaptation, and migration can influence these impacts. Recent developments in Earth system models support increasingly realistic simulations of vegetation dynamics. In parallel, emerging remote sensing datasets promise qualitatively new and more abundant data on the underlying processes and consequences for vegetation structure. When combined, these advances hold promise for improving the scientific understanding of changes in vegetation demographics and disturbances.

**T**he interplay of vegetation demography—recruitment, growth, and mortality—with environmental conditions and disturbances drives forest dynamics of biomass, function, and species composition (see Box 1 for definitions). In old-growth forests that approximate steady-state demographics, the recruitment, growth, and mortality of trees are approximately balanced; in contrast, rapid recruitment often follows widespread disturbance-induced mortality (1). Vegetation dynamics may now be changing because the environmental context in which plant demography and disturbances interact is shifting with anthropogenic change. The interaction between episodic forest disturbances, such as windthrow or wildfire, and chronically changing drivers, such as rising temperature, vapor pressure deficit (VPD), and CO<sub>2</sub>, together with land-use change (LUC) (2), leads to both compounding and antagonistic impacts that alter demographic rates (3), with consequences for terrestrial biogeochemical cycles and climate (4, 5). Understanding the drivers of vegetation

dynamics is thus critical for accurate prediction of global terrestrial biogeochemistry under future conditions (6).

The impacts of global change on forest demographic rates may already be materializing. In mature ecosystems, tree mortality rates have doubled throughout much of the Americas and in Europe over the past four decades (7–9). Simultaneously, global carbon budgets indicate either a growing or constant terrestrial carbon sink (10–12), which implies increased or constant vegetation production rates (13, 14). However, satellite evidence suggests that forests might be switching from a CO<sub>2</sub> fertilization-dominated period to a VPD-dominated period (15). Terrestrial greening indices indicate a shift from a CO<sub>2</sub>-driven increase in greenness in the late 20th century to a VPD-driven decrease in the past decade (16). Thus, increasing mortality due to anthropogenic changes and potentially increasing or stable growth and recruitment due to CO<sub>2</sub> fertilization (5) represent opposing processes that are co-occurring globally, leaving the fate of future forests uncertain.

In addition to changing vegetation dynamics in intact or relatively undisturbed forests, episodic disturbances are tending to be larger, more severe, and in some regions more frequent under global climate change (17–20). Similarly, the rates and types of LUC vary widely (21) but have, on average, increased globally in the past few centuries (2, 22, 23). Thus, at the global scale, disturbances and LUC have likely amplified tree mortality beyond what is suggested by the doubling of background mortality rates in undisturbed forests (7–9). Current understanding of the net balance of tree losses (mortality) and gains (recruitment and growth) under a changing environment characterized by more-extreme drivers and disturbances is limited, preventing prediction of whether recruitment and growth can balance increased mortality rates in the future.

To evaluate whether environmental changes and increasing disturbances are causing globally widespread shifts in vegetation demography, we reviewed global observations of recruitment, growth, and mortality of forests and woodlands. Our expert-derived compilation of the state-of-the-art knowledge on vegetation dynamics, their drivers, and disturbances, allowed us to address four questions: (i) Is there evidence for shifts in demography over recent decades? (ii) What physiological and disturbance-mediated processes underlie these demographic shifts? (iii) What are the potential consequences of disturbance-mediated changes in demography for climate forcing? (iv) How can global predictions of future vegetation dynamics best be improved?

## Evidence for changing drivers and disturbances and their impact on demography

Determining the impacts of changing drivers on demography is difficult given the lack of global observation platforms. However, evidence abounds from individual published studies on the drivers and their impacts on plant communities, and new modeling and observational efforts now enable a more complete picture of disturbances and forest demography (24–26). In this section, we first examine whether there are global trends in stand ages and test the sensitivity of the stand-age distribution to changes in disturbance rate

<sup>1</sup>Pacific Northwest National Laboratory, Richland, WA 99354, USA. <sup>2</sup>U.S. Geological Survey, Fort Collins Science Center, New Mexico Landscapes Field Station, Los Alamos, NM 87544, USA.

<sup>3</sup>Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, VA 22630, USA. <sup>4</sup>Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Republic of Panama. <sup>5</sup>Department of Entomology, University of Minnesota, St. Paul, MN 55108, USA. <sup>6</sup>Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park, MD 20740, USA. <sup>7</sup>Department of Geographical Sciences, University of Maryland, College Park, MD 20742, USA. <sup>8</sup>Nicholas School of the Environment, Duke University, Durham, NC 27708, USA. <sup>9</sup>Department of Earth and Environment, Boston University, Boston, MA 02215, USA. <sup>10</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland. <sup>11</sup>Energy and Resources Group, University of California, Berkeley, Berkeley, CA 94720, USA. <sup>12</sup>Department of Earth System Science, Woods Institute for the Environment, and Precourt Institute for Energy, Stanford University, Stanford, CA 94305, USA. <sup>13</sup>School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, USA. <sup>14</sup>Division of Climate and Ecosystem Sciences, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA. <sup>15</sup>Department of Biology, University of Florida, Gainesville, FL 32611, USA. <sup>16</sup>School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ 86001, USA. <sup>17</sup>Biospheric Sciences Laboratory, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA. <sup>18</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, B15 2TT Birmingham, UK. <sup>19</sup>Birmingham Institute of Forest Research, University of Birmingham, B15 2TT Birmingham, UK.

<sup>20</sup>Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences Vienna, 1180 Vienna, Austria. <sup>21</sup>School of Life Sciences, Technical University of Munich, 85354 Freising, Germany. <sup>22</sup>Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI 53706, USA. <sup>23</sup>Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA. <sup>24</sup>Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN 37831, USA. <sup>25</sup>Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA.

\*Corresponding author. Email: nate.mcdowell@pnnl.gov

### Box 1. Vegetation dynamics definitions.

We focus on three main plant demographic processes: recruitment, growth, and mortality. Recruitment (including reproduction) determines the seedling and sapling composition of a plant community after disturbance (152). Growth from sapling to mature plant results in development of mature forests and includes competitive processes. Mortality is a key rate controlling carbon storage and species composition in a plant community and is a dominant demographic rate during a pulse disturbance (153, 154).

**Abiotic drivers.** Physical factors that cause changes in demography and that respond to global change or to disturbances, such as light, CO<sub>2</sub>, soil moisture, humidity, temperature, etc.

**Biotic drivers.** Biological factors that may drive changes in demography, such as pathogens, insects, herbivores, or competition with other individuals.

**Chronic environmental change.** Persistently changing drivers of demographic rates. These drivers have a nonstable and directional trajectory, such as rising CO<sub>2</sub>, temperature, and VPD.

**Demographic rate.** Any individual-, population-, or community-level parameter that affects the age and/or size structure of a population or community, including rates of recruitment, growth, and death.

**Demographic driver.** An abiotic or biotic factor that, when undergoing a change itself, also leads to change(s) in one or more demographic rates.

**Disturbance.** The destruction of live plant biomass in a discrete event (155, 156).

**Disturbance regimes.** Spatial and temporal characteristics of disturbances in a landscape over a long time period, including frequency, return interval, duration, intensity, severity, and size.

**Growth.** The rate of biomass production over time, at the individual or ecosystem scale (i.e., net primary production in grams of carbon per square meter per year).

**Land-use and land-cover change.** Anthropogenic shifts in forms of cultivation or in vegetation cover due to, for example, forestry or conversion of woodlands to crop ecosystems.

**Mortality.** Defined herein as the complete loss of a plant's ability to reproduce and ultimately the loss of cellular metabolism.

**Recruitment.** The rates of transition of plants from one size class to another (typically in units of individuals per square meter per year). Recruitment results from the birth and growth of individuals. Herein, we consider recruitment from the stage of seed dispersal through seedling growth into the sapling stage.

**Self-thinning.** Reduction in the number of live plants within a stand, occurring via competition for resources.

**Vegetation dynamics.** The net outcome of the interplay between disturbances and vegetation demographic rates.

using global datasets on LUC (27) and non-LUC (25, 28) disturbances. We subsequently draw upon the wealth of published studies on changes in forest demographics and their drivers to investigate the potential changes leading to global stand-age trends. Ultimately, the combination of our global estimates and the large literature base allows us to generate testable hypotheses regarding trends and impacts of the drivers of forest demographics.

#### Is disturbance changing forest demography at the global scale?

We reanalyzed the Land-use Harmonization (LUHV2) dataset (27) with respect to forest age, revealing that the area of young forest stands (here defined as stands younger than 140 years old) resulting directly from LUC (conversion of forest to nonforest) or wood harvest (forest retention with reduction of biomass and age) has increased from 4.8 million km<sup>2</sup> in 1900 to 12.5 million km<sup>2</sup> in 2015 (or from 11.3 to 33.6% of forest area) (Fig. 1A). The results were insensitive to assumptions regarding the link of disturbance likelihood to stand age (Fig. 1A). These forest stand-age distributions exhibit different trajectories in different regions. Tropical forests have pro-

gressively lost old-growth area owing to LUC over the course of the 20th century (Fig. 2A, black dashed line). Wood harvest has increased from a minor driver of tropical forest age distribution in 1900 to a major one in 2015 (difference between solid and dashed lines). The split between deforestation and shifting cultivation drivers is broadly consistent with a satellite-based analysis for the period 2001–2015 (29). Temperate and Mediterranean forest ages are strongly influenced by wood harvest, which has made old-growth forests increasingly scarce in these regions. LUC has had minimal influence on stand age in boreal forests, but wood harvest has substantially shifted boreal forest age distribution toward young growth.

In reality, old-growth forests are made scarcer by more than just LUC and wood harvest (Figs. 1A and 2), they are threatened by other disturbances that have shifted landscapes from old to young growth-dominated stands (14), such as wildfire (29), windthrow (30), and biotic outbreaks (31). To address these additional disturbances, we integrated recent observation-based estimates of non-LUC disturbance for closed-canopy forests (25, 28) with LUC from LUHV2 to obtain a first-principles

estimate of the combined effect of human and natural disturbances on forest age structure (Fig. 1B). A twofold increase in non-LUC disturbance rates over the period 2015–2050 would result in a substantial increase in the fraction of young forests (Fig. 1, B and C). Thus, realistic shifts in disturbance rates can substantially affect the age structure of forests in the future. As discussed below, such an increase in disturbance rate is consistent with the magnitude of changes observed or predicted in individual ecosystems.

