

## Pervasive shifts in forest dynamics in a changing world

McDowell, Nate; Allen, Craig; Anderson-Teixeira, Kristina; Aukema, Brian; Bond-Lamberty, Ben; Chini, Louise; Clark, James; Dietze, Michael; Grossiord, Charlotte; Hanbury-Brown, Adam; Hurtt, George; Jackson, Robert; Johnson, Daniel; Kueppers, Lara; Lichstein, Jeremy; Ogle, Kiona; Poulter, Ben; Pugh, Thomas; Seidl, Rupert; Turner, Monica

DOI:

[10.1126/science.aaz9463](https://doi.org/10.1126/science.aaz9463)

License:

Other (please specify with Rights Statement)

*Document Version*

Peer reviewed version

*Citation for published version (Harvard):*

McDowell, N, Allen, C, Anderson-Teixeira, K, Aukema, B, Bond-Lamberty, B, Chini, L, Clark, J, Dietze, M, Grossiord, C, Hanbury-Brown, A, Hurtt, G, Jackson, R, Johnson, D, Kueppers, L, Lichstein, J, Ogle, K, Poulter, B, Pugh, T, Seidl, R, Turner, M, Uriarte, M, Walker, A & Xu, C 2020, 'Pervasive shifts in forest dynamics in a changing world', *Science*, vol. 368, no. 6494, eaaz9463. <https://doi.org/10.1126/science.aaz9463>

[Link to publication on Research at Birmingham portal](#)

### **Publisher Rights Statement:**

This is the author's version of the work. It is posted here by permission of the AAAS for personal use, not for redistribution. The definitive version was published in *Science* in Vol 368, Issue 6494 on 29 May 2020, DOI: 10.1126/science.aaz9463

### **General rights**

Unless a licence is specified above, all rights (including copyright and moral rights) in this document are retained by the authors and/or the copyright holders. The express permission of the copyright holder must be obtained for any use of this material other than for purposes permitted by law.

- Users may freely distribute the URL that is used to identify this publication.
- Users may download and/or print one copy of the publication from the University of Birmingham research portal for the purpose of private study or non-commercial research.
- User may use extracts from the document in line with the concept of 'fair dealing' under the Copyright, Designs and Patents Act 1988 (?)
- Users may not further distribute the material nor use it for the purposes of commercial gain.

Where a licence is displayed above, please note the terms and conditions of the licence govern your use of this document.

When citing, please reference the published version.

### **Take down policy**

While the University of Birmingham exercises care and attention in making items available there are rare occasions when an item has been uploaded in error or has been deemed to be commercially or otherwise sensitive.

If you believe that this is the case for this document, please contact [UBIRA@lists.bham.ac.uk](mailto:UBIRA@lists.bham.ac.uk) providing details and we will remove access to the work immediately and investigate.

1 **Pervasive shifts in forest dynamics in a changing world**

2 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  
3 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  
4 Hanbury-Brown<sup>11</sup>, George C. Hurtt<sup>7</sup>, Robert B. Jackson<sup>12</sup>, Daniel J. Johnson<sup>13</sup>, Lara  
5 Kueppers<sup>11,14</sup>, Jeremy W. Lichstein<sup>15</sup>, Kiona Ogle<sup>16</sup>, Ben Poulter<sup>17</sup>, Thomas A.M. Pugh<sup>18,19</sup>,  
6 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>

7 <sup>1</sup>Pacific Northwest National Laboratory, Richland, WA, 99354, USA

8 <sup>2</sup>US Geological Survey, Fort Collins Science Center, New Mexico Landscapes Field Station,  
9 Los Alamos, New Mexico, USA

10 <sup>3</sup>Conservation Ecology Center; Smithsonian Conservation Biology Institute; Front Royal,  
11 Virginia, USA

12 <sup>4</sup>Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical  
13 Research Institute, Republic of Panama

14 <sup>5</sup>Department of Entomology, University of Minnesota, St. Paul, MN 55108, USA

15 <sup>6</sup>Joint Global Change Research Institute, Pacific Northwest National Laboratory, 5825  
16 University Research Ct. #3500, College Park, MD 20740, USA

17 <sup>7</sup>Department of Geographical Sciences, University of Maryland, College Park, MD 20742

18 <sup>8</sup>Nicholas School of the Environment, Duke University, Durham, NC 27708, USA

19 <sup>9</sup>Department of Earth and Environment, Boston University, Boston, MA 02215, USA

20 <sup>10</sup>Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111,  
21 8903 Birmensdorf, Switzerland

22 <sup>11</sup>Energy and Resources Group, University of California, Berkeley, 310 Barrows Hall #3050,  
23 Berkeley, CA, 94720, USA

24 <sup>12</sup>Department of Earth System Science, Woods Institute for the Environment, and Precourt  
25 Institute for Energy, Stanford University, Stanford, CA 94305, USA

26 <sup>13</sup>School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611

27 <sup>14</sup>Division of Climate and Ecosystem Sciences, Lawrence Berkeley National Laboratory, 1  
28 Cyclotron Road, Berkeley, CA 94720, USA

29 <sup>15</sup>Department of Biology, University of Florida, Gainesville, FL 32611, USA

30 <sup>16</sup>School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff,  
31 AZ 86001, USA

32 <sup>17</sup>NASA Goddard Space Flight Center, Biospheric Sciences Lab., Greenbelt, MD 20771, USA

33 <sup>18</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, B15 2TT  
34 Birmingham, United Kingdom;

35 <sup>19</sup>Birmingham Institute of Forest Research, University of Birmingham, B15 2TT Birmingham,  
36 United Kingdom;

37 <sup>20</sup>Department of Forest and Soil Sciences, University of Natural Resources and Life Sciences  
38 Vienna, Austria

39 <sup>21</sup>School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2,  
40 85354 Freising, Germany

41 <sup>22</sup>Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706,  
42 USA

43 <sup>23</sup>Department of Ecology, Evolution & Environmental Biology, Columbia University, New  
44 York, NY 10027, USA

45 <sup>24</sup>Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National  
46 Laboratory, Oak Ridge, TN 37831, USA

47 <sup>25</sup>Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos,  
48 NM 87545, USA

49

50

51 **Enhanced abstract.**

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

64 **Advances:** We reviewed the literature of forest demographic responses to chronic drivers and  
65 transient disturbances to generate hypotheses on future trajectories of these factors and their  
66 subsequent impacts on vegetation dynamics, with a focus on forested ecosystems. We  
67 complemented this review with analyses of global land-use change and disturbance datasets to  
68 independently evaluate the implications of changing drivers and disturbances on global-scale tree  
69 demographics. Ongoing changes in environmental drivers and disturbance regimes are  
70 consistently increasing mortality and forcing forests towards shorter and younger stands,  
71 reducing potential carbon storage. Acclimation, adaptation, and migration may partially mitigate  
72 these effects. These increased forest impacts are due to natural disturbances (e.g. wildfire,  
73 drought, windthrow, insect/pathogen outbreaks) and land-use change, both of which are  
74 predicted to increase in magnitude in the future. Tree growth, and potentially recruitment, may  
75 have increased globally in the 20<sup>th</sup> century based on atmospherically derived estimates of the  
76 terrestrial carbon sink and based on remote sensing data, but the growth of this carbon sink has  
77 slowed. Variability in growth stimulation due to CO<sub>2</sub> fertilization is evident globally, with  
78 observations and experiments suggesting that forests benefit from CO<sub>2</sub> primarily in early stages  
79 of secondary succession. Furthermore, increased tree growth typically requires sufficient water  
80 and nutrients to take advantage of rising CO<sub>2</sub>. Collectively, the evidence reveals that it is highly  
81 likely that tree mortality rates will continue to increase while recruitment and growth will  
82 respond to changing drivers in a spatially and temporally variable manner. The net impact will  
83 be a reduction in forest canopy cover and biomass.

84 **Outlook:** Pervasive shifts in forest vegetation dynamics are already occurring and are likely to  
85 accelerate under future global changes, with consequences for biodiversity and climate forcing.  
86 This conclusion is robust with respect to the abundant literature evidence and our global  
87 assessment of historical demographic changes, but it also forms the basis for hypotheses  
88 regarding the patterns and processes underlying the shifts in forest dynamics. These hypotheses  
89 will be directly testable using emerging terrestrial and satellite-based observation networks. The  
90 existing evidence and new observations provide a critical test of Earth system models that  
91 continue to improve in their ability to simulate forest dynamics and resulting climate forcing.

92 Ultimately, forest managers and natural resource policies must confront the consequences of  
93 changing climate and disturbance regimes to ensure sustainable forests and accrue their  
94 associated benefits.

95

96 **Abstract:** Forest dynamics arise from the interplay of environmental drivers and disturbances  
97 with the demographic processes of recruitment, growth, and mortality, subsequently driving the  
98 biomass and species composition of terrestrial ecosystems. However, forest disturbances and  
99 subsequent recovery are shifting with global changes in climate and land use, altering forest  
100 dynamics. Ongoing changes in environmental drivers, land use, and disturbance regimes are  
101 forcing forests towards younger, shorter stands. Rising CO<sub>2</sub>, acclimation, adaptation, and  
102 migration can influence these impacts. Recent developments in Earth system models support  
103 increasingly realistic simulations of vegetation dynamics. In parallel, emerging remote sensing  
104 datasets promise qualitatively new and more abundant data on the underlying processes and  
105 consequences for vegetation structure. When combined, these advances hold promise to improve  
106 the scientific understanding of changes in vegetation demographics and disturbances. Pervasive  
107 shifts in forest dynamics are already occurring and are likely to accelerate under future global  
108 changes, with consequences for climate forcing.

109

## 110 **Introduction**

111           The interplay of vegetation demography—recruitment, growth, and mortality—with  
112 environmental conditions and disturbances drives forest dynamics of biomass, function, and  
113 species composition (Figure 1; see Box 1 for definitions). In old-growth forests that approximate  
114 steady-state demographics, the recruitment, growth, and mortality of trees are approximately  
115 balanced; in contrast, rapid recruitment often follows widespread disturbance-induced mortality  
116 (1). Vegetation dynamics may now be changing because the environmental context in which  
117 plant demography and disturbances interact is shifting with anthropogenic change (Figure 1).  
118 The interaction between episodic forest disturbances such as wind-throw or wildfire, and  
119 chronically changing drivers such as rising temperature, vapor pressure deficit (*VPD*), and  $\text{CO}_2$ ,  
120 together with land-use change (2), leads to both compounding and antagonistic impacts that alter  
121 demographic rates (3), with consequences for terrestrial biogeochemical cycles and climate (4,5).  
122 Understanding the drivers of vegetation dynamics is thus critical for accurate prediction of global  
123 terrestrial biogeochemistry under future conditions (6).

124           The impacts of global change on forest demographic rates may already be materializing.  
125 In mature ecosystems, tree mortality rates have doubled throughout much of the Americas and in  
126 Europe over the last four decades (7-9). Simultaneously, global carbon budgets indicate either a  
127 growing or constant terrestrial carbon sink (10-12), which implies increased or constant  
128 vegetation production rates (13,14). However, satellite evidence suggests that forests might be  
129 switching from a  $\text{CO}_2$  fertilization dominated period to a *VPD* dominated period (15). Terrestrial  
130 greening indices indicate a shift from a  $\text{CO}_2$ -driven increase in greenness in the late 20<sup>th</sup> century  
131 to a *VPD*-driven decrease in the last decade (16). Thus, increasing mortality due to  
132 anthropogenic changes, along with potentially increasing or stable growth and recruitment due to

133 CO<sub>2</sub> fertilization (5), represent opposing processes that are co-occurring globally, leaving the fate  
134 of future forests uncertain.

135         Beyond changing vegetation dynamics within “intact” or relatively undisturbed forests,  
136 episodic disturbances are tending to be larger, more severe and, in some regions, more frequent  
137 under global change(17-20). Similarly, the rates and types of land-use change (*LUC*) vary widely  
138 (21) but have, on average, increased globally in the past few centuries (2,22,23). Thus, at the  
139 global scale, disturbances and *LUC* have likely amplified tree mortality beyond that suggested by  
140 the doubling of background mortality rates in undisturbed forests (7-9). Current understanding  
141 of the net balance of tree losses (mortality) and gains (recruitment and growth) under a changing  
142 environment characterized by more extreme drivers and disturbances is limited, preventing  
143 prediction of whether recruitment and growth can balance increased mortality rates in the future.

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

## 152 **Evidence for changing drivers and disturbances and their impact on demography.**

153         Determining the impacts of changing drivers on demography is difficult given the lack of  
154 global observation platforms. However, evidence abounds from individual published studies on  
155 the drivers and their impacts on plant communities, and new modeling and observational efforts



156 now enable a more complete picture of disturbances and forest demography (24-26). In this  
157 section, we first examine if there are global trends in stand ages and test the sensitivity of the  
158 stand-age distribution to changes in disturbance rate using global datasets on *LUC* (27) and non-  
159 *LUC* (25,28) disturbances. We subsequently draw upon the wealth of published studies on  
160 changes in forest demographics and their drivers to investigate the potential changes leading to  
161 global age-trends. Ultimately, the combination of our global estimates along with the large  
162 literature base allows us to generate testable hypotheses regarding trends and impacts of the  
163 drivers of forest demographics.

164

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

166 We re-analysed the Land-use Harmonization (*LUHv2*) dataset (28) with respect to forest  
167 age, revealing that the area of young forest stands (here defined as <140 years old) resulting  
168 directly from *LUC* (conversion of forest to non-forest) or wood harvest (reduction of biomass  
169 and age but retained as forest) has increased from 4.8 million km<sup>2</sup> in 1900 to 12.5 million km<sup>2</sup> in  
170 2015 (or from 11.3% to 33.6% of forest area; Figure 2A). The results were insensitive to  
171 assumptions regarding the link of disturbance likelihood to stand age (Figure 2A). These forest  
172 stand age distributions exhibit different trajectories in different regions. Tropical forests have  
173 progressively lost old-growth area due to *LUC* over the 20<sup>th</sup> century (Figure 3a, black dashed  
174 line). Wood harvest has increased from a minor driver of tropical forest age distribution in 1900  
175 to a major one in 2015 (difference between solid and dashed lines). The split between  
176 deforestation and shifting cultivation drivers is broadly consistent with a satellite-based analysis  
177 for the period 2001-2015 (29). Temperate and Mediterranean forest ages are strongly influenced  
178 by wood harvest, which has made old-growth forests increasingly scarce in these regions. Boreal

179 forests saw little influence of *LUC* on stand age, but wood harvest has substantially shifted the  
180 age distribution towards young forests.

181 In reality, old-growth forest are scarcer than that due to *LUC* and wood harvest (Figures  
182 2a and 3), due to other disturbances that have shifted landscapes from old- to young-dominated  
183 stands (14), such as wildfire (29), windthrows (30), and biotic outbreaks (31). To address these  
184 additional disturbances, we integrated recent observation-based estimates of non-*LUC*  
185 disturbance for closed-canopy forests (25,28) with *LUC* from *LUHv2*, to obtain a first principles  
186 estimate of the combined effect of human and natural disturbances on forest age structure (Figure  
187 2B). A twofold increase in non-*LUC* disturbance rates over the period 2015-2050 would result in  
188 a substantial increase in the fraction of young forests (Figure 2B, C). Thus, realistic shifts in  
189 disturbance rates can have substantial impacts on the age structure of forests in the future. As  
190 discussed below, such an increase in disturbance rate is consistent with the magnitude of changes  
191 observed or predicted in individual ecosystems.

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

197 ***Chronically changing drivers:*** *Atmospheric CO<sub>2</sub>* has risen more than 125 ppm since the  
198 industrial revolution (11), and is projected to rise an additional 50 to 200 ppm by 2100. Higher  
199 CO<sub>2</sub> increases leaf-level water use efficiency, and rising CO<sub>2</sub> has positive but uncertain  
200 feedbacks on plant demographic rates (Figure 4A-B). Maturation and seed production can be  
201 accelerated under elevated CO<sub>2</sub> (33); however, seedling growth is not always stimulated by CO<sub>2</sub>

202 (34). Recruitment response to rising CO<sub>2</sub> is variable (35,36). Forest inventory and tree-ring  
203 studies show limited evidence for CO<sub>2</sub> fertilization of growth (37-43), potentially due to the  
204 overwhelming influence of increasing drought and nutrient limitations (44). Ecosystem-scale  
205 CO<sub>2</sub> enrichment experiments in young forests suggest a 30% gain in decadal biomass increment  
206 (45), but experiments in mature forests have found minimal growth stimulation (46,47). This is  
207 consistent with evidence for an initially strong CO<sub>2</sub>-related growth stimulation in young forests  
208 that decreases with tree age and size<sup>39</sup> due perhaps to nutrient (7,48) and hydraulic path-length  
209 limitations (49).

210         Limited studies suggest elevated CO<sub>2</sub> causes increased mortality or no change in  
211 mortality. Mortality rates of saplings during experimental drought were not mitigated by  
212 elevated CO<sub>2</sub> (50,51) while accelerated self-thinning due to CO<sub>2</sub> fertilization-induced stand  
213 density increases may lead to higher mortality (6,52,53) (Figure 4B). The latter process would  
214 be consistent with increases in recruitment at large scales. Because tree mortality is dominated  
215 by large size classes i.e. (54) (for details see section on size-related mortality below) faster  
216 growth via CO<sub>2</sub> fertilization may expose trees to size-related mortality risks earlier (7). Such  
217 CO<sub>2</sub>-induced increases in mortality may be global (55). Furthermore, faster growth is often  
218 associated with lower wood density (56), rendering fast growing trees more susceptible to high  
219 winds. Thus, future CO<sub>2</sub> fertilization could increase recruitment, growth, and mortality (Figure  
220 4B), though there is significant uncertainty about these effects.

221

222 ***Chronically changing drivers: Temperature and vapor pressure deficit*** are rising globally and  
223 will continue to rise into the future (57). Both temperature and *VPD* can have impacts on  
224 demographic rates. Rising temperature forces an exponential rise in *VPD*, which prompts

225 stomatal closure and limits photosynthesis, leading to lower growth, higher mortality (58), and  
226 reduced regeneration (59), and ultimately driving community shifts (60,61). These observations  
227 are consistent with hydraulic theory, which suggests that as *VPD* rises, potential maximum tree  
228 height declines (62) (Figure 5). This results from the dependency of water transport limitations  
229 on tree size (49) that are exacerbated by elevated *VPD* (Figure 5), making short stature  
230 advantageous with rising *VPD*. Because most plants cannot reduce their size (beyond limited  
231 reductions in leaf area or crown dieback), forests respond through increased mortality of large  
232 plants, which are replaced by smaller ones (62), as has been observed in many studies (26,54).  
233 While rising air temperature may also increase respiratory carbon loss, leaving less carbon for  
234 growth (63), warming in wetter and cooler regions may actually stimulate reproductive output,  
235 recruitment, and growth (64-66). Changes in temperature and *VPD* also can produce asynchrony  
236 in floral and pollinator phenology (67) and can reduce cold stratification (68), both of which  
237 reduce seed abundance (69), and negatively affect recruitment (70,71). Sapling mortality is  
238 accelerated by elevated temperature (71,72), but recruitment has increased in moist areas (73).  
239 Thus, rising temperature and *VPD* may be beneficial in cooler or wetter areas, but most evidence  
240 suggests negative impacts on plant demographic rates (Figure 4C, D; Figure 5).

241  
242 ***Changing disturbance regimes: Droughts*** are anticipated to increase in frequency, duration,  
243 and severity globally (Figure 4E-F) and are more stressful to plants due to increases in  
244 temperature, *VPD*, and associated water loss (57). Drought can directly cause tree death or  
245 indirectly lead to mortality through associated increases in insect or pathogen attack (51).  
246 Hydraulic failure and carbon starvation remain the most likely, mutually inclusive, underlying  
247 physiological mechanisms for drought-induced mortality (74) and both processes are likely to  
248 increase tree susceptibility to biotic agents (75). Evidence suggests that drought-induced

249 mortality occurs more rapidly under warmer conditions (51.72). Consistent with these empirical  
250 results, models suggest far greater mortality of temperate conifer trees in the future (76).  
251 Reproductive output is often reduced by drought (but see (64)), which combined with drought  
252 impacts on seedling survival, leads to reduced recruitment (77). However, growth was relatively  
253 stable across a drought in Amazonia (78), while mortality increased. Thus, like rising  
254 temperature and *VPD*, it appears that drought may increase mortality regardless of location,  
255 while having variable impacts on recruitment and growth (Figure 4F).

256

257 ***Changing disturbance regimes: Land-use change*** and forest management have reduced  
258 vegetation stature and biomass, and altered species composition, with profound consequences for  
259 forest dynamics (Figures 2A, 4G-H). Today's global vegetation biomass stocks may amount to  
260 only ~50% of their potential due to *LUC* (79). Wood harvest and shifting cultivation are the  
261 land-use activities primarily responsible for the conversion from primary to secondary vegetation  
262 cover and associated demographic shifts (2). For systems that return to wild-vegetation or to  
263 managed forest after human clearing, demographic rates are typically accelerated. The increased  
264 resource availability after forest removal facilitates establishment of early-successional species,  
265 reduces species diversity (80,81), and causes a transition to younger, smaller plants (82). Post-  
266 deforestation recruitment is often prolific even in the absence of management (83). Globally, the  
267 recovery of harvested forests and abandoned agricultural land, along with establishment of new  
268 plantations, has resulted in younger forests (Figure 2A), with associated reductions in tree size  
269 and biomass (84). Such post-deforestation recruitment may be limited by elevated *VPD* or  
270 drought, as is the case with recruitment following all natural disturbances. Overall the net effect

271 of historical *LUC* and wood harvest has resulted in a substantial loss of forest area, along with  
272 altered demographic rates, leading to younger, shorter, less diverse ecosystems (Figure 4H).  
273

274 ***Changing disturbance regimes: Wildfire*** is increasing in many forests worldwide (85) (Figure  
275 4I), although human management of landscapes has led to wildfire suppression in some biomes  
276 (86). Given sufficient fuel, burned area increases exponentially with aridity (87), and future fire  
277 frequencies may exceed those documented over the past 10,000 years (88). Increased fire  
278 activity causes increased mortality and potentially higher recruitment and growth of either pre-  
279 existing or new species, but rates of recruitment and growth may be slowed under climate  
280 warming. Forests characterized by stand-replacing fire regimes are dominated by obligate  
281 seeders, and typically have effective seedling recruitment (89). However, high-severity and high-  
282 frequency fires can reduce recruitment by reducing seed supply through the repeated and severe  
283 loss of reproductively mature vegetation (90), and high frequency fires can cause recruitment  
284 losses via direct mortality of the seedbank, seedlings, and saplings (91), which is worsened by  
285 elevated *VPD* (92). Woody species that can resprout following fire, including shrubs that  
286 suppress tree regeneration (92), may be favored by increased fire frequency and severity.  
287 Increased fire severity results in high tree mortality in forests historically adapted to low-severity  
288 fires, and subsequent recruitment and growth may be slow or absent, resulting in conversion of  
289 forests to low-biomass ecosystems (93). Thus, wildfire can result in higher demographic rates,  
290 though rising temperature and *VPD* can negatively impact recruitment and growth (Figure 4J).  
291

292 ***Changing disturbance regimes: Wind throw*** from cyclonic storms represents the dominant  
293 natural disturbance in coastal forests across the globe (94). Cyclonic storms are expected to

294 increase in frequency, wind velocities, and precipitation intensity (95) (Figure 4K), with more  
295 extreme flooding that promotes tree instability. Wind throw also results from convective  
296 thunderstorms and topographically mediated winds, and warming is expected to increase the  
297 frequency of atmospheric conditions conducive to severe thunderstorms (96). Canopy damage  
298 and whole-tree mortality are the most immediate impacts of wind throw (97) (Figure 4L). Larger  
299 trees dominate mortality from storms (98), and the loss of large canopy trees during wind  
300 disturbance favors growth of surviving trees (98,99) and advances regeneration, recruitment of  
301 early successional species (100), or resprouting of trees broken by wind (101). Depending on the  
302 resprouting or seeding capacity of surviving species, wind damage may slow or accelerate  
303 succession (102). We note that storms may also be associated with lightning, which may be a  
304 significant cause of large-tree mortality (103). Thus, windstorms should result in changes in all  
305 three demographic rates, though with large uncertainty at the global scale (Figure 4L).

306

307 ***Changing disturbance regimes: Biotic agents*** Biotic disturbances from insects, insect-pathogen  
308 complexes, and other biotic agents have been increasing in frequency, severity, and extent in  
309 recent decades (17,104,105) (Figure 3M). Such trends reflect a changing climate (106), altered  
310 land use (107), and introductions of non-indigenous insects and pathogens (108). Climate change  
311 is expected to further amplify biotic disturbances (109) in part through enhanced host  
312 vulnerability (Figure 4M). However, shifts in frequency or dampening of disturbance regimes  
313 could also emerge (110), leading to some uncertainty in outbreak dynamics under future  
314 conditions (Figure 4M). While insects and associated pathogens are globally widespread, lianas,  
315 or vines that use other plants as host structures, are increasing in abundance and are thought to be  
316 causing increasing mortality in the tropics (7,111).

317           Response of insects and pathogens to climate change is likely to increase plant mortality  
318 (4), with variable impacts on growth and recruitment (Figure 4N). Tree mortality can result from  
319 girdling of the phloem and xylem by bark beetles (75) and from repeated defoliation events that  
320 exhaust the capacity of trees to recover (112). Tree mortality during outbreaks is usually partial  
321 at the stand-level because many biotic agents preferentially attack trees of specific size- or  
322 health-classes, or are host-specific (16). Suppressed, smaller trees and non-host tree species may  
323 survive and grow rapidly when released from competition for resources (113,114). Thus, similar  
324 to many other disturbances, mortality increases while recruitment and growth show variable  
325 responses to biotic disturbances, including a dependency on post-disturbance temperature, *VPD*,  
326 and drought.

327

328 ***On size and age demographics.*** The combination of *LUC*, disturbances, and chronic drivers is  
329 likely to have already shifted forests to younger and shorter stands, with these impacts increasing  
330 under expected future changes in drivers and disturbances (Figure 2A-C). These results are  
331 consistent with our review of the literature (Figure 4). Large trees are the most susceptible to die  
332 from *LUC*-caused forest fragmentation (115,116), drought (26), rising temperature or *VPD*  
333 (54,62) (Figure 5), windthrow (117,118), biotic attacks (119), and lightning (103), with variable  
334 size-impacts of fire (120). The abundance of size-dependent mortality drivers and disturbances  
335 should logically push stands towards younger/smaller distributions of trees and shorter statured  
336 species assemblages (121).

337           There are exceptions to the pattern of climate drivers and disturbances reducing tree  
338 height and stand age. Non-stand-replacing fires that kill smaller trees and leave the larger, older  
339 trees will shift forests towards larger size distributions. Similarly, on occasions when droughts



340 preferentially kill younger but fast-growing trees, this would impact the subsequent size  
341 distribution and rate of carbon accumulation. Rising CO<sub>2</sub> and increased precipitation in some  
342 areas also counter the general decrease in size because they may lead to faster growth and hence  
343 taller trees (122). Thus, the antagonistic drivers promoting larger trees (e.g. rising CO<sub>2</sub>) vs  
344 smaller trees (e.g. rising *VPD*, increasing disturbances) co-occur, but the general pattern of  
345 decreasing size and younger ages reveals that processes driving down size and age (Figures 2-5)  
346 are dominant globally.

347

### 348 **Mitigation of demographic-disturbance impacts**

349

350 The literature patterns suggest most drivers and disturbances will increase tree mortality  
351 now and in the future, with variable effects on recruitment and growth (Figure 4). The  
352 uncertainty grows, however, when we consider multiple feedbacks that can mitigate the changes  
353 in forest demography induced by chronically changing drivers and disturbance regimes. These  
354 processes include acclimation, adaptation, migration, and compensatory mechanisms of resource  
355 use. With global change, forests will be influenced by a combination of phenotypic plasticity  
356 (i.e. acclimation (123)), adaptation to novel biotic and abiotic stresses (124), and the ability to  
357 migrate as conditions change (125). Failure to acclimate, adapt, or migrate, including due to  
358 human infrastructure (126), could lead to recruitment and growth reductions and local  
359 extinctions. Plants have demonstrated acclimation of phenology, seed longevity, and metabolic  
360 processes to single and/or multiple stressors (127-130). Acclimation and adaptation will likely  
361 depend on an array of factors including genetic variation, fecundity, dispersal, population size,  
362 and environmental variability (123). Many tree species have migrated in response to past  
363 climatic cycles but at rates slower than the current pace of climate change (131). Regarding

364 resource use, reductions in stand density as a result of increased mortality or reduced recruitment  
365 should allow greater resource availability to surviving individuals, and therefore subsequently  
366 higher growth and survival rates (132). Such stand-resource mechanisms can manifest at the  
367 landscape scale, as most disturbances are patchy (133), and the size, shape, and arrangement of  
368 surviving forest patches can play a key role in recovery of the disturbed landscape (20). Taken  
369 together, the mitigating factors can play a significant role in buffering the impacts of changing  
370 drivers on plant survival, but it remains unclear if these factors will enable trees to keep pace  
371 with ongoing climate change (50,123). Ultimately, the uncertainty around future demographic  
372 rates shown in Figure 3 is partially because of the influence of these mitigating factors.

373

#### 374 **Consequences for community assembly and for climate forcing**

375

376 The widespread shift in vegetation dynamics begets questions regarding consequences for  
377 community assembly and climate forcing. Hydraulic theory suggests that under rising *VPD*,  
378 functional traits of high conductance, low stature, and low leaf area should best enable survival,  
379 all of which are characteristics of pioneer, shrub and weed species (62). Consistent with this,  
380 diversity (e.g. species richness) temporarily increases post-disturbance for many systems, as  
381 short-statured, opportunistic species invade (134). If forest communities shift towards trait  
382 assemblages better suited to the new disturbance regime, such shifts may confer some resistance  
383 to future disturbances (134,135). Alternatively, if disturbance regimes shift faster than  
384 recruitment, growth, and subsequent community assembly can respond, resistance to future  
385 disturbances will likely decline.

386 Climate forcing responds to changing vegetation dynamics in complex ways. Changes in  
387 forest disturbance regimes and vegetation dynamics can affect climate via biogeochemical,

388 hydrological, and land-surface energy budgets (136). Reductions in biomass result in a loss of  
389 carbon to the atmosphere despite younger, shorter stands often having higher gross  
390 photosynthesis; this is due to the loss of carbon through decomposition of necromass, which is a  
391 particularly large flux from mortality of older, larger trees such as those in old-growth forests  
392 (137), and reduced landscape-mean carbon storage under an intensified disturbance regime  
393 (138). The time required to re-achieve the same live carbon storage of an ecosystem after  
394 disturbance can be decades to centuries, particularly if the disturbance cycle is increased, thus the  
395 net effect of the biomass loss is increased CO<sub>2</sub> to the atmosphere and hence greater climate  
396 forcing. This impact may be mitigated by increased carbon uptake due to CO<sub>2</sub> fertilization (139)  
397 or enhanced recruitment. Calculations of the terrestrial carbon sink from atmospheric inversions  
398 indicate that the sink grew over recent decades<sup>12</sup> due in part to increased leaf area (13),  
399 consistent with increased recruitment and growth. However, evidence suggests that forests are  
400 switching from a CO<sub>2</sub> fertilization dominated period to a *VPD* dominated period (15,16), despite  
401 sustained high gross photosynthesis at the global scale (140). The increased mortality  
402 throughout much of the terrestrial biosphere (7-9) further minimizes potential carbon storage  
403 through the enhanced biomass loss. Ultimately, the terrestrial contribution to climate forcing  
404 through carbon uptake and release results from the antagonistic process of rising CO<sub>2</sub> and forest  
405 recovery from *LUC*, which enhance the carbon sink, and rising *VPD* and disturbances that reduce  
406 the carbon sink.

407        Changing vegetation dynamics also influence regional and global surface energy budgets  
408 and hydrological cycles. Disturbances frequently shift albedo of ecosystems from darker to  
409 lighter, resulting in a decline in radiative forcing through less light absorption (141). The rate of  
410 recruitment post disturbance influences the temporal period of this negative feedback (142). The

411 impact of changing vegetation dynamics on the water cycle is particularly complex. Evaporation  
412 from canopies shifts as stands become taller because taller trees transpire less (per unit leaf area)  
413 than smaller trees (49), but larger trees often have better rooting access to water sources and have  
414 greater total leaf area. The net effect of disturbance is a transient decrease in evaporative loading  
415 to the atmosphere along with albedo shifts, causing a feedback of decreasing precipitation  
416 downwind (143,144). Ultimately, carbon storage is at least transiently reduced by disturbances,  
417 with mixed impacts on the water and energy budgets.

418

### 419 **The path to improved prediction**

420 Changes in the global drivers of temperature, CO<sub>2</sub>, *VPD*, and disturbances including  
421 *LUC*, drought, wildfire, windstorms, and insect outbreaks, should all force forests towards  
422 shorter, younger, lower biomass ecosystems. This trend is supported by hydraulic theory (62)  
423 (Figure 5) and by abundant empirical evidence demonstrating a consistent increase in mortality  
424 across the global-spectrum of drivers and disturbances and variable but often declining  
425 recruitment and growth (Figure 4). While the bulk of evidence points to reduced plant stature  
426 due to changing drivers, large uncertainty remains in the magnitude and slope of demographic  
427 trajectories in the future (Figure 4). Given these trajectories, and the large uncertainties around  
428 them, what are the critical next steps to allow improved global prediction? Continued long-term  
429 observations (ground and remotely sensed) are essential to reveal the patterns of demographic  
430 responses to drivers and disturbances; likewise, manipulative experiments are needed that alter  
431 conditions such as CO<sub>2</sub> or drought to provide cause-and-effect understanding of the interactions  
432 among mechanisms of demographic responses. However, for global-scale prediction of

433 responses and climate consequences we need to mainstream insights from observations and  
434 experiments into Earth system models (*ESMs*).

435 *ESMs* simulate the exchange of fluxes between the atmosphere, land, and ocean and  
436 stores of carbon, water, and energy; the land-surface modules of *ESMs* simulate the vegetation.  
437 *ESMs* have made great progress in simulating land use, disturbances, and demography, including  
438 representation of wildfire (145), drought-induced mortality (146), and cohort-age structured  
439 models that enable representation of succession and associated shifts in physiological traits (6).  
440 The global Coupled Model Intercomparison Project CMIP6 now includes a dedicated model  
441 intercomparison activity focused on the effects of changes of land-use on carbon and climate  
442 (147). Advances in remote sensing and forest inventory integration are enhancing global  
443 datasets of forest structure (148) and age (32) that can be used in model initialization, data  
444 assimilation benchmarking, and sensitivity analyses (Figure 2A-C). These advancements set the  
445 stage for developments in *ESMs* such as the prediction of disturbances and demographic rate  
446 responses under climate and *LUC* scenarios.

447 The newest generation of *ESMs* utilize size or age-structured approaches to explicitly  
448 model demography in the Earth system (6), which should ultimately enable model-based  
449 representation of observed shifts in age structure (e.g. Figure 2). However, representation of  
450 vegetation demographic rates remains relatively simplistic. Simulation of growth responses to  
451 global change requires model refinement in light capture, belowground water and nutrient  
452 acquisition, and responses of respiration to temperature (6). Recruitment, including reproduction  
453 and dispersal, is the most undeveloped demographic process in *ESM* simulations. Reproductive  
454 allocation is invariant with plant functional type (*PFT*), and seed is assumed to mix evenly  
455 throughout a grid cell (but see (149)). Environmental constraints to *PFT* establishment are

456 derived from prior distributions of major taxa, and while recruitment rates can be influenced by  
457 light or space availability, they are not responsive to temperature, CO<sub>2</sub>, or soil moisture  
458 (150,151). Simplistic dispersal assumptions are typically either overly permissive or restrictive.  
459 Improvements in representing recruitment under global change are critical for improving  
460 predictions of vegetation dynamics. These advancements will require data synthesis and new  
461 data collection to support *PFT*-specific, environmentally sensitive parameterizations of  
462 regeneration processes, such as reproductive allocation; effective dispersal; seedling  
463 establishment, survival and growth; and post-disturbance recovery strategies (e.g., serotiny and  
464 resprouting).

465         Disturbance-induced mortality is better developed for landscape-scale models than for  
466 *ESMs*. *ESM* modeling of disturbance-induced mortality exists for wildfire and drought  
467 (145,146), although significant challenges remain to represent both reliably globally, while *ESMs*  
468 are under-developed for wind and insect mortality. Currently only one *ESM* to our knowledge  
469 represents canopy damage (152); this causes *ESMs* to potentially underestimate the impacts of  
470 drought and wind, as both disturbances cause lagged tree mortality associated with canopy loss  
471 years after the inciting event (153,154). For insects, there have been prescriptive studies  
472 examining the impact of insect outbreaks on land processes within *ESMs*, but no *ESM* has yet  
473 explicitly considered the interaction between plant defense and insect population dynamics for  
474 prediction of large-scale insect-induced tree mortality. For predicting wildfire, models should be  
475 sensitive to both fuels and climate interactions and represent spatial patterns of burn severity  
476 because the burn mosaic strongly influences postfire vegetation dynamics (145). Next-  
477 generation demographic models are evolving to include explicit, mechanistic representations of  
478 drought-associated mortality, including carbon starvation and hydraulic failure (155). The

479 evaluation of new hydraulics models (155) for prediction of mortality is an essential next step.  
480 Ultimately, model formulations that include environmentally sensitive, *PFT*-specific processes  
481 compatible with the cohort-based approach are likely to provide the best compromise between  
482 process-detail and parsimony and therefore most likely to capture changes in large-scale forest  
483 dynamics under future conditions.

484

485 **Summary** Forest vegetation dynamics (Figure 1) are already strongly influenced by global  
486 change (Figure 2) and will continue to be affected in the future (Figures 2-5) by changes in land  
487 use, chronic drivers such as CO<sub>2</sub> and *VPD*, and increasing frequency and severity of transient  
488 disturbances such as windthrow, wildfire, and insect outbreaks. Effects on forests are driven  
489 largely by consistent increases in tree mortality from these drivers, and variable responses of  
490 recruitment and growth depending on stand-age, disturbance type, and geographic location  
491 (Figure 4). The consequences of changing demographics suggest an increasing constraint in  
492 terrestrial carbon storage due, at least, to the consistent increase in mortality. Any declines in  
493 recruitment or growth, especially when disturbance-recovery cycles are disrupted, will  
494 exacerbate this carbon-cycle constraint. Shifts in other terrestrial radiative forcing terms such as  
495 energy and water budgets are also likely. While well-supported by the literature, data, and  
496 sensitivity analysis (Figure 2), the trends in Figure (4) represent hypotheses to be tested by the  
497 next-generation of observational platforms, both terrestrial and space-borne. Forest management  
498 must ultimately confront the elevated mortality and uncertainty in recruitment and growth when  
499 considering options for sustaining forest benefits to society into the future.

500 **References**

- 501 1. Turner, M. G., Whitby, T. G., Tinker, D. B. & Romme, W. H. Twenty-four years after the  
502 Yellowstone Fires: Are postfire lodgepole pine stands converging in structure and  
503 function? *Ecology* **97**, 1260-1273 (2016).
- 504 2. Hurtt, G. C., Chini, L. P., Frolking, S., Betts, R. A., Feddema, J., Fischer, G., et al.  
505 Harmonization of land-use scenarios for the period 1500–2100: 600 years of global  
506 gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic*  
507 *Change*. <http://doi.org/10.1007/s10584-011-0153-2>. (2011)
- 508 3. Anderson-Teixeira, K. J. et al. Altered dynamics of forest recovery under a changing climate.  
509 *Glob. Chang. Ecol.* **19**, 2001-2021 (2013).
- 510 4. Reichstein, M. et al. Climate extremes and the carbon cycle. *Nature* **500**, 287-295 (2013).
- 511 5. Seidl, R. et al. Forest disturbances under climate change. *Nat. Clim. Change* **7**, 395-402  
512 (2017).
- 513 6. Fisher, R. A. et al. Vegetation demographics in earth system models: a review of progress and  
514 priorities. *Glob. Chang. Ecol.* **24**, 35-54 (2017).
- 515 7. McDowell, N. G. et al. Drivers and mechanisms of tree mortality in moist tropical forests.  
516 *New Phytol.* **219**, 851-869 (2018).
- 517 8. Carnicer, J. et al. Widespread crown condition decline, food web disruption, and amplified  
518 tree mortality with increased climate change-type drought. *Proc. Natl Acad. Sci.* **108**,  
519 1474-1478 (2011).
- 520 9. Senf C. et al. Canopy mortality has doubled in Europe’s temperate forests over the last three  
521 decades. *Nat. Comm.* **9**, 4978 (2018).
- 522 10. Fernández-Martínez, M. et al. Global trends in carbon sinks and their relationships with CO<sub>2</sub>  
523 and temperature. *Nat. Clim. Change* **9**, 73-79 (2019).
- 524 11. Friedlingstein, P. et al. Global Carbon Budget 2019. *Earth System Science Data* **11**, 1783-  
525 1838 (2019).
- 526 12. Ciais, P., Tan, J., Wang, X., Roedenbeck, C., Chevallier, F., Piao, S.L., Moriarty, R., Broquet,  
527 G., Le Quéré, C., Canadell, J.G. and Peng, S., 2019. Five decades of northern land carbon  
528 uptake revealed by the interhemispheric CO<sub>2</sub> gradient. *Nature*, 568(7751), p.221.
- 529 13. Chen JM, W Ju, P Ciais, N Viovy, R Liu, Y Liu, X Lu, Vegetation structural change since  
530 1981 significantly enhanced the terrestrial carbon sink. *Nature Communications* 10 (1), 1-  
531 713.
- 532 14. Pugh, T. A. M. et al. Role of forest regrowth in global carbon sink dynamics. *Proc. Natl*  
533 *Acad. Sci.* **116**, 4382-4387 (2019).
- 534 15. Peñuelas, J., Ciais, P., Canadell, J.G., Janssens, I.A., Fernández-Martínez, M., Carnicer, J.,  
535 Obersteiner, M., Piao, S., Vautard, R. and Sardans, J., 2017. Shifting from a fertilization-  
536 dominated to a warming-dominated period. *Nature Ecology & Evolution*, 1(10), p.1438.



- 537 16. Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G.,  
538 Dong, W., Hu, Z. and Jain, A.K., 2019. Increased atmospheric vapor pressure deficit  
539 reduces global vegetation growth. *Science Advances*, 5(8), p.eaax1396.
- 540 17. Raffa, K. F. et al. Cross-scale drivers of natural disturbances prone to anthropogenic  
541 amplification: the dynamics of bark beetle eruptions. *Bioscience* **58**, 501-517 (2008).
- 542 18. Tippet, M. K., Lepore, C. & Cohen, J. E. More tornadoes in the most extreme US tornado  
543 outbreaks. *Science* **354**, 1419-1423 (2016).
- 544 19. van der Werf, G. R. et al. Global fire emissions estimates during 1997-2016. *Earth System*  
545 *Science Data* **9**, 697-720 (2017).
- 546 20. Sommerfeld, A. et al. Patterns and drivers of recent disturbances across the temperate forest  
547 biome. *Nature Communications* **9**, 4355 (2018).
- 548 21. Houghton, R. A. & Nassikas, A. A. Global and regional fluxes of carbon from land use and  
549 land cover change 1850-2015. *Global Biogeochemical Cycles* **31**, 456-472 (2017).
- 550 22. Foley, J. A. et al. Global consequences of land use. *Science* **309**, 570-574 (2005).
- 551 23. Perring, M. et al. Global environmental change effects on ecosystems: the importance of  
552 land-use legacies. *Glob. Chang. Biol.* **22**, 1361-1371 (2015).
- 553 24. Hartmann H, Schuldt B, Sanders TGM, Macinnis-Ng C, Boehmer HJ, Allen CD, Bolte A,  
554 Crowther TW, Hansen MC, Medlyn BE, Ruehr NK, Anderegg WRL. 2018. Monitoring  
555 global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales  
556 and disciplines to identify global trends of tree mortality as indicators of forest  
557 health'. *New Phytologist* **217**: 984–987.
- 558 25. Pugh, T.A., Arneeth, A., Kautz, M., Poulter, B. and Smith, B., 2019. Important role of forest  
559 disturbances in the global biomass turnover and carbon sinks. *Nature Geoscience*, pp.1-6.
- 560 26. Stovall, A.E., Shugart, H. and Yang, X., 2019. Tree height explains mortality risk during an  
561 intense drought. *Nature Communications*, 10(1), pp.1-6.
- 562 27. Hurtt G, Chini L, Sahajpal R, Frohking S (2017) Harmonization of global land-use change  
563 and management for the period 850-2100. Available at [luh.umd.edu/data.shtml](http://luh.umd.edu/data.shtml). Accessed  
564 October 24th, 2019.
- 565 28. Hansen, M.C., et al. 2013. High-resolution global maps of 21st-century forest cover  
566 change. *Science*, 342(6160), pp.850-853.
- 567 29. Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A. and Hansen, M.C., 2018. Classifying  
568 drivers of global forest loss. *Science*, 361(6407), pp.1108-1111.
- 569 30. Frohking, S. et al. Forest disturbance and recovery: a general review in the context of  
570 spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *J.*  
571 *Geophys. Res.* **114**, G00E02 (2009).

- 572 31. Kautz, M., Meddens, A. J. H., Hall, R. J. & Arneeth, A. Biotic disturbances in Northern  
573 Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest  
574 monitoring and modelling. *Glob. Ecol. Biogeogr.* **26**, 533–552 (2017).
- 575 32. Poulter, B. et al. *The Global Forest Age Dataset and its Uncertainties (GFADv1.1)*  
576 (PANGAEA, 2019); <https://doi.org/10.1594/PANGAEA.897392>
- 577 33. LaDeau, S. L. & Clark, J. S. Rising CO<sub>2</sub> levels and the fecundity of forest trees. *Science* **292**,  
578 95-98 (2001).
- 579 34. Mohan, J. E., Clark, J. S., & Schlesinger, W. H. Long-term CO<sub>2</sub> enrichment of a forest  
580 ecosystem: implications for forest regeneration and succession. *Ecol. Appl.* **17**, 1198-1212  
581 (2007).
- 582 35. Perry, L. G., Shafroth, P. B., Blumenthal, D. M., Morgan, J. A. & LeCain, D. R. Elevated  
583 CO<sub>2</sub> does not offset greater water stress predicted under climate change for native and  
584 exotic riparian plants. *New Phytol.* **197**, 532-543 (2013).
- 585 36. Saintilan, N. & Rogers, L. Woody plant encroachment of grasslands: a comparison of  
586 terrestrial and wetland settings. *New Phytol.* **197**, 1062-1070 (2015).
- 587 37. McMahon, S. M., Parker, G. G. & Miller, D. R. Evidence for a recent increase in forest  
588 growth. *Proc. Natl Acad. Sci. USA* **107**, 3611-3615 (2010).
- 589 38. Camarero, J. J., Gazol, A., Galvan, J. D., Sanguesa-Barreda, G. & Gutierrez, E. Disparate  
590 effects of global-change drivers on mountain conifer forests: warming-induced growth  
591 enhancement in young trees vs. CO<sub>2</sub> fertilization in old trees from wet sites. *Glob. Chang.*  
592 *Biol.* **21**, 738-749 (2015).
- 593 39. Voelker, S. L., Muzika, R. M., Guyette, R. P. & Stambaugh, M. C. Historical CO<sub>2</sub> growth  
594 enhancement declines with age in *Quercus* and *Pinus*. *Ecological Monogr.* **76**, 549-564  
595 (2006).
- 596 40. Penuelas, J., Canadell, J. G. & Ogaya, R. Increased water-use efficiency during the 20<sup>th</sup>  
597 century did not translate into enhanced tree growth. *Global Ecol. Biogeography* **20**, 597-  
598 608 (2011).
- 599 41. van der Sleen, P. et al. No growth stimulation of tropical trees by 150 years of CO<sub>2</sub>  
600 fertilization but water-use efficiency increased. *Nature Geoscience* **8**, 24-28 (2015).
- 601 42. Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., et  
602 al. (2016). No growth stimulation of Canada's boreal forest under half-century of  
603 combined warming and CO<sub>2</sub> fertilization. *PNAS*, 113, E8406–E8414.
- 604 43. Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., et al.  
605 (2015). Long-term decline of the Amazon carbon sink. *Nature*, 519, 344–348.
- 606 44. Gedalof, Z. & Berg, A. Tree ring evidence for limited direct CO<sub>2</sub> fertilization of forests over  
607 the 20<sup>th</sup> century. *Glob. Biogeochem. Cycles* **24**, GB3027 (2010).

- 608 45. Walker, A. P. et al. Decadal biomass increment in early secondary succession woody  
609 ecosystems is increased by CO<sub>2</sub> enrichment. *Nature Communications* **10**, 454 (2019).
- 610 46. Bader, M. K. F. et al. Central European hardwood trees in a high-CO<sub>2</sub> future: synthesis of an  
611 8-year forest canopy CO<sub>2</sub> enrichment project. *J. Ecol.* **101**, 1509-1519 (2013).
- 612 47. Ellsworth, D. S. et al. Elevated CO<sub>2</sub> does not increase eucalypt forest productivity on a low-  
613 phosphorus soil. *Nat. Clim. Change* **7**, 279-282 (2017).
- 614 48. Norby, R. J. et al. Net primary productivity of a CO<sub>2</sub>-enriched deciduous forest and the  
615 implications for carbon storage. *Ecol. Appl.* **12**, 1261-1266 (2002).
- 616 49. McDowell, N. G., Bond, B. J., Dickman, L. T., Ryan, M. G. & Whitehead, D. Relationships  
617 between tree height and carbon isotope discrimination. in *Size- and Age-Related Changes*  
618 *in Tree Structure and Function* (eds Meinzer, F. C. et al.) 255-286 (Springer, Dordrecht,  
619 2011).
- 620 50. Duan, H. et al. Elevated [CO<sub>2</sub>] does not ameliorate the negative effects of elevated  
621 temperature on drought-induced mortality in *Eucalyptus radiata* seedlings. *Plant Cell*  
622 *Environ.* **37**, 1598-1613 (2014).
- 623 51. Allen, C. D., Breshears, D. D. & McDowell, N. G. On underestimation of global  
624 vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene.  
625 *Ecosphere* **6** 1-55 (2015).
- 626 52. Körner, C., 2017. A matter of tree longevity. *Science*, 355(6321), pp.130-131.
- 627 53. Büntgen, U., Krusic, P.J., Piermattei, A., Coomes, D.A., Esper, J., Myglan, V.S., Kirilyanov,  
628 A.V., Camarero, J.J., Crivellaro, A. and Körner, C., 2019. Limited capacity of tree growth  
629 to mitigate the global greenhouse effect under predicted warming. *Nature*  
630 *communications*, 10(1), p.2171.
- 631 54. Bennett, A. C., McDowell, N. G., Allen, C. D. & Anderson-Teixeira, K. J. Larger trees suffer  
632 most during drought in forests worldwide. *Nature Plants* **1**, 15139 (2015).
- 633 55. Yu, K., Smith, W.K., Trugman, A.T., Condit, R., Hubbell, S.P., Sardans, J., Peng, C., Zhu,  
634 K., Peñuelas, J., Cailleret, M. and Levanic, T., 2019. Pervasive decreases in living  
635 vegetation carbon turnover time across forest climate zones. *Proceedings of the National*  
636 *Academy of Sciences*, 116(49), pp.24662-24667.
- 637 56. Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J. & Uhl, E. Wood density reduced while  
638 wood volume growth accelerated in Central European forests since 1870. *For. Ecol.*  
639 *Manage.* **429**, 589-616 (2018).
- 640 57. Trenberth, K. E. et al. Global warming and changes in drought. *Nat. Clim. Change* **4**, 17-22  
641 (2014).
- 642 58. Williams, A. P. et al. Temperature as a potent driver of regional forest drought stress and tree  
643 mortality. *Nat. Clim. Change* **3**, 292-297 (2013).

- 644 59. Tepley, A. J., Thompson, J. R., Epstein, H. E. & Anderson-Teixeira, K. J. Vulnerability to  
645 forest loss through altered postfire recovery dynamics in a warming climate in the Klamath  
646 Mountains. *Glob. Chang. Biol.* **23**, 4117-4132 (2017).
- 647 60. Serra-Diaz, J. M. et al. Disequilibrium of fire-prone forests sets the stage for a rapid decline  
648 in conifer dominance during the 21<sup>st</sup> century. *Scientific Reports* **8**, 6749 (2018).
- 649 61. Uriarte, M, Lasky, J. R., Boukili, V. K. & Chazdon, R. L. A trait-mediated, neighbourhood  
650 approach to quantify climate impacts on successional dynamics of tropical rainforests.  
651 *Funct. Ecol.* **30**, 157-167 (2016).
- 652 62. McDowell, N. G. & Allen, C. D. Darcy's law predicts widespread forest mortality under  
653 climate warming. *Nat. Clim. Change* **5**, 669-672 (2015).
- 654 63. Liu, J. et al. Contrasting carbon cycle response of the tropical continents to the 2015-2016 El  
655 Niño. *Science* **358**, eeam5690 (2017).
- 656 64. Wright, S. J. & Calderón, O. Seasonal, El Niño and longer term changes in flower and seed  
657 production in a moist tropical forest. *Ecol. Lett.* **9**, 35-44 (2006).
- 658 65. Anderson-Teixeira, K. J. et al. Altered dynamics of forest recovery under a changing climate.  
659 *Glob. Chang. Ecol.* **19**, 2001-2021 (2013).
- 660 66. Keenan, T. F. & Riley, W. J. Greening of the land surface in the world's cold regions  
661 consistent with recent warming. *Nat. Clim. Change* **8**, 825-828 (2018).
- 662 67. Forrest, J.R., 2015. Plant–pollinator interactions and phenological change: what can we learn  
663 about climate impacts from experiments and observations?. *Oikos*, **124**(1), pp.4-13.
- 664 68. Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K. & Poschlod, P. Climate change  
665 and plant regeneration from seed. *Glob. Chang. Biol.* **17**, 2145-2161 (2011).
- 666 69. Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. Global warming and the disruption  
667 of plant-pollinator interactions. *Ecol. Lett.* **10**, 710-717 (2007).
- 668 70. Kueppers, L. M. et al. Warming and provenance limit tree recruitment across and beyond the  
669 elevation range of subalpine forest. *Glob. Chang. Biol.* **23**, 2383-2395 (2017).
- 670 71. Hansen, W. D. & Turner, M. G. Origins of abrupt change? Postfire subalpine conifer  
671 regeneration declines nonlinearly with warming and drying. *Ecological Monogr.* **89**,  
672 e01340 (2019).
- 673 72. Adams, H. D. et al. Temperature sensitivity of drought-induced tree mortality portends  
674 increased regional die-off under global-change-type drought. *Proc. Natl Acad. Sci.* **106**,  
675 7063-7066 (2009).
- 676 73. Hember, R. A. et al. Accelerating regrowth of temperate-maritime forests due to  
677 environmental change. *Glob. Clim. Change* **18**, 2026-2040 (2012).
- 678 74. Adams, H.D., Zeppel, M.J., Anderegg, W.R., Hartmann, H., