REVIEW

FOREST ECOLOGY

Pervasive shifts in forest dynamics in a changing world

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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.

The 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_2, 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_2 fertilization–dominated period to a VPD-dominated period (*15*). Terrestrial greening indices indicate a shift from a CO_2-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_2 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

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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$_2$, 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$_2$, 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^2 in 1900 to 12.5 million km^2 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 progressively 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^2 of old-growth forest and 26.3 million km^2 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$_2$

Atmospheric CO$_2$ 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$_2$ increases leaf-level water-use efficiency, and rising CO$_2$ has positive but uncertain feedbacks on plant demographic rates (Fig. 3, A and B). Maturation and seed production can be accelerated under elevated CO$_2$ (*33*); however, seedling growth is not always stimulated by CO$_2$ (*34*). Recruitment response to rising CO$_2$ is variable (*35*, *36*). Forest inventory and tree-ring studies show limited evidence for CO$_2$ fertilization of growth (*37*–*43*), potentially because of the overwhelming influence of increasing drought and nutrient limitations (*44*). Ecosystem-scale CO$_2$ 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$_2$-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$_2$ causes increased mortality or no change in mortality. Mortality rates of saplings during experimental drought were not mitigated by elevated CO$_2$ (*50*, *51*), while accelerated self-thinning due to CO$_2$ 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$_2$ fertilization may

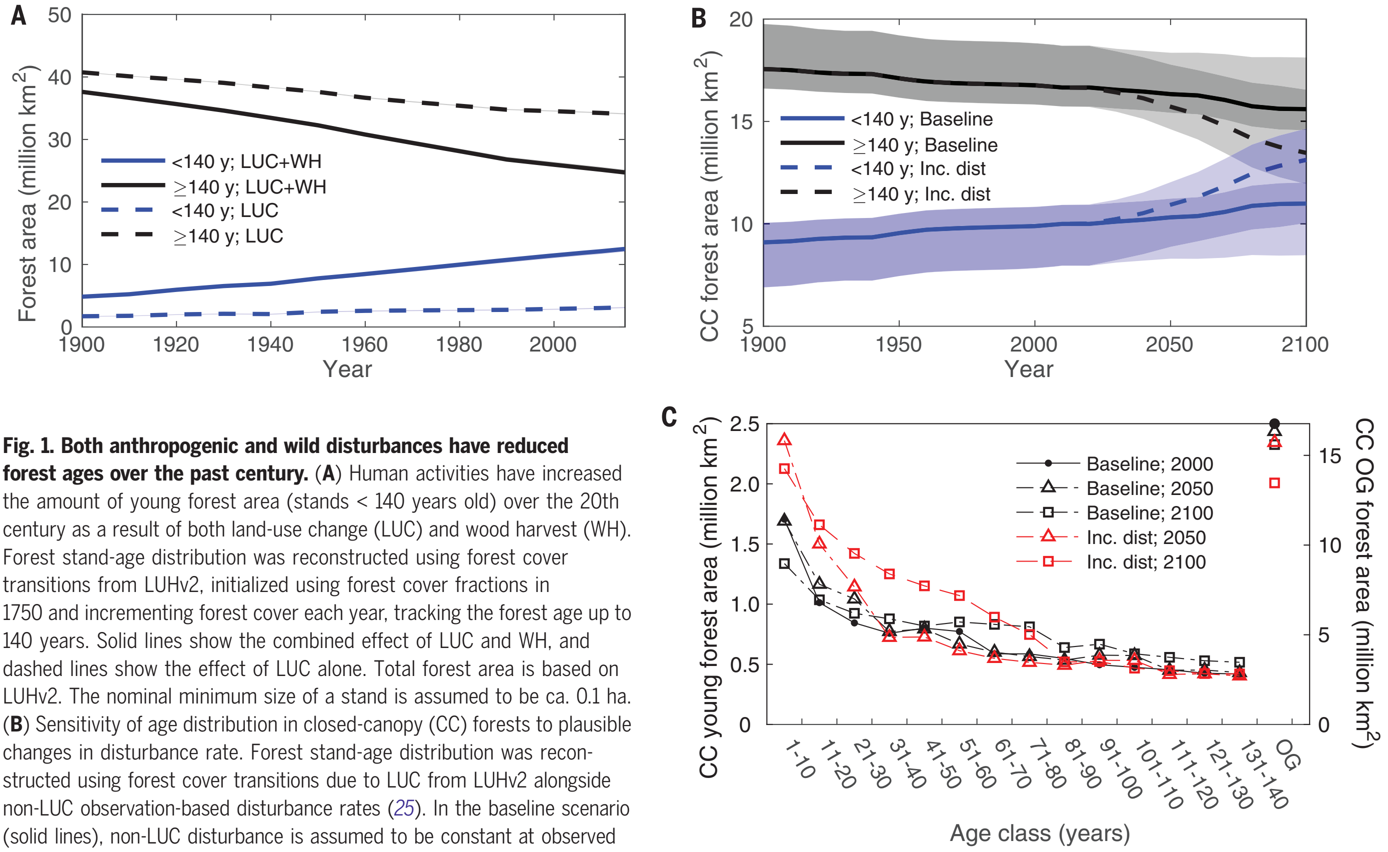

Fig. 1. Both anthropogenic and wild disturbances have reduced forest ages over the past century. (**A**) Human activities have increased the amount of young forest area (stands < 140 years old) over the 20th century as a result of both land-use change (LUC) and wood harvest (WH). Forest stand-age distribution 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$_2$ 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.

expose trees to size-related mortality risks earlier (*7*). Such CO$_2$-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$_2$ 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 observations 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

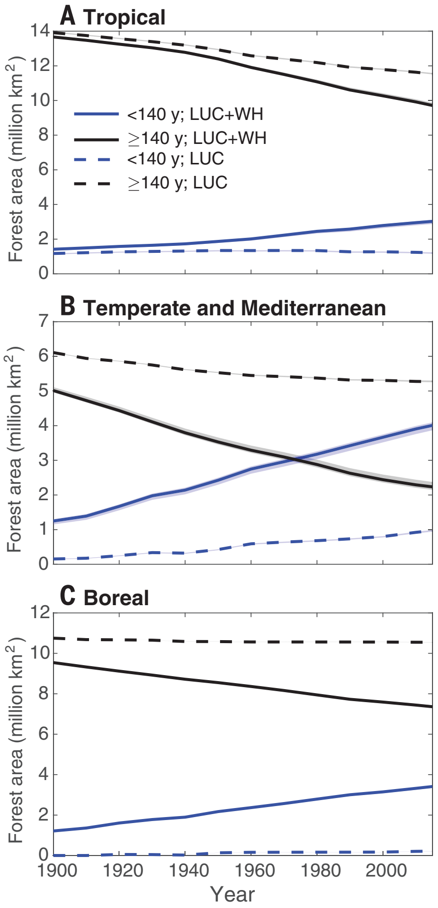

Fig. 2. Human activities have increased the amount of young forest area irrespective of biome. As in Fig. 1A, but broken down by biome (*157*): (**A**) tropical, (**B**) temperate and Mediterranean, and (**C**) boreal.

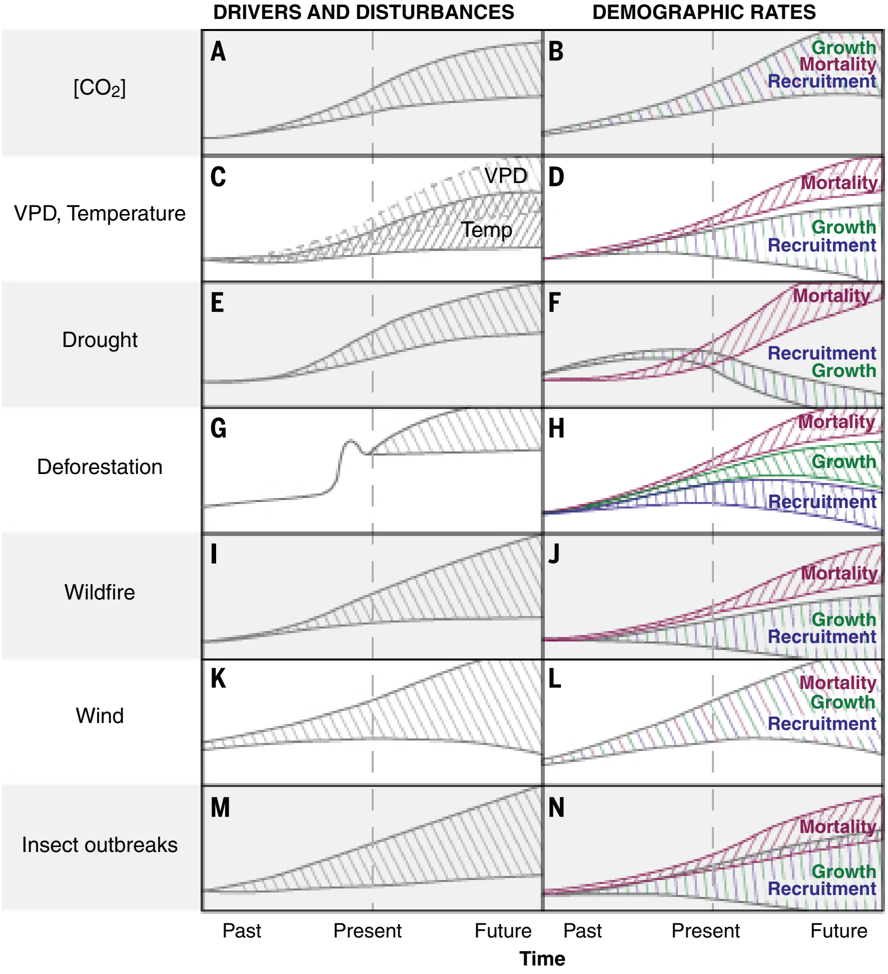

Fig. 3. Drivers, disturbances, and demographics are changing both historically and into the future. A graphical summary of the literature evidence of changing drivers and disturbances (left-hand column) and subsequent demographic rates (right-hand column). Shown are the chronically changing drivers (**A** and **B**) CO$_2$ 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.

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 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 plantations, 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

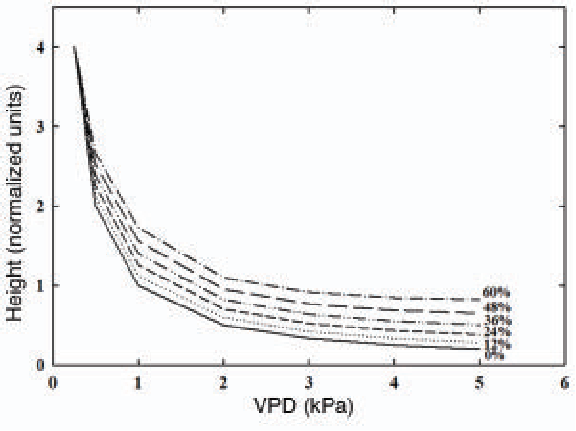

Fig. 4. Rising VPD forces declines in potential plant stature. Predictions of plant height in response to rising VPD from the hydraulic corollary to Darcy's law. The equation is $h = (A_s \times k_s \times \Delta\Psi)/(G \times A_l \times \text{VPD})$, where h is height, A_s is sapwood area, k_s is specific 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 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 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 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 reachieve 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_2 to the atmosphere and hence greater climate forcing. This impact may be mitigated by increased carbon uptake due to CO_2 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_2 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_2 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_2, 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_2 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_2, 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 sensitive, 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_2 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.

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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