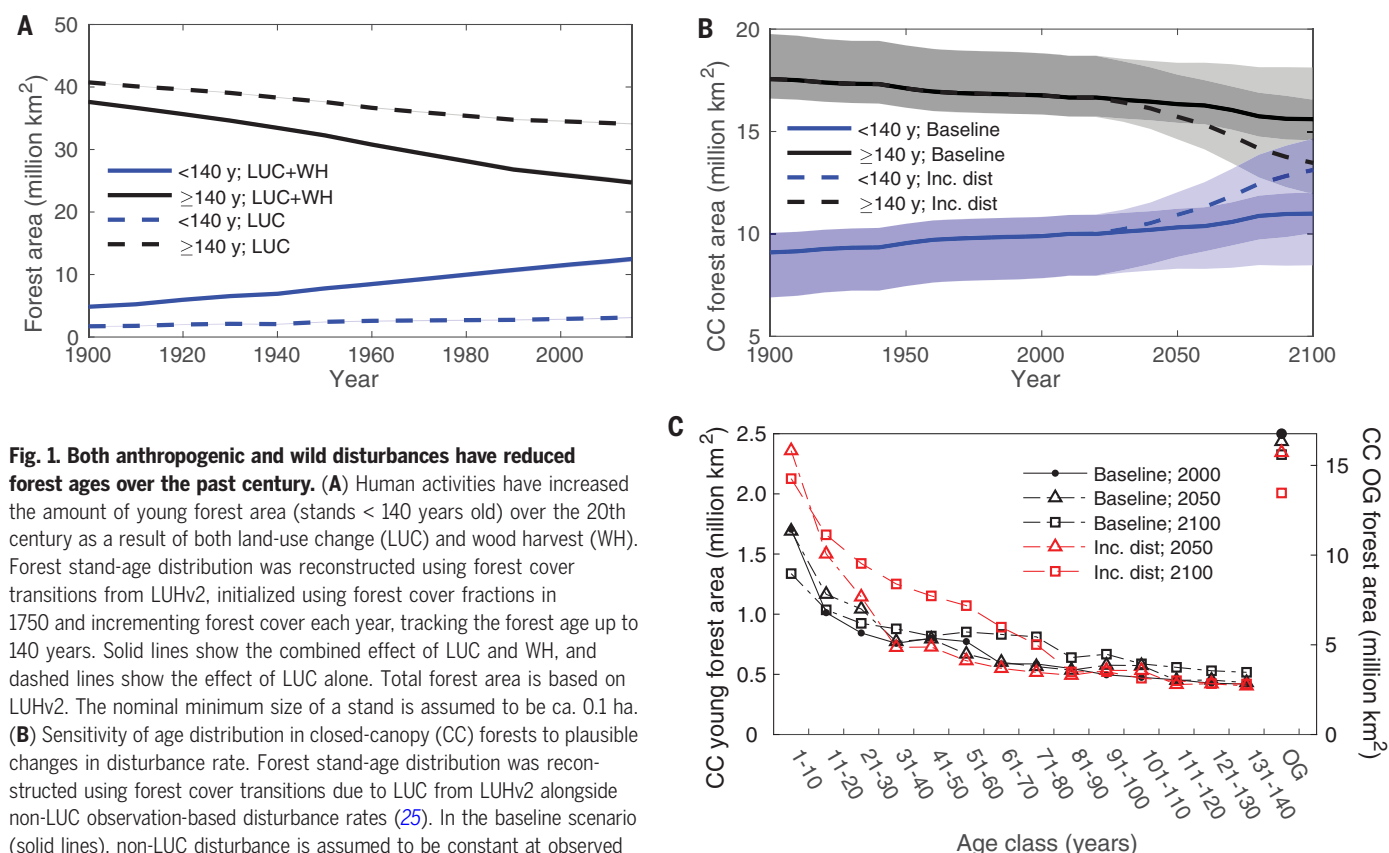
Notably, calculations based on the Global Forest Age Dataset (GFAD) v1.1 (14, 32) yielded 16.5 million km<sup>2</sup> of old-growth forest and 26.3 million km<sup>2</sup> of young forest (32), which differs from what is shown in Fig. 1, B and C. This disparity is likely attributable to consideration of different forest types (closed-canopy forests versus all forests) and to differences in definitions of stand size and age used in inventories versus those used in satellite-based estimates.

#### Chronically changing drivers Atmospheric CO<sub>2</sub>

Atmospheric CO<sub>2</sub> has risen more than 125 parts per million (ppm) since the industrial revolution (11) and is projected to rise an additional 50 to 200 ppm by 2100. Higher CO<sub>2</sub> increases leaf-level water-use efficiency, and rising CO<sub>2</sub> has positive but uncertain feedbacks on plant demographic rates (Fig. 3, A and B). Maturation and seed production can be accelerated under elevated CO<sub>2</sub> (33); however, seedling growth is not always stimulated by CO<sub>2</sub> (34). Recruitment response to rising CO<sub>2</sub> is variable (35, 36). Forest inventory and tree-ring studies show limited evidence for CO<sub>2</sub> fertilization of growth (37–43), potentially because of the overwhelming influence of increasing drought and nutrient limitations (44). Ecosystem-scale CO<sub>2</sub> enrichment experiments in young forests suggest a 30% gain in decadal biomass increment (45), but experiments in mature forests have found minimal growth stimulation (46, 47). This is consistent with evidence for an initially strong CO<sub>2</sub>-related growth stimulation in young forests that decreases with tree age and size (39) perhaps due to nutrient (7, 48) and hydraulic path-length limitations (49).

A limited number of studies suggest that elevated CO<sub>2</sub> causes increased mortality or no change in mortality. Mortality rates of saplings during experimental drought were not mitigated by elevated CO<sub>2</sub> (50, 51), while accelerated self-thinning due to CO<sub>2</sub> fertilization-induced stand density increases may lead to higher mortality (6, 52, 53) (Fig. 3B). The latter process would be consistent with increases in recruitment at large scales. Because tree mortality is dominated by large size classes [i.e., (54)] (for details see section on size-related mortality below), faster growth via CO<sub>2</sub> fertilization may





**Fig. 1. Both anthropogenic and wild disturbances have reduced forest ages over the past century. (A)** Human activities have increased the amount of young forest area (stands < 140 years old) over the 20th century as a result of both land-use change (LUC) and wood harvest (WH). Forest stand-age distribution was reconstructed using forest cover transitions from LUHv2, initialized using forest cover fractions in 1750 and incrementing forest cover each year, tracking the forest age up to 140 years. Solid lines show the combined effect of LUC and WH, and dashed lines show the effect of LUC alone. Total forest area is based on LUHv2. The nominal minimum size of a stand is assumed to be ca. 0.1 ha. **(B)** Sensitivity of age distribution in closed-canopy (CC) forests to plausible changes in disturbance rate. Forest stand-age distribution was reconstructed using forest cover transitions due to LUC from LUHv2 alongside non-LUC observation-based disturbance rates (25). In the baseline scenario (solid lines), non-LUC disturbance is assumed to be constant at observed 2001–2014 values throughout. In the incremented distribution scenario ("Inc. dist"; dashed lines), disturbance rates are incremented linearly to 200% of the 2001–2014 values over the period 2015–2050 and held constant at that level thereafter. The underlying LUC scenario is Global Change Assessment Model Representative Concentration Pathway 3.4 (GCAM RCP 3.4), which includes land-based mitigation for CO<sub>2</sub> emissions. Results are presented for CC forests only (25), which is why total forest area is lower in (B) than in (A), as non-LUC disturbance rate information is not currently available for open-canopy forests. The shaded areas in (A) and (B) indicate the effect of assuming that disturbances are five times more likely to affect young forests than old-growth

forests, or vice versa, as opposed to an even probability across ages (solid lines). The apparent large dampening of this assumption in (A) versus (B) is primarily due to the different y-axis scales. **(C)** Changes in the disturbance regime propagate through forest age structure at decadal time scales. CC young (<140 years old) forest area is shown on the left-hand y axis. Old-growth (OG; >140 years old) forest area is shown on the right-hand y axis (same units) and refers to the data points in the upper right-hand corner of the panel. Scripts used and additional methods can be accessed at [https://github.com/pughtam/AgeClassReconst\\_rel.git](https://github.com/pughtam/AgeClassReconst_rel.git).

expose trees to size-related mortality risks earlier (7). Such CO<sub>2</sub>-induced increases in mortality may be global (55). Furthermore, faster growth is often associated with lower wood density (56), rendering fast growing trees more susceptible to high winds. Thus, future CO<sub>2</sub> fertilization could increase recruitment, growth, and mortality (Fig. 4B), although there is considerable uncertainty about these effects.

#### Temperature and vapor pressure deficit

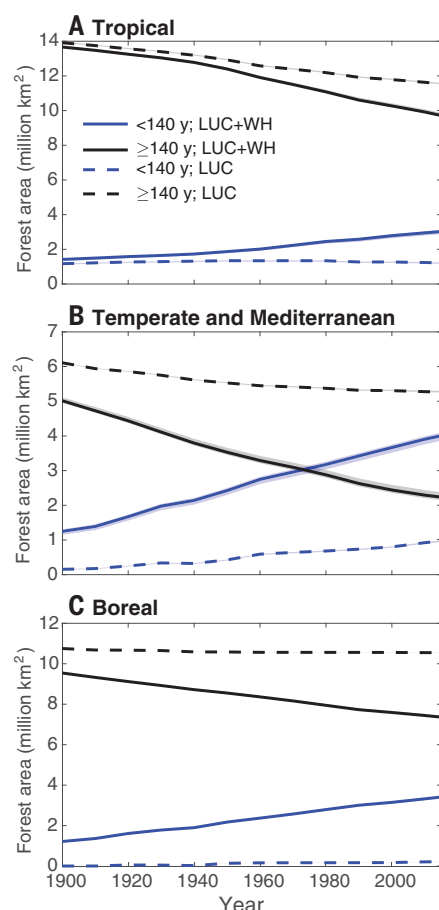
Temperature and VPD are rising globally and will continue to rise into the future (57). Both temperature and VPD can have impacts on demographic rates. Rising temperature forces an exponential rise in VPD, which prompts stomatal closure and limits photosynthesis, leading to lower growth, higher mortality (58), and reduced regeneration (59) and ultimately driving community shifts (60, 61). These ob-

servations are consistent with hydraulic theory, which suggests that as VPD rises, potential maximum tree height declines (62) (Fig. 4). This results from the dependency of water transport limitations on tree size (49) that are exacerbated by elevated VPD (Fig. 4), making short stature advantageous with rising VPD. Because most plants cannot reduce their size (beyond limited reductions in leaf area or crown dieback), forests respond through increased mortality of large plants, which are replaced by smaller ones (62), as has been observed in many studies (26, 54). While rising air temperature may also increase respiratory carbon loss, leaving less carbon for growth (63), warming in wetter and cooler regions may actually stimulate reproductive output, recruitment, and growth (3, 64, 65). Changes in temperature and VPD also can produce asynchrony in floral and pollinator phenology (66) and can reduce cold stratification (67),

both of which reduce seed abundance (68), and negatively affect recruitment (69, 70). Sapling mortality is accelerated by elevated temperature (70, 71), but recruitment has increased in moist areas (72). Thus, rising temperature and VPD may be beneficial in cooler or wetter areas, but most evidence suggests negative impacts on plant demographic rates (Figs. 3, C and D, and 4).

#### Changing disturbance regimes Droughts

Droughts are anticipated to increase in frequency, duration, and severity globally (Fig. 3, E and F) and are more stressful to plants owing to increases in temperature, VPD, and associated water loss (57). Drought can directly cause tree death or indirectly lead to mortality through associated increases in insect or pathogen attack (51). Hydraulic failure and carbon starvation remain the most likely, mutually

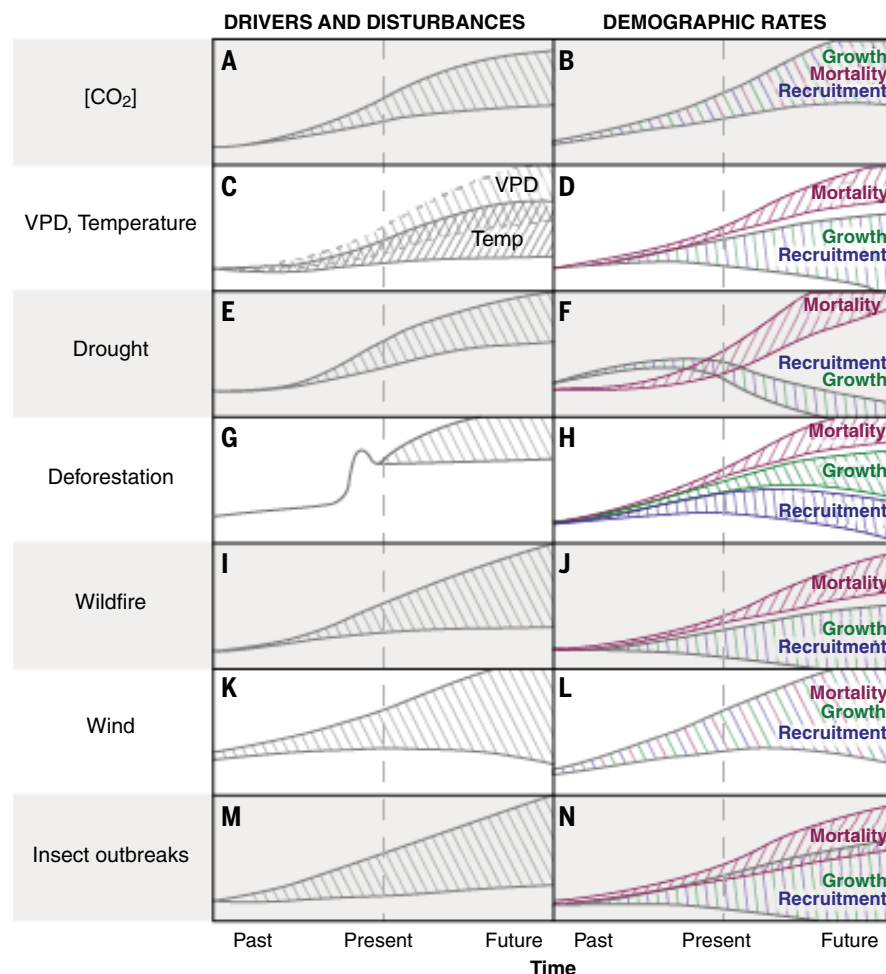


**Fig. 2. Human activities have increased the amount of young forest area irrespective of biome.** As in Fig. 1A, but broken down by biome (157): (A) tropical, (B) temperate and Mediterranean, and (C) boreal.

inclusive, underlying physiological mechanisms for drought-induced mortality (73), and both processes are likely to increase tree susceptibility to biotic agents (74). Evidence suggests that drought-induced mortality occurs more rapidly under warmer conditions (51, 71). Consistent with these empirical results, models suggest far greater mortality of temperate conifer trees in the future (75). Reproductive output is often reduced by drought [but see (64)], which, combined with drought impacts on seedling survival, leads to reduced recruitment (76). However, growth was relatively stable across a drought in Amazonia (77) while mortality increased. Thus, like rising temperature and VPD, it appears that drought may increase mortality regardless of location, while having variable impacts on recruitment and growth (Fig. 3F).

#### Land-use change

LUC and forest management have reduced vegetation stature and biomass and have altered species composition, with profound consequences for forest dynamics (Figs. 1A



**Fig. 3. Drivers, disturbances, and demographics are changing both historically and into the future.**

A graphical summary of the literature evidence of changing drivers and disturbances (left-hand column) and subsequent demographic rates (right-hand column). Shown are the chronically changing drivers (A and B) CO<sub>2</sub> and (C and D) VPD and temperature, as well as the more transient disturbances of (E and F) drought (low precipitation), (G and H) deforestation, (I and J) wildfire, (K and L) wind, and (M and N) insect outbreaks. Each driver or disturbance's corresponding demographic responses (shown as carbon fluxes per unit area over time) are shown in the corresponding right-hand panels.

and 3, G and H). Today's global vegetation biomass stocks may amount to only ~50% of their potential because of LUC (78). Wood harvest and shifting cultivation are the land-use activities primarily responsible for the conversion from primary to secondary vegetation cover and associated demographic shifts (2). In systems that return to wild vegetation or to managed forest after human clearing, demographic rates are typically accelerated. The increased resource availability after forest removal facilitates establishment of early successional species, reduces species diversity (79, 80), and triggers a transition to younger, smaller plants (81). Post-deforestation recruitment is often prolific even in the absence of management (82). Globally, the recovery of harvested forests and abandoned agricultural land, along with establishment of new planta-

tions, has resulted in younger forests (Fig. 1A), with associated reductions in tree size and biomass (83). Such post-deforestation recruitment may be limited by elevated VPD or drought, as is the case with recruitment after all-natural disturbances. Overall, the net effect of historical LUC and wood harvest has resulted in a substantial loss of forest area, along with altered demographic rates, leading to younger, shorter, less diverse ecosystems (Fig. 3H).

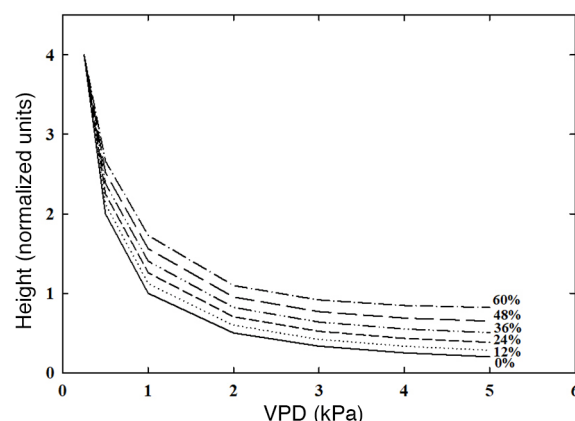
#### Wildfire

Wildfire is increasing in many forests worldwide (84) (Fig. 3I), although human management of landscapes has led to wildfire suppression in some biomes (85). Given sufficient fuel, burned area increases exponentially with aridity (86), and future fire frequencies may exceed those documented over the past

**Fig. 4. Rising VPD forces declines in potential plant stature.**

Predictions of plant height in response to rising VPD from the hydraulic corollary to Darcy's law. The equation is  $h = (A_s \times k_s \times \Delta\Psi) / (G \times A_l \times \text{VPD})$ , where  $h$  is height,  $A_s$  is sapwood area,  $k_s$  is specific conductivity,  $\Delta\Psi$  is the leaf-to-soil water potential gradient,  $G$  is stomatal conductance, and  $A_l$  is leaf area (53). The different lines represent different levels of acclimation of  $A_s$ ,  $k_s$ ,  $\Delta\Psi$ ,  $G$ , and  $A_l$ , all allowed to adjust simultaneously from 0 to 60% of their initial values.

In the case of  $G$ , it is assumed to decrease because of rising atmospheric  $\text{CO}_2$ . Acclimation can help, but not completely mitigate, the impact of rising VPD on plant stature.



10,000 years (87). Increased fire activity causes increased mortality and potentially higher recruitment and growth of either preexisting or newly introduced species, but rates of recruitment and growth may be slowed under climate warming. Forests characterized by stand-replacing fire regimes are dominated by obligate seeders and typically have effective seedling recruitment (88). However, high-severity and high-frequency fires can reduce recruitment by reducing seed supply through the repeated and severe loss of reproductively mature vegetation (89), and high-frequency fires can cause recruitment losses via direct mortality of the seedbank, seedlings, and saplings (90), which is worsened by elevated VPD (59). Woody species that can resprout after fire, including shrubs that suppress tree regeneration (59), may be favored by increased fire frequency and severity. Increased fire severity results in high tree mortality in forests historically adapted to low-severity fires, and subsequent recruitment and growth may be slow or absent, resulting in conversion of forests to low-biomass ecosystems (91). Thus, wildfire can result in higher demographic rates, although rising temperature and VPD can negatively affect recruitment and growth (Fig. 3J).

#### Windthrow

Windthrow from cyclonic storms represents the dominant natural disturbance in coastal forests across the globe (92). Cyclonic storms are expected to increase in frequency, wind velocities, and precipitation intensity (93) (Fig. 3K), resulting in more extreme flooding that promotes tree instability. Windthrow also results from convective thunderstorms and topographically mediated winds, and warming is expected to increase the frequency of atmospheric conditions conducive to severe thunderstorms (94). Canopy damage and

whole-tree mortality are the most immediate impacts of windthrow (95) (Fig. 3L). Storm-induced mortality is greatest for larger trees (96), and the loss of large canopy trees during wind disturbance favors growth of surviving trees (96, 97) and advances regeneration, recruitment of early successional species (98), or resprouting of trees broken by wind (99). Depending on the resprouting or seeding capacity of surviving species, wind damage may either slow or accelerate succession (100). We note that storms may also be associated with lightning, which may be a prominent cause of large-tree mortality (101). Thus, windstorms should result in changes in all three demographic rates, although with large uncertainty at the global scale (Fig. 3L).

#### Biotic agents

Biotic disturbances from insects, insect-pathogen complexes, and other biotic agents have been increasing in frequency, severity, and extent in recent decades (17, 31, 102) (Fig. 3M). Such trends reflect a changing climate (103), altered land use (104), and introductions of nonindigenous insects and pathogens (105). Climate change is expected to further amplify biotic disturbances (106), in part through enhanced host vulnerability (Fig. 3M). However, shifts in frequency or dampening of disturbance regimes could also emerge (107), leading to some uncertainty in outbreak dynamics under future conditions (Fig. 3M). Whereas insects and associated pathogens are globally widespread, lianas, or vines that use other plants as host structures, are increasing in abundance and are thought to be causing increasing mortality in the tropics (7, 108).

Response of insects and pathogens to climate change is likely to increase plant mortality (4), with variable impacts on growth and recruitment (Fig. 3N). Tree mortality can result from girdling of the phloem and xylem by

bark beetles (74) and from repeated defoliation events that exhaust the capacity of trees to recover (109). Tree mortality during outbreaks is usually partial at the stand level because many biotic agents preferentially attack trees of specific size or health classes or are host-specific (16). Suppressed, smaller trees and nonhost tree species may survive and grow rapidly when released from competition for resources (110, 111). Thus, similar to many other disturbances, mortality increases while recruitment and growth show variable responses to biotic disturbances, including a dependency on post-disturbance temperature, VPD, and drought.

#### On size and age demographics

The combination of LUC, disturbances, and chronic drivers is likely to have already shifted forests to younger and shorter stands, with these impacts increasing under expected future changes in drivers and disturbances (Fig. 1, A to C). These results are consistent with our review of the literature (Fig. 3). Large trees are the most susceptible to die from LUC-induced forest fragmentation (112, 113), drought (26), rising temperature or VPD (54, 62) (Fig. 4), windthrow (114, 115), biotic attacks (116), and lightning (101), with variable size impacts of fire (117). The abundance of size-dependent mortality drivers and disturbances should logically push stands toward younger and smaller distributions of trees and shorter-statured species assemblages (118).

There are exceptions to the pattern of climate drivers and disturbances reducing tree height and stand age. Non-stand-replacing fires that kill smaller trees but spare the larger, older trees will shift forests toward larger size distributions. Similarly, on occasions when droughts preferentially kill younger but fast-growing trees, subsequent size distribution and rate of carbon accumulation would be affected. Rising  $\text{CO}_2$  and increased precipitation in some areas also counter the general decrease in size, because they may lead to faster growth and hence taller trees (119). Thus, the antagonistic drivers promoting larger trees (e.g., rising  $\text{CO}_2$ ) and smaller trees (e.g., rising VPD, increasing disturbances) co-occur, but the general pattern of decreasing size and younger ages reveals that processes driving down size and age (Figs. 1 to 4) are dominant globally.

#### Mitigation of demographic-disturbance impacts

The literature patterns suggest that most drivers and disturbances will increase tree mortality now and in the future, with variable effects on recruitment and growth (Fig. 3). This supposition becomes uncertain, however, when we consider multiple feedbacks that can mitigate the changes in forest demography induced by chronically changing drivers and disturbance regimes. These processes include



acclimation, adaptation, migration, and compensatory mechanisms of resource use. With global change, forests will be influenced by a combination of phenotypic plasticity [i.e., acclimation (120)], adaptation to novel biotic and abiotic stresses (121), and the ability to migrate as conditions change (122). Failure to acclimate, adapt, or migrate—including failure due to human infrastructure (123)—could lead to recruitment and growth reductions and local extinctions. Plants have demonstrated acclimation of phenology, seed longevity, and metabolic processes to single and/or multiple stressors (124–127). Acclimation and adaptation will likely depend on an array of factors including genetic variation, fecundity, dispersal, population size, and environmental variability (120). Many tree species have migrated in response to past climatic cycles but at rates slower than the current pace of climate change (128). Regarding resource use, reductions in stand density as a result of increased mortality or reduced recruitment should allow greater resource availability to surviving individuals and therefore subsequently higher growth and survival rates (129). Such stand resource mechanisms can manifest at the landscape scale, as most disturbances are patchy (130), and the size, shape, and arrangement of surviving forest patches can play a key role in recovery of the disturbed landscape (20). Taken together, the mitigating factors can play a substantial role in buffering the impacts of changing drivers on plant survival, but it remains unclear whether these factors will enable trees to keep pace with ongoing climate change (50, 120). Ultimately, the uncertainty surrounding future demographic rates shown in Fig. 3 is partially due to the influence of these mitigating factors.

### Consequences for community assembly and for climate forcing

The widespread shift in vegetation dynamics begets questions regarding consequences for community assembly and climate forcing. Hydraulic theory suggests that under rising VPD, functional traits of high conductance, low stature, and low leaf area should best enable survival, all of which are characteristics of pioneer, shrub, and weed species (62). Consistent with this theory, diversity (e.g., species richness) temporarily increases post-disturbance for many systems, as short-statured, opportunistic species invade (131). If forest communities shift toward trait assemblages better suited to the new disturbance regime, such shifts may confer some resistance to future disturbances (131, 132). Alternatively, if disturbance regimes shift faster than recruitment, growth, and subsequent community assembly can respond, resistance to future disturbances will likely decline.

Climate forcing responds to changing vegetation dynamics in complex ways. Changes

in forest disturbance regimes and vegetation dynamics can affect climate via biogeochemical, hydrological, and land-surface energy budgets (133). Reductions in biomass result in a loss of carbon to the atmosphere despite younger, shorter stands often having higher gross photosynthesis; this is due to the loss of carbon through decomposition of necromass, which is a particularly large flux from mortality of older, larger trees, such as those in old-growth forests (134), and reduced landscape-mean carbon storage under an intensified disturbance regime (135). The time required for an ecosystem to reacheive the same live carbon storage after disturbance can be decades to centuries, particularly if the disturbance cycle is increased, thus the net effect of the biomass loss is increased CO<sub>2</sub> to the atmosphere and hence greater climate forcing. This impact may be mitigated by increased carbon uptake due to CO<sub>2</sub> fertilization (119) or enhanced recruitment. Calculations of the terrestrial carbon sink from atmospheric inversions indicate that the sink grew over recent decades (12) in part because of increased leaf area (13), which is consistent with increased recruitment and growth. However, evidence suggests that forests are switching from a CO<sub>2</sub> fertilization-dominated period to a VPD-dominated period (15, 16), despite sustained high gross photosynthesis at the global scale (136). The increased mortality throughout much of the terrestrial biosphere (7–9) further minimizes potential carbon storage through enhanced biomass loss. Ultimately, the terrestrial contribution to climate forcing through carbon uptake and release results from the antagonistic process of rising CO<sub>2</sub> and forest recovery from LUC, which enhance the carbon sink, and rising VPD and disturbances that reduce the carbon sink.

Changing vegetation dynamics also influence regional and global surface energy budgets and hydrological cycles. Disturbances frequently shift albedo of ecosystems from darker to lighter, resulting in a decline in radiative forcing through less light absorption (137). The rate of recruitment after disturbance influences the temporal period of this negative feedback (138). The impact of changing vegetation dynamics on the water cycle is particularly complex. Evaporation from canopies shifts as stands become taller, because taller trees transpire less (per unit leaf area) than smaller trees (49), but larger trees often have better rooting access to water sources and have greater total leaf area. The net effect of disturbance is a transient decrease in evaporative loading to the atmosphere along with albedo shifts, causing a feedback of decreasing precipitation downwind (139, 140). Ultimately, carbon storage is at least transiently reduced by disturbances,

with mixed impacts on the water and energy budgets.

### The path to improved prediction

Changes in global drivers (temperature, CO<sub>2</sub>, and VPD) and disturbances (including LUC, drought, wildfire, windstorms, and insect outbreaks) should all force forests toward shorter, younger, lower-biomass ecosystems. This trend is supported by hydraulic theory (62) (Fig. 4) and by abundant empirical evidence demonstrating a consistent increase in mortality across the global spectrum of drivers and disturbances and variable, but often declining, recruitment and growth (Fig. 3). While the bulk of the evidence points to reduced plant stature owing to changing drivers, large uncertainty remains in the magnitude and slope of demographic trajectories in the future (Fig. 3). Given these trajectories, and the large uncertainties around them, what are the critical next steps to allow improved global prediction? Continued long-term observations (both on the ground and remotely sensed) are essential to reveal the patterns of demographic responses to drivers and disturbances. Likewise, manipulative experiments are needed that alter conditions such as CO<sub>2</sub> or drought to provide cause-and-effect understanding of the interactions among mechanisms of demographic responses. However, for global-scale prediction of responses and climate consequences, we need to mainstream insights from observations and experiments into Earth system models (ESMs).

ESMs simulate the exchange of fluxes between the atmosphere, land, and ocean and stores of carbon, water, and energy; the land-surface modules of ESMs simulate vegetation. ESMs have made great progress in simulating land use, disturbances, and demography, including representation of wildfire (141), drought-induced mortality (142), and cohort-age structured models that enable representation of succession and associated shifts in physiological traits (6). The global Coupled Model Intercomparison Project CMIP6 now includes a dedicated model intercomparison activity focused on the effects of changes of land use on carbon and climate (143). Advances in remote sensing and forest inventory integration are enhancing global datasets of forest structure (144) and age (32) that can be used in model initialization, data assimilation benchmarking, and sensitivity analyses (Fig. 1, A to C). These advancements set the stage for developments in ESMs, such as the prediction of disturbances and demographic rate responses under climate and LUC scenarios.

The newest generation of ESMs uses size or age-structured approaches to explicitly model demography in the Earth system (6), which should ultimately enable model-based representation of observed shifts in age structure

(e.g., Fig. 1). However, representation of vegetation demographic rates remains relatively simplistic. Simulation of growth responses to global change requires model refinement in light capture, belowground water and nutrient acquisition, and responses of respiration to temperature (6). Recruitment, including reproduction and dispersal, is the most undeveloped demographic process in ESM simulations. Reproductive allocation is invariant with plant functional type (PFT), and seed is assumed to mix evenly throughout a grid cell [but see (145)]. Environmental constraints to PFT establishment are derived from prior distributions of major taxa, and while recruitment rates can be influenced by light or space availability, they are not responsive to temperature, CO<sub>2</sub>, or soil moisture (146, 147). Simplistic dispersal assumptions are typically either overly permissive or overly restrictive. Improvements in representing recruitment under global change are critical for improving predictions of vegetation dynamics. These advancements will require data synthesis and additional data collection to support PFT-specific, environmentally sensitive parameterizations of regeneration processes, such as reproductive allocation; effective dispersal; seedling establishment, survival, and growth; and post-disturbance recovery strategies (e.g., serotiny and resprouting).

Disturbance-induced mortality is better developed for landscape-scale models than for ESMs. ESM modeling of disturbance-induced mortality exists for wildfire and drought (141, 142), although considerable challenges remain to reliably represent both disturbances globally, while ESMs are underdeveloped for wind and insect mortality. To our knowledge, only one ESM currently represents canopy damage (148); this causes ESMs to potentially underestimate the impacts of drought and wind, as both disturbances cause lagged tree mortality associated with canopy loss years after the inciting event (149, 150). As for insects, there have been prescriptive studies examining the impact of insect outbreaks on land processes within ESMs, but no ESM has yet explicitly considered the interaction between plant defense and insect population dynamics for prediction of large-scale insect-induced tree mortality. For predicting wildfire, models should be sensitive to both fuels and climate interactions and represent spatial patterns of burn severity, because the burn mosaic strongly influences postfire vegetation dynamics (141). Next-generation demographic models are evolving to include explicit, mechanistic representations of drought-associated mortality, including carbon starvation and hydraulic failure (151). The evaluation of new hydraulics models (151) for prediction of mortality is an essential next step. Ultimately, model formulations that include environmentally sen-

sitive, PFT-specific processes compatible with the cohort-based approach are likely to provide the best compromise between process detail and parsimony and are therefore most likely to capture changes in large-scale forest dynamics under future conditions.

## Outlook

Forest vegetation dynamics are already strongly influenced by global change (Fig. 1) and will continue to be affected in the future (Figs. 1 to 4) by changes in land use, chronic drivers such as CO<sub>2</sub> and VPD, and increasing frequency and severity of transient disturbances such as windthrow, wildfire, and insect outbreaks. Effects on forests are driven largely by consistent increases in tree mortality from these drivers, and variable responses of recruitment and growth depending on stand age, disturbance type, and geographic location (Fig. 3). The consequences of changing demographics suggest an increasing constraint in terrestrial carbon storage due, at least, to the consistent increase in mortality. Any declines in recruitment or growth, especially when disturbance-recovery cycles are disrupted, will exacerbate this carbon-cycle constraint. Shifts in other terrestrial radiative forcing terms such as energy and water budgets are also likely. Although well supported by the literature, data, and sensitivity analysis (Fig. 1), the trends in Fig. 3 represent hypotheses to be tested by the next generation of observational platforms, both terrestrial and spaceborne. Forest management must ultimately confront the elevated mortality and uncertainty in recruitment and growth when considering options for sustaining the societal benefits of forests into the future.

## REFERENCES AND NOTES

1. M. G. Turner, T. G. Whittby, D. B. Tinker, W. H. Romme, Twenty-four years after the Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and function? *Ecology* **97**, 1260–1273 (2016). doi: [10.1890/151585.1](https://doi.org/10.1890/151585.1); pmid: [27349102](https://pubmed.ncbi.nlm.nih.gov/27349102/)
2. G. C. Hurtt *et al.*, Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change* **109**, 117–161 (2011). doi: [10.1007/s10584-011-0153-2](https://doi.org/10.1007/s10584-011-0153-2)
3. K. J. Anderson-Teixeira *et al.*, Altered dynamics of forest recovery under a changing climate. *Glob. Change Biol.* **19**, 2001–2021 (2013). doi: [10.1111/gcb.12194](https://doi.org/10.1111/gcb.12194); pmid: [23529980](https://pubmed.ncbi.nlm.nih.gov/23529980/)
4. M. Reichstein *et al.*, Climate extremes and the carbon cycle. *Nature* **500**, 287–295 (2013). doi: [10.1038/nature12350](https://doi.org/10.1038/nature12350); pmid: [23955228](https://pubmed.ncbi.nlm.nih.gov/23955228/)
5. R. Seidl *et al.*, Forest disturbances under climate change. *Nat. Clim. Change* **7**, 395–402 (2017). doi: [10.1038/nclimate3303](https://doi.org/10.1038/nclimate3303); pmid: [28861124](https://pubmed.ncbi.nlm.nih.gov/28861124/)
6. R. A. Fisher *et al.*, Vegetation demographics in Earth System Models: A review of progress and priorities. *Glob. Change Biol.* **24**, 35–54 (2018). doi: [10.1111/gcb.13910](https://doi.org/10.1111/gcb.13910); pmid: [28921829](https://pubmed.ncbi.nlm.nih.gov/28921829/)
7. N. McDowell *et al.*, Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol.* **219**, 851–869 (2018). doi: [10.1111/nph.15027](https://doi.org/10.1111/nph.15027); pmid: [29451313](https://pubmed.ncbi.nlm.nih.gov/29451313/)
8. J. Carnicer *et al.*, Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 1474–1478 (2011). doi: [10.1073/pnas.1010070108](https://doi.org/10.1073/pnas.1010070108); pmid: [21220333](https://pubmed.ncbi.nlm.nih.gov/21220333/)
9. C. Senf *et al.*, Canopy mortality has doubled in Europe's temperate forests over the last three decades. *Nat. Commun.* **9**, 4978 (2018). doi: [10.1038/s41467-018-07539-6](https://doi.org/10.1038/s41467-018-07539-6); pmid: [30478255](https://pubmed.ncbi.nlm.nih.gov/30478255/)
10. M. Fernández-Martínez *et al.*, Global trends in carbon sinks and their relationships with CO<sub>2</sub> and temperature. *Nat. Clim. Change* **9**, 73–79 (2019). doi: [10.1038/s41558-018-0367-7](https://doi.org/10.1038/s41558-018-0367-7)
11. P. Friedlingstein *et al.*, Global carbon budget 2019. *Earth Syst. Sci. Data* **11**, 1783–1838 (2019). doi: [10.5194/essd-11-1783-2019](https://doi.org/10.5194/essd-11-1783-2019)
12. P. Clais *et al.*, Five decades of northern land carbon uptake revealed by the interhemispheric CO<sub>2</sub> gradient. *Nature* **568**, 221–225 (2019). doi: [10.1038/s41586-019-1078-6](https://doi.org/10.1038/s41586-019-1078-6); pmid: [30944480](https://pubmed.ncbi.nlm.nih.gov/30944480/)
13. J. M. Chen *et al.*, Vegetation structural change since 1981 significantly enhanced the terrestrial carbon sink. *Nat. Commun.* **10**, 4259 (2019). doi: [10.1038/s41467-019-12257-8](https://doi.org/10.1038/s41467-019-12257-8); pmid: [31534135](https://pubmed.ncbi.nlm.nih.gov/31534135/)
14. T. A. M. Pugh *et al.*, Role of forest regrowth in global carbon sink dynamics. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 4382–4387 (2019). doi: [10.1073/pnas.1810512116](https://doi.org/10.1073/pnas.1810512116); pmid: [30782807](https://pubmed.ncbi.nlm.nih.gov/30782807/)
15. J. Peñuelas *et al.*, Shifting from a fertilization-dominated to a warming-dominated period. *Nat. Ecol. Evol.* **1**, 1438–1445 (2017). doi: [10.1038/s41559-017-0274-8](https://doi.org/10.1038/s41559-017-0274-8); pmid: [29185529](https://pubmed.ncbi.nlm.nih.gov/29185529/)
16. W. Yuan *et al.*, Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Sci. Adv.* **5**, eaax1396 (2019). doi: [10.1126/sciadv.aax1396](https://doi.org/10.1126/sciadv.aax1396); pmid: [31453338](https://pubmed.ncbi.nlm.nih.gov/31453338/)
17. K. F. Raffa *et al.*, Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *Bioscience* **58**, 501–517 (2008). doi: [10.1641/B580607](https://doi.org/10.1641/B580607)
18. M. K. Tippett, C. Lepore, J. E. Cohen, More tornadoes in the most extreme U.S. tornado outbreaks. *Science* **354**, 1419–1423 (2016). doi: [10.1126/science.aah7393](https://doi.org/10.1126/science.aah7393); pmid: [27934705](https://pubmed.ncbi.nlm.nih.gov/27934705/)
19. G. R. van der Werf *et al.*, Global fire emissions estimates during 1997–2016. *Earth Syst. Sci. Data* **9**, 697–720 (2017). doi: [10.5194/essd-9-697-2017](https://doi.org/10.5194/essd-9-697-2017)
20. A. Sommerfeld *et al.*, Patterns and drivers of recent disturbances across the temperate forest biome. *Nat. Commun.* **9**, 4355 (2018). doi: [10.1038/s41467-018-06788-9](https://doi.org/10.1038/s41467-018-06788-9); pmid: [30341309](https://pubmed.ncbi.nlm.nih.gov/30341309/)
21. R. A. Houghton, A. A. Nassikas, Global and regional fluxes of carbon from land use and land cover change 1850–2015. *Global Biogeochem. Cycles* **31**, 456–472 (2017). doi: [10.1002/2016GB005546](https://doi.org/10.1002/2016GB005546)
22. J. A. Foley *et al.*, Global consequences of land use. *Science* **309**, 570–574 (2005). doi: [10.1126/science.1111772](https://doi.org/10.1126/science.1111772); pmid: [16040698](https://pubmed.ncbi.nlm.nih.gov/16040698/)
23. M. P. Perring *et al.*, Global environmental change effects on ecosystems: The importance of land-use legacies. *Glob. Change Biol.* **22**, 1361–1371 (2016). doi: [10.1111/gcb.13146](https://doi.org/10.1111/gcb.13146); pmid: [26546049](https://pubmed.ncbi.nlm.nih.gov/26546049/)
24. H. Hartmann *et al.*, Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health'. *New Phytol.* **217**, 984–987 (2018). doi: [10.1111/nph.14988](https://doi.org/10.1111/nph.14988); pmid: [29334597](https://pubmed.ncbi.nlm.nih.gov/29334597/)
25. T. A. M. Pugh, A. Arneeth, M. Kautz, B. Poulter, B. Smith, Important role of forest disturbances in the global biomass turnover and carbon sinks. *Nat. Geosci.* **12**, 730–735 (2019). doi: [10.1038/s41561-019-0427-2](https://doi.org/10.1038/s41561-019-0427-2); pmid: [31478009](https://pubmed.ncbi.nlm.nih.gov/31478009/)
26. A. E. L. Stovall, H. Shugart, X. Yang, Tree height explains mortality risk during an intense drought. *Nat. Commun.* **10**, 4385 (2019). doi: [10.1038/s41467-019-12380-6](https://doi.org/10.1038/s41467-019-12380-6); pmid: [31558795](https://pubmed.ncbi.nlm.nih.gov/31558795/)
27. G. C. Hurtt *et al.*, Harmonization of Global Land-Use Change and Management for the Period 850–2100 (LUH2) for CMIP6. *Geosci. Model Dev. Discuss.* 10.5194/gmd-2019-360 (2020).
28. M. C. Hansen *et al.*, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013). doi: [10.1126/science.1244693](https://doi.org/10.1126/science.1244693); pmid: [24233722](https://pubmed.ncbi.nlm.nih.gov/24233722/)
29. P. G. Curtis, C. M. Slay, N. L. Harris, A. Tyukavina, M. C. Hansen, Classifying drivers of global forest loss. *Science* **361**, 1108–1111 (2018). doi: [10.1126/science.aau3445](https://doi.org/10.1126/science.aau3445); pmid: [30213911](https://pubmed.ncbi.nlm.nih.gov/30213911/)
30. S. Frolik *et al.*, Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J. Geophys. Res.* **114**, G00E02 (2009). doi: [10.1029/2008JG000911](https://doi.org/10.1029/2008JG000911)
31. M. Kautz, A. J. H. Meddens, R. J. Hall, A. Arneeth, Biotic disturbances in Northern Hemisphere forests—A synthesis of recent data, uncertainties and implications for forest



- monitoring and modelling. *Glob. Ecol. Biogeogr.* **26**, 533–552 (2017). doi: [10.1111/geb.12558](https://doi.org/10.1111/geb.12558)
32. B. Poulter *et al.*, The Global Forest Age Dataset and its Uncertainties (GFADv1.1), NASA National Aeronautics and Space Administration, PANGAEA (2019). doi: [10.1594/PANGAEA.897392](https://doi.org/10.1594/PANGAEA.897392)
  33. S. L. LaDeau, J. S. Clark, Rising CO<sub>2</sub> levels and the fecundity of forest trees. *Science* **292**, 95–98 (2001). doi: [10.1126/science.1057547](https://doi.org/10.1126/science.1057547); pmid: [11292871](https://pubmed.ncbi.nlm.nih.gov/11292871/)
  34. J. E. Mohan, J. S. Clark, W. H. Schlesinger, Long-term CO<sub>2</sub> enrichment of a forest ecosystem: Implications for forest regeneration and succession. *Ecol. Appl.* **17**, 1198–1212 (2007). doi: [10.1890/05-1690](https://doi.org/10.1890/05-1690); pmid: [17555228](https://pubmed.ncbi.nlm.nih.gov/17555228/)
  35. L. G. Perry, P. B. Shafroth, D. M. Blumenthal, J. A. Morgan, D. R. LeCain, Elevated CO<sub>2</sub> does not offset greater water stress predicted under climate change for native and exotic riparian plants. *New Phytol.* **197**, 532–543 (2013). doi: [10.1111/nph.12030](https://doi.org/10.1111/nph.12030); pmid: [23171384](https://pubmed.ncbi.nlm.nih.gov/23171384/)
  36. N. Saintilan, K. Rogers, Woody plant encroachment of grasslands: A comparison of terrestrial and wetland settings. *New Phytol.* **205**, 1062–1070 (2015). doi: [10.1111/nph.13147](https://doi.org/10.1111/nph.13147); pmid: [25729806](https://pubmed.ncbi.nlm.nih.gov/25729806/)
  37. S. M. McMahon, G. G. Parker, D. R. Miller, Evidence for a recent increase in forest growth. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 3611–3615 (2010). doi: [10.1073/pnas.0912376107](https://doi.org/10.1073/pnas.0912376107); pmid: [20133710](https://pubmed.ncbi.nlm.nih.gov/20133710/)
  38. J. J. Camarero, A. Gazol, J. D. Galván, G. Sangüesa-Barreda, E. Gutiérrez, Disparate effects of global-change drivers on mountain conifer forests: Warming-induced growth enhancement in young trees vs. CO<sub>2</sub> fertilization in old trees from wet sites. *Glob. Change Biol.* **21**, 738–749 (2015). doi: [10.1111/gcb.12787](https://doi.org/10.1111/gcb.12787); pmid: [25362899](https://pubmed.ncbi.nlm.nih.gov/25362899/)
  39. S. L. Voecker, R. M. Muzika, R. P. Guyette, M. C. Stambaugh, Historical CO<sub>2</sub> growth enhancement declines with age in *Quercus* and *Pinus*. *Ecol. Monogr.* **76**, 549–564 (2006). doi: [10.1890/0012-9615\(2006\)076\[0549:HCGEDW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0549:HCGEDW]2.0.CO;2)
  40. J. Peñuelas, J. G. Canadell, R. Ogaya, Increased water-use efficiency during the 20<sup>th</sup> century did not translate into enhanced tree growth. *Glob. Ecol. Biogeogr.* **20**, 597–608 (2011). doi: [10.1111/j.1466-8238.2010.00608.x](https://doi.org/10.1111/j.1466-8238.2010.00608.x)
  41. P. van der Sleen *et al.*, No growth stimulation of tropical trees by 150 years of CO<sub>2</sub> fertilization but water-use efficiency increased. *Nat. Geosci.* **8**, 24–28 (2015). doi: [10.1038/ngeo2313](https://doi.org/10.1038/ngeo2313)
  42. M. P. Girardin *et al.*, No growth stimulation of Canada's boreal forest under half-century of combined warming and CO<sub>2</sub> fertilization. *Proc. Natl. Acad. Sci. U.S.A.* **113**, E8406–E8414 (2016). doi: [10.1073/pnas.1610156113](https://doi.org/10.1073/pnas.1610156113); pmid: [27956624](https://pubmed.ncbi.nlm.nih.gov/27956624/)
  43. R. J. W. Brienen *et al.*, Long-term decline of the Amazon carbon sink. *Nature* **519**, 344–348 (2015). doi: [10.1038/nature14283](https://doi.org/10.1038/nature14283); pmid: [25788097](https://pubmed.ncbi.nlm.nih.gov/25788097/)
  44. Z. Gedalof, A. Berg, Tree ring evidence for limited direct CO<sub>2</sub> fertilization of forests over the 20th century. *Global Biogeochem. Cycles* **24**, GB3027 (2010). doi: [10.1029/2009GB003699](https://doi.org/10.1029/2009GB003699)
  45. A. P. Walker *et al.*, Decadal biomass increment in early secondary succession woody ecosystems is increased by CO<sub>2</sub> enrichment. *Nat. Commun.* **10**, 454 (2019). doi: [10.1038/s41467-019-08348-1](https://doi.org/10.1038/s41467-019-08348-1); pmid: [30765702](https://pubmed.ncbi.nlm.nih.gov/30765702/)
  46. M. K. F. Bader *et al.*, Central European hardwood trees in a high-CO<sub>2</sub> future: Synthesis of an 8-year forest canopy CO<sub>2</sub> enrichment project. *J. Ecol.* **101**, 1509–1519 (2013). doi: [10.1111/1365-2745.12149](https://doi.org/10.1111/1365-2745.12149)
  47. D. S. Ellsworth *et al.*, Elevated CO<sub>2</sub> does not increase eucalypt forest productivity on a low-phosphorus soil. *Nat. Clim. Change* **7**, 279–282 (2017). doi: [10.1038/nclimate3235](https://doi.org/10.1038/nclimate3235)
  48. R. J. Norby *et al.*, Net primary productivity of a CO<sub>2</sub>-enriched deciduous forest and the implications for carbon storage. *Ecol. Appl.* **12**, 1261–1266 (2002). doi: [10.1890/1051-0761\(2002\)012\[1261:NPP0AC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[1261:NPP0AC]2.0.CO;2)
  49. N. G. McDowell, B. J. Bond, L. T. Dickman, M. G. Ryan, D. Whitehead, "Relationships between tree height and carbon isotope discrimination" in *Size- and Age-Related Changes in Tree Structure and Function*, F. C. Meinzer, B. Lachenbruch, T. E. Dawson, Eds. (Springer, 2011), pp. 255–286.
  50. H. Duan *et al.*, Elevated [CO<sub>2</sub>] does not ameliorate the negative effects of elevated temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant Cell Environ.* **37**, 1598–1613 (2014). doi: [10.1111/pce.12260](https://doi.org/10.1111/pce.12260); pmid: [24372529](https://pubmed.ncbi.nlm.nih.gov/24372529/)
  51. C. D. Allen, D. D. Breshears, N. G. McDowell, On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 129 (2015). doi: [10.1890/ES15-00203.1](https://doi.org/10.1890/ES15-00203.1)
  52. C. Körner, A matter of tree longevity. *Science* **355**, 130–131 (2017). doi: [10.1126/science.aal2449](https://doi.org/10.1126/science.aal2449); pmid: [28082545](https://pubmed.ncbi.nlm.nih.gov/28082545/)
  53. U. Buntgen *et al.*, Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. *Nat. Commun.* **10**, 2171 (2019). doi: [10.1038/s41467-019-10174-4](https://doi.org/10.1038/s41467-019-10174-4); pmid: [31092831](https://pubmed.ncbi.nlm.nih.gov/31092831/)
  54. A. C. Bennett, N. G. McDowell, C. D. Allen, K. J. Anderson-Teixeira, Larger trees suffer most during drought in forests worldwide. *Nat. Plants* **1**, 15139 (2015). doi: [10.1038/nplants.2015.139](https://doi.org/10.1038/nplants.2015.139); pmid: [27251391](https://pubmed.ncbi.nlm.nih.gov/27251391/)
  55. K. Yu *et al.*, Pervasive decreases in living vegetation carbon turnover time across forest climate zones. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 24662–24667 (2019). doi: [10.1073/pnas.1821387116](https://doi.org/10.1073/pnas.1821387116); pmid: [31740604](https://pubmed.ncbi.nlm.nih.gov/31740604/)
  56. H. Pretzsch, P. Biber, G. Schütze, J. Kemmerer, E. Uhl, Wood density reduced while wood volume growth accelerated in Central European forests since 1870. *For. Ecol. Manage.* **429**, 589–616 (2018). doi: [10.1016/j.foreco.2018.07.045](https://doi.org/10.1016/j.foreco.2018.07.045)
  57. K. E. Trenberth *et al.*, Global warming and changes in drought. *Nat. Clim. Change* **4**, 17–22 (2014). doi: [10.1038/nclimate2067](https://doi.org/10.1038/nclimate2067)
  58. A. Park Williams *et al.*, Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* **3**, 292–297 (2013). doi: [10.1038/nclimate1693](https://doi.org/10.1038/nclimate1693)
  59. A. J. Tepley, J. R. Thompson, H. E. Epstein, K. J. Anderson-Teixeira, Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. *Glob. Change Biol.* **23**, 4117–4132 (2017). doi: [10.1111/gcb.13704](https://doi.org/10.1111/gcb.13704); pmid: [28447370](https://pubmed.ncbi.nlm.nih.gov/28447370/)
  60. J. M. Serra-Diaz *et al.*, Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21<sup>st</sup> century. *Sci. Rep.* **8**, 6749 (2018). doi: [10.1038/s41598-018-24642-2](https://doi.org/10.1038/s41598-018-24642-2); pmid: [29712940](https://pubmed.ncbi.nlm.nih.gov/29712940/)
  61. M. Uriarte, J. R. Lasky, V. K. Boukili, R. L. Chazdon, A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. *Funct. Ecol.* **30**, 157–167 (2016). doi: [10.1111/1365-2435.12576](https://doi.org/10.1111/1365-2435.12576)
  62. N. G. McDowell, C. D. Allen, Darcy's law predicts widespread forest mortality under climate warming. *Nat. Clim. Change* **5**, 669–672 (2015). doi: [10.1038/nclimate2641](https://doi.org/10.1038/nclimate2641)
  63. J. Liu *et al.*, Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. *Science* **358**, eaam5690 (2017). doi: [10.1126/science.aam5690](https://doi.org/10.1126/science.aam5690); pmid: [29026011](https://pubmed.ncbi.nlm.nih.gov/29026011/)
  64. S. J. Wright, O. Calderón, Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* **9**, 35–44 (2006). pmid: [16958866](https://pubmed.ncbi.nlm.nih.gov/16958866/)
  65. T. F. Keenan, W. J. Riley, Greening of the land surface in the world's cold regions consistent with recent warming. *Nat. Clim. Change* **8**, 825–828 (2018). doi: [10.1038/s41558-018-0258-y](https://doi.org/10.1038/s41558-018-0258-y); pmid: [30319714](https://pubmed.ncbi.nlm.nih.gov/30319714/)
  66. J. R. Forrest, Plant–pollinator interactions and phenological change: What can we learn about climate impacts from experiments and observations? *Oikos* **124**, 4–13 (2015). doi: [10.1111/oik.01386](https://doi.org/10.1111/oik.01386)
  67. J. L. Walck, S. N. Hidayati, K. W. Dixon, K. Thompson, P. Poschlod, Climate change and plant regeneration from seed. *Glob. Change Biol.* **17**, 2145–2161 (2011). doi: [10.1111/j.1365-2486.2010.02368.x](https://doi.org/10.1111/j.1365-2486.2010.02368.x)
  68. J. Memmott, P. G. Craze, N. M. Waser, M. V. Price, Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717 (2007). doi: [10.1111/j.1461-0248.2007.01061.x](https://doi.org/10.1111/j.1461-0248.2007.01061.x); pmid: [17594426](https://pubmed.ncbi.nlm.nih.gov/17594426/)
  69. L. M. Kueppers *et al.*, Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Glob. Change Biol.* **23**, 2383–2395 (2017). doi: [10.1111/gcb.13561](https://doi.org/10.1111/gcb.13561); pmid: [27976819](https://pubmed.ncbi.nlm.nih.gov/27976819/)
  70. W. D. Hansen, M. G. Turner, Origins of abrupt change? Postfire subalpine conifer regeneration declines nonlinearly with warming and drying. *Ecol. Monogr.* **89**, e01340 (2019). doi: [10.1002/ecm.1340](https://doi.org/10.1002/ecm.1340)
  71. H. D. Adams *et al.*, Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 7063–7066 (2009). doi: [10.1073/pnas.0901438106](https://doi.org/10.1073/pnas.0901438106); pmid: [19365070](https://pubmed.ncbi.nlm.nih.gov/19365070/)
  72. R. A. Hember *et al.*, Accelerating regrowth of temperate-maritime forests due to environmental change. *Glob. Clim. Change* **18**, 2026–2040 (2012). doi: [10.1111/j.1365-2486.2012.02669.x](https://doi.org/10.1111/j.1365-2486.2012.02669.x)
  73. H. D. Adams *et al.*, A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat. Ecol. Evol.* **1**, 1285–1291 (2017). doi: [10.1038/s41559-017-0248-x](https://doi.org/10.1038/s41559-017-0248-x); pmid: [29046541](https://pubmed.ncbi.nlm.nih.gov/29046541/)
  74. M. L. Gaylor *et al.*, Drought predisposes piñon-juniper woodlands to insect attacks and mortality. *New Phytol.* **198**, 567–578 (2013). doi: [10.1111/nph.12174](https://doi.org/10.1111/nph.12174); pmid: [23421561](https://pubmed.ncbi.nlm.nih.gov/23421561/)
  75. N. G. McDowell *et al.*, Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat. Clim. Change* **6**, 295–300 (2016). doi: [10.1038/nclimate2873](https://doi.org/10.1038/nclimate2873)
  76. B. M. J. Engelbrecht, T. A. Kursar, Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* **136**, 383–393 (2003). doi: [10.1007/s00442-003-1290-8](https://doi.org/10.1007/s00442-003-1290-8); pmid: [12811534](https://pubmed.ncbi.nlm.nih.gov/12811534/)
  77. C. E. Doughty *et al.*, Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature* **519**, 78–82 (2015). doi: [10.1038/nature14213](https://doi.org/10.1038/nature14213); pmid: [25739631](https://pubmed.ncbi.nlm.nih.gov/25739631/)
  78. K. H. Erb *et al.*, Land management: Data availability and process understanding for global change studies. *Glob. Change Biol.* **23**, 512–533 (2017). doi: [10.1111/gcb.13443](https://doi.org/10.1111/gcb.13443); pmid: [27447350](https://pubmed.ncbi.nlm.nih.gov/27447350/)
  79. P. A. Martin, A. C. Newton, M. Pfeifer, M. Khoo, J. M. Bullock, Impacts of tropical selective logging on carbon storage and tree species richness: A meta-analysis. *For. Ecol. Manage.* **356**, 224–233 (2015). doi: [10.1016/j.foreco.2015.07.010](https://doi.org/10.1016/j.foreco.2015.07.010)
  80. A. Chaudhary, Z. Burivalova, L. P. Koh, S. Hellweg, Impact of forest management on species richness: Global meta-analysis and economic trade-offs. *Sci. Rep.* **6**, 23954 (2016). doi: [10.1038/srep23954](https://doi.org/10.1038/srep23954); pmid: [27040604](https://pubmed.ncbi.nlm.nih.gov/27040604/)
  81. M. J. Duveneck, J. R. Thompson, E. J. Gustafson, Y. Liang, A. M. G. de Bruijn, Recovery dynamics and climate change effects to future New England forests. *Landscape* **32**, 1385–1397 (2017). doi: [10.1007/s10980-016-0415-5](https://doi.org/10.1007/s10980-016-0415-5)
  82. D. Thom, W. Rammer, R. Garstenauer, R. Seidl, Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. *Biogeosciences* **15**, 5699–5713 (2018). doi: [10.5194/bg-15-5699-2018](https://doi.org/10.5194/bg-15-5699-2018)
  83. T. Vilen *et al.*, Reconstructed forest age structure in Europe 1950–2010. *For. Ecol. Manage.* **286**, 203–218 (2012). doi: [10.1016/j.foreco.2012.08.048](https://doi.org/10.1016/j.foreco.2012.08.048)
  84. W. M. Jolly *et al.*, Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat. Commun.* **6**, 7537 (2015). doi: [10.1038/ncomms8537](https://doi.org/10.1038/ncomms8537); pmid: [26172867](https://pubmed.ncbi.nlm.nih.gov/26172867/)
  85. N. Andela *et al.*, A human-driven decline in global burned area. *Science* **356**, 1356–1362 (2017). doi: [10.1126/science.aal4108](https://doi.org/10.1126/science.aal4108); pmid: [28663495](https://pubmed.ncbi.nlm.nih.gov/28663495/)
  86. J. T. Abatzoglou, A. P. Williams, Impact of anthropogenic climate change on wildfire across western US forests. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11770–11775 (2016). doi: [10.1073/pnas.1607171113](https://doi.org/10.1073/pnas.1607171113); pmid: [27791053](https://pubmed.ncbi.nlm.nih.gov/27791053/)
  87. A. L. Westerling, M. G. Turner, E. A. H. Smithwick, W. H. Romme, M. G. Ryan, Continued warming could transform Greater Yellowstone fire regimes by mid-21<sup>st</sup> century. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 13165–13170 (2011). doi: [10.1073/pnas.110199108](https://doi.org/10.1073/pnas.110199108); pmid: [21788495](https://pubmed.ncbi.nlm.nih.gov/21788495/)
  88. D. Bowman, G. J. Williamson, L. D. Prior, B. P. Murphy, The relative importance of intrinsic and extrinsic factors in the decline of obligate seeder forests. *Glob. Ecol. Biogeogr.* **25**, 1166–1172 (2016). doi: [10.1111/geb.12484](https://doi.org/10.1111/geb.12484)
  89. J. F. Johnstone *et al.*, Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* **14**, 369–378 (2016). doi: [10.1002/fee.1311](https://doi.org/10.1002/fee.1311)
  90. M. G. Turner, K. H. Braziliunas, W. D. Hansen, B. J. Harvey, Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 11319–11328 (2019). doi: [10.1073/pnas.1902841116](https://doi.org/10.1073/pnas.1902841116); pmid: [31110003](https://pubmed.ncbi.nlm.nih.gov/31110003/)
  91. T. Kitzberger *et al.*, Fire-vegetation feedbacks and alternative states: Common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. *N. Z. J. Bot.* **54**, 247–272 (2016). doi: [10.1080/002825X.2016.1151903](https://doi.org/10.1080/002825X.2016.1151903)
  92. A. E. Lugo, Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral Ecol.* **33**, 368–398 (2008). doi: [10.1111/j.1442-9993.2008.01894.x](https://doi.org/10.1111/j.1442-9993.2008.01894.x)
  93. K. Balaguru, G. R. Foltz, L. R. Leung, Increasing magnitude of hurricane rapid intensification in the central and eastern tropical Atlantic. *Geophys. Res. Lett.* **45**, 4238–4247 (2018). doi: [10.1029/2018GL077597](https://doi.org/10.1029/2018GL077597)
  94. N. S. Diefenbaugh, M. Scherer, R. J. Trapp, Robust increases in severe thunderstorm environments in response to greenhouse forcing. *Proc. Natl. Acad. Sci. U.S.A.* **110**,

- 16361–16366 (2013). doi: [10.1073/pnas.1307758110](https://doi.org/10.1073/pnas.1307758110); pmid: [24062439](https://pubmed.ncbi.nlm.nih.gov/24062439/)
95. M. Uriarte, C. D. Canham, J. Thompson, J. K. Zimmerman, A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* **74**, 591–614 (2004). doi: [10.1890/03-4031](https://doi.org/10.1890/03-4031)
  96. B. Gardiner, P. Berry, B. Mouli, Review: Wind impacts on plant growth, mechanics and damage. *Plant Sci.* **245**, 94–118 (2016). doi: [10.1016/j.plantsci.2016.01.006](https://doi.org/10.1016/j.plantsci.2016.01.006); pmid: [26940495](https://pubmed.ncbi.nlm.nih.gov/26940495/)
  97. M. Uriarte *et al.*, Natural disturbances and human land use as determinants of tropical forest dynamics: Results from a forest simulator. *Ecol. Monogr.* **79**, 423–443 (2009). doi: [10.1890/08-0707.1](https://doi.org/10.1890/08-0707.1)
  98. L. S. Comita *et al.*, Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J. Ecol.* **97**, 1346–1359 (2009). doi: [10.1111/j.1365-2745.2009.01551.x](https://doi.org/10.1111/j.1365-2745.2009.01551.x)
  99. M. Uriarte *et al.*, Multidimensional trade-offs in species responses to disturbance: Implications for diversity in a subtropical forest. *Ecology* **93**, 191–205 (2012). doi: [10.1890/10-2422.1](https://doi.org/10.1890/10-2422.1); pmid: [22486099](https://pubmed.ncbi.nlm.nih.gov/22486099/)
  100. D. F. B. Flynn *et al.*, Hurricane disturbance alters secondary forest recovery in Puerto Rico. *Biotropica* **42**, 149–157 (2010). doi: [10.1111/j.1744-7429.2009.00581.x](https://doi.org/10.1111/j.1744-7429.2009.00581.x)
  101. S. P. Yanoviak *et al.*, Lightning is a major cause of large tree mortality in a lowland neotropical forest. *New Phytol.* **225**, 1936–1944 (2020). doi: [10.1111/nph.16260](https://doi.org/10.1111/nph.16260); pmid: [31610011](https://pubmed.ncbi.nlm.nih.gov/31610011/)
  102. R. Seidl, M. J. Schelhaas, W. Rammer, P. J. Verkerk, Increasing forest disturbances in Europe and their impact on carbon storage. *Nat. Clim. Change* **4**, 806–810 (2014). doi: [10.1038/nclimate2318](https://doi.org/10.1038/nclimate2318); pmid: [25737744](https://pubmed.ncbi.nlm.nih.gov/25737744/)
  103. K. F. Raffa *et al.*, “Responses of tree-killing bark beetles to a changing climate” in *Climate Change and Insect Pests*, C. Björkman, P. Niemelä, Eds., vol. 7 of *CABI Climate Change Series* (CABI International, 2015), pp. 173–201.
  104. J. S. Schurman *et al.*, Large-scale disturbance legacies and the climate sensitivity of primary *Picea abies* forests. *Glob. Change Biol.* **24**, 2169–2181 (2018). doi: [10.1111/gcb.14041](https://doi.org/10.1111/gcb.14041); pmid: [29322582](https://pubmed.ncbi.nlm.nih.gov/29322582/)
  105. D. W. Rosenberger, R. C. Venette, B. H. Aukema, Development of an aggressive bark beetle on novel hosts: Implications for outbreaks in an invaded range. *J. Appl. Ecol.* **55**, 1526–1537 (2018). doi: [10.1111/1365-2664.13064](https://doi.org/10.1111/1365-2664.13064)
  106. R. Seidl *et al.*, Invasive alien pests threaten the carbon stored in Europe’s forests. *Nat. Commun.* **9**, 1626 (2018). doi: [10.1038/s41467-018-04096-w](https://doi.org/10.1038/s41467-018-04096-w); pmid: [29691396](https://pubmed.ncbi.nlm.nih.gov/29691396/)
  107. D. M. Johnson *et al.*, Climatic warming disrupts recurrent Alpine insect outbreaks. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 20576–20581 (2010). doi: [10.1073/pnas.1010270107](https://doi.org/10.1073/pnas.1010270107); pmid: [21059922](https://pubmed.ncbi.nlm.nih.gov/21059922/)
  108. M. di Porcia e Brugnera *et al.*, Modeling the impact of liana infestation on the demography and carbon cycle of tropical forests. *Glob. Change Biol.* **25**, 3767–3780 (2019). doi: [10.1111/gcb.14769](https://doi.org/10.1111/gcb.14769); pmid: [31310429](https://pubmed.ncbi.nlm.nih.gov/31310429/)
  109. D. S. Pureswaran, R. Johns, S. B. Heard, D. Quiring, Paradigms in eastern spruce budworm (Lepidoptera: Tortricidae) population ecology: a century of debate. *Environ. Entomol.* **45**, 1333–1342 (2016). doi: [10.1093/ee/nwv103](https://doi.org/10.1093/ee/nwv103); pmid: [28028079](https://pubmed.ncbi.nlm.nih.gov/28028079/)
  110. G. V. J. Virgin, D. A. MacLean, Five decades of balsam fir stand development after spruce budworm-related mortality. *For. Ecol. Manage.* **400**, 129–138 (2017). doi: [10.1016/j.foreco.2017.05.057](https://doi.org/10.1016/j.foreco.2017.05.057)
  111. M. Macek *et al.*, Life and death of *Picea abies* after bark-beetle outbreak: Ecological processes driving seedling recruitment. *Ecol. Appl.* **27**, 156–167 (2017). doi: [10.1002/eap.1429](https://doi.org/10.1002/eap.1429); pmid: [28052495](https://pubmed.ncbi.nlm.nih.gov/28052495/)
  112. W. F. Laurance, P. Delamônica, S. G. Laurance, H. L. Vasconcelos, T. E. Lovejoy, Rainforest fragmentation kills big trees. *Nature* **404**, 836 (2000). doi: [10.1038/35009032](https://doi.org/10.1038/35009032); pmid: [10786782](https://pubmed.ncbi.nlm.nih.gov/10786782/)
  113. D. B. Lindenmayer, W. F. Laurance, J. F. Franklin, Global decline in large old trees. *Science* **338**, 1305–1306 (2012). doi: [10.1126/science.1231070](https://doi.org/10.1126/science.1231070); pmid: [23224548](https://pubmed.ncbi.nlm.nih.gov/23224548/)
  114. C. J. Peterson, Catastrophic wind damage to North American forests and the potential impact of climate change. *Sci. Total Environ.* **262**, 287–311 (2000). doi: [10.1016/S0048-9697\(00\)00529-5](https://doi.org/10.1016/S0048-9697(00)00529-5); pmid: [11087033](https://pubmed.ncbi.nlm.nih.gov/11087033/)
  115. C. D. Canham, M. J. Papaik, E. F. Latty, Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. *Can. J. For. Res.* **31**, 1–10 (2001). doi: [10.1139/x00-124](https://doi.org/10.1139/x00-124)
  116. J. Boone, B. H. Aukema, J. Bohlmann, A. L. Carroll, K. F. Raffa, Efficacy of tree defense physiology varies with bark beetle population density: A basis for positive feedback in eruptive species. *Can. J. For. Res.* **41**, 1174–1188 (2011). doi: [10.1139/x11-041](https://doi.org/10.1139/x11-041)
  117. N. G. McDowell *et al.*, Predicting chronic climate-driven disturbances and their mitigation. *Trends Ecol. Evol.* **33**, 15–27 (2018). doi: [10.1016/j.tree.2017.10.002](https://doi.org/10.1016/j.tree.2017.10.002); pmid: [29146414](https://pubmed.ncbi.nlm.nih.gov/29146414/)
  118. D. J. Johnson *et al.*, Climate sensitive size-dependent survival in tropical trees. *Nat. Ecol. Evol.* **2**, 1436–1442 (2018). doi: [10.1038/s41559-018-0626-z](https://doi.org/10.1038/s41559-018-0626-z); pmid: [30104751](https://pubmed.ncbi.nlm.nih.gov/30104751/)
  119. H. Pretzsch, P. Biber, G. Schütze, E. Uhl, T. Rötzer, Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* **5**, 4967 (2014). doi: [10.1038/ncomms5967](https://doi.org/10.1038/ncomms5967); pmid: [25216297](https://pubmed.ncbi.nlm.nih.gov/25216297/)
  120. A. B. Nicotra *et al.*, Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* **15**, 684–692 (2010). doi: [10.1016/j.jplants.2010.09.008](https://doi.org/10.1016/j.jplants.2010.09.008); pmid: [20970368](https://pubmed.ncbi.nlm.nih.gov/20970368/)
  121. S. N. Aitken, S. Yeaman, J. A. Holliday, T. Wang, S. Curtis-McLane, Adaptation, migration or extirpation: Climate change outcomes for tree populations. *Evol. Appl.* **1**, 95–111 (2008). doi: [10.1111/j.1752-4571.2007.00013.x](https://doi.org/10.1111/j.1752-4571.2007.00013.x); pmid: [25567494](https://pubmed.ncbi.nlm.nih.gov/25567494/)
  122. A. L. Angert *et al.*, Do species’ traits predict recent shifts at expanding range edges? *Ecol. Lett.* **14**, 677–689 (2011). doi: [10.1111/j.1461-0248.2011.01620.x](https://doi.org/10.1111/j.1461-0248.2011.01620.x); pmid: [21535340](https://pubmed.ncbi.nlm.nih.gov/21535340/)
  123. K. M. Miller, B. J. McGill, Land use and life history limit migration capacity of eastern tree species. *Glob. Ecol. Biogeogr.* **27**, 57–67 (2018). doi: [10.1111/geb.12671](https://doi.org/10.1111/geb.12671)
  124. M. Slot, K. Kitajima, General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types. *Oecologia* **177**, 885–900 (2015). doi: [10.1007/s00442-014-3159-4](https://doi.org/10.1007/s00442-014-3159-4); pmid: [25481817](https://pubmed.ncbi.nlm.nih.gov/25481817/)
  125. I. Rieu, D. Twell, N. Firon, Pollen development at high temperature: From acclimation to collapse. *Plant Physiol.* **173**, 1967–1976 (2017). doi: [10.1104/pp.16.01644](https://doi.org/10.1104/pp.16.01644); pmid: [28246296](https://pubmed.ncbi.nlm.nih.gov/28246296/)
  126. H. D. Adams *et al.*, Experimental drought and heat can delay phenological development and reduce foliar and shoot growth in semiarid trees. *Glob. Change Biol.* **21**, 4210–4220 (2015). doi: [10.1111/gcb.13030](https://doi.org/10.1111/gcb.13030); pmid: [26149972](https://pubmed.ncbi.nlm.nih.gov/26149972/)
  127. C. Grossiord *et al.*, Warming combined with more extreme precipitation regimes modifies the water sources used by trees. *New Phytol.* **213**, 584–596 (2017). doi: [10.1111/nph.14192](https://doi.org/10.1111/nph.14192); pmid: [27612306](https://pubmed.ncbi.nlm.nih.gov/27612306/)
  128. J. S. McLachlan, J. J. Hellmann, M. W. Schwartz, A framework for debate of assisted migration in an era of climate change. *Conserv. Biol.* **21**, 297–302 (2007). doi: [10.1111/j.1523-1739.2007.00676.x](https://doi.org/10.1111/j.1523-1739.2007.00676.x); pmid: [17391179](https://pubmed.ncbi.nlm.nih.gov/17391179/)
  129. F. Lloret, A. Escudero, J. M. Iriondo, J. Martínez-Vilalta, F. Valladares, Extreme climatic events and vegetation: The role of stabilizing processes. *Glob. Change Biol.* **18**, 797–805 (2012). doi: [10.1111/j.1365-2486.2011.02624.x](https://doi.org/10.1111/j.1365-2486.2011.02624.x)
  130. K. B. Kemp, P. E. Higuera, P. Morgan, Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landsc. Ecol.* **31**, 619–636 (2016). doi: [10.1038/nature15374](https://doi.org/10.1038/nature15374); pmid: [26466564](https://pubmed.ncbi.nlm.nih.gov/26466564/)
  131. D. Thom, W. Rammer, R. Seidl, The impact of future forest dynamics on climate: Interactive effects of changing vegetation and disturbance regimes. *Ecol. Monogr.* **87**, 665–684 (2017). doi: [10.1002/ecm.1272](https://doi.org/10.1002/ecm.1272); pmid: [29628526](https://pubmed.ncbi.nlm.nih.gov/29628526/)
  132. T. L. Powell *et al.*, Variation in hydroclimate sustains tropical forest biomass and promotes functional diversity. *New Phytol.* **219**, 932–946 (2018). doi: [10.1111/nph.15271](https://doi.org/10.1111/nph.15271); pmid: [29923303](https://pubmed.ncbi.nlm.nih.gov/29923303/)
  133. G. B. Bonan, Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444–1449 (2008). doi: [10.1126/science.1155121](https://doi.org/10.1126/science.1155121); pmid: [18556546](https://pubmed.ncbi.nlm.nih.gov/18556546/)
  134. S. Luysaert *et al.*, Old-growth forests as global carbon sinks. *Nature* **455**, 213–215 (2008). doi: [10.1038/nature07276](https://doi.org/10.1038/nature07276); pmid: [18784722](https://pubmed.ncbi.nlm.nih.gov/18784722/)
  135. M. E. Harmon, Carbon sequestration in forests: Addressing the scale question. *J. For.* **99**, 24–29 (2001).
  136. J. E. Campbell *et al.*, Large historical growth in global terrestrial gross primary production. *Nature* **544**, 84–87 (2017). doi: [10.1038/nature22030](https://doi.org/10.1038/nature22030); pmid: [28382993](https://pubmed.ncbi.nlm.nih.gov/28382993/)
  137. J. T. Randerson *et al.*, The impact of boreal forest fire on climate warming. *Science* **314**, 1130–1132 (2006). doi: [10.1126/science.1132075](https://doi.org/10.1126/science.1132075); pmid: [17110574](https://pubmed.ncbi.nlm.nih.gov/17110574/)
  138. X. Lee *et al.*, Observed increase in local cooling effect of deforestation at higher latitudes. *Nature* **479**, 384–387 (2011). doi: [10.1038/nature10588](https://doi.org/10.1038/nature10588); pmid: [22094699](https://pubmed.ncbi.nlm.nih.gov/22094699/)
  139. N. Devaraju, G. Bala, A. Modak, Effects of large-scale deforestation on precipitation in the monsoon regions: Remote versus local effects. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 3257–3262 (2015). doi: [10.1073/pnas.1423439112](https://doi.org/10.1073/pnas.1423439112); pmid: [25733889](https://pubmed.ncbi.nlm.nih.gov/25733889/)
  140. Q. Lejeune, E. L. Davin, B. P. Guillod, S. I. Seneviratne, Influence of Amazonian deforestation on the future evolution of regional surface fluxes, circulation, surface temperature and precipitation. *Clim. Dyn.* **44**, 2769–2786 (2015). doi: [10.1007/s00382-014-2203-8](https://doi.org/10.1007/s00382-014-2203-8)
  141. Y. Le Page, D. Morton, B. Bond-Lamberty, J. M. C. Pereira, G. Hurtt, HESFIRE: A global fire model to explore the role of anthropogenic and weather drivers. *Biogeosciences* **12**, 887–903 (2015). doi: [10.5194/bg-12-887-2015](https://doi.org/10.5194/bg-12-887-2015)
  142. N. G. McDowell *et al.*, Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytol.* **200**, 304–321 (2013). doi: [10.1111/nph.12465](https://doi.org/10.1111/nph.12465); pmid: [24004027](https://pubmed.ncbi.nlm.nih.gov/24004027/)
  143. D. Lawrence *et al.*, The Land Use Model Intercomparison Project (LUMP) contribution to CMIP6: Rationale and experimental design. *Geosci. Model Dev.* **9**, 2973–2998 (2016). doi: [10.5194/gmd-9-2973-2016](https://doi.org/10.5194/gmd-9-2973-2016)
  144. M. Simard, N. Pinto, J. B. Fisher, A. Baccini, Mapping forest canopy height globally with spaceborne lidar. *J. Geophys. Res. Biogeosci.* **116**, G04021 (2011).
  145. V. Lehsten, M. Mischorow, E. Lindström, D. Lehsten, H. Lischke, LPJ-GM 1.0: Simulating migration efficiently in a dynamic vegetation model. *Geosci. Model Dev.* **12**, 893–908 (2019). doi: [10.5194/gmd-12-893-2019](https://doi.org/10.5194/gmd-12-893-2019)
  146. B. Smith, I. C. Prentice, M. T. Sykes, Representation of vegetation dynamics in the modelling of terrestrial ecosystems: Comparing two contrasting approaches within European climate space. *Glob. Ecol. Biogeogr.* **10**, 621–637 (2001). doi: [10.1046/j.1466-822X.2001.00256.x](https://doi.org/10.1046/j.1466-822X.2001.00256.x)
  147. R. A. Fisher *et al.*, Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geosci. Model Dev.* **8**, 3593–3619 (2015). doi: [10.5194/gmd-8-3593-2015](https://doi.org/10.5194/gmd-8-3593-2015)
  148. Y. Chen *et al.*, Simulating damage for wind storms in the land surface model ORCHIDEE-CAN (revision 4262). *Geosci. Model Dev.* **11**, 771–791 (2018). doi: [10.5194/gmd-11-771-2018](https://doi.org/10.5194/gmd-11-771-2018)
  149. T. K. Henkel, J. Q. Chambers, D. A. Baker, Delayed tree mortality and Chinese tallow (*Triadica sebifera*) population explosion in a Louisiana bottomland hardwood forest following Hurricane Katrina. *For. Ecol. Manage.* **378**, 222–232 (2016). doi: [10.1016/j.foreco.2016.07.036](https://doi.org/10.1016/j.foreco.2016.07.036)
  150. J. P. Roccaforte *et al.*, Delayed tree mortality, bark beetle activity, and regeneration dynamics five years following the Wallow Fire, Arizona, USA: Assessing trajectories towards resiliency. *For. Ecol. Manage.* **428**, 20–26 (2018). doi: [10.1016/j.foreco.2018.06.012](https://doi.org/10.1016/j.foreco.2018.06.012)
  151. D. Kennedy *et al.*, Implementing plant hydraulics in the Community Land Model, version 5. *J. Adv. Model. Earth Syst.* **11**, 485–513 (2019). doi: [10.1029/2018MS001500](https://doi.org/10.1029/2018MS001500)
  152. P. J. Grubb, The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev. Camb. Philos. Soc.* **52**, 107–145 (1977). doi: [10.1111/j.1469-185X.1977.tb01347.x](https://doi.org/10.1111/j.1469-185X.1977.tb01347.x)
  153. B. D. Amiro *et al.*, Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res. Biogeosci.* **115**, G00K02 (2010).
  154. J. A. Hicke *et al.*, Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Glob. Change Biol.* **18**, 7–34 (2012). doi: [10.1111/j.1365-2486.2011.02543.x](https://doi.org/10.1111/j.1365-2486.2011.02543.x)
  155. J. P. Grime, *Plant Strategies and Vegetation Processes* (Wiley, 1979).
  156. A. Jentsch, P. White, A theory of pulse dynamics and disturbance in ecology. *Ecology* **100**, e02734 (2019). doi: [10.1002/ecy.2734](https://doi.org/10.1002/ecy.2734); pmid: [31018013](https://pubmed.ncbi.nlm.nih.gov/31018013/)
  157. D. M. Olson *et al.*, Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* **51**, 933–938 (2001). doi: [10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)

# ACKNOWLEDGMENTS

**Funding:** This manuscript was derived from the Department of Energy (DOE) Workshop “Disturbance and vegetation dynamics in Earth System Models” held March 2018 in Washington, D.C. Funding was provided by: the DOE’s Next Generation Ecosystem Experiment-Tropics (NGEE-Tropics) and Pacific Northwest National Lab’s (PNNL’s) LDRD program (N.G.M.), McIntire-Stennis MIN-17-095 (B.H.A.), the U.S. Geological Survey’s Ecosystems and Land Resources mission areas (C.D.A.), the Joint Fire Science Program (16-3-01-4) and the University of Wisconsin–Madison

Vilas Trust (M.G.T.), sabbatical fellowship support from sDiv (J.W.L.), the Synthesis Centre of iDiv (DFG FZT 118), DOE's NGEE-Tropics and the University of California's Laboratory Fees Research Program (grant LFR-18-542511 to C.X.), the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant 758873, TreeMort, to

T.A.M.P.), paper number 43 of the Birmingham Institute of Forest Research, PNNL's LDRD program (B.B.-L.), sabbatical support from Stanford's Center for Advanced Study in the Behavioral Sciences and financial support from the Gordon and Betty Moore Foundation (R.B.J.), the NASA Carbon Monitoring System and NASA Interdisciplinary Science Programs (G.C.H. and B.P.). Oak

Ridge National Laboratory is operated by UT-Battelle, LLC, under contract DE-AC05-00OR22725 to the United States Department of Energy. **Competing interests:** The authors have no competing interests to declare.

10.1126/science.aaz9463



## Pervasive shifts in forest dynamics in a changing world

Nate G. McDowell, Craig D. Allen, Kristina Anderson-Teixeira, Brian H. Aukema, Ben Bond-Lamberty, Louise Chini, James S. Clark, Michael Dietze, Charlotte Grossiord, Adam Hanbury-Brown, George C. Hurtt, Robert B. Jackson, Daniel J. Johnson, Lara Kueppers, Jeremy W. Lichstein, Kiona Ogle, Benjamin Poulter, Thomas A. M. Pugh, Rupert Seidl, Monica G. Turner, Maria Uriarte, Anthony P. Walker and Chonggang Xu

*Science* **368** (6494), eaaz9463.  
DOI: 10.1126/science.aaz9463

### Shifting forest dynamics

Forest dynamics are the processes of recruitment, growth, death, and turnover of the constituent tree species of the forest community. These processes are driven by disturbances both natural and anthropogenic. McDowell *et al.* review recent progress in understanding the drivers of forest dynamics and how these are interacting and changing in the context of global climate change. The authors show that shifts in forest dynamics are already occurring, and the emerging pattern is that global forests are tending toward younger stands with faster turnover as old-growth forest with stable dynamics are dwindling.

*Science*, this issue p. eaaz9463

#### ARTICLE TOOLS

<http://science.sciencemag.org/content/368/6494/eaaz9463>

#### REFERENCES

This article cites 152 articles, 25 of which you can access for free  
<http://science.sciencemag.org/content/368/6494/eaaz9463#BIBL>

#### PERMISSIONS

<http://www.sciencemag.org/help/reprints-and-permissions>

Use of this article is subject to the [Terms of Service](#)

---

*Science* (print ISSN 0036-8075; online ISSN 1095-9203) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science* is a registered trademark of AAAS.

Copyright © 2020 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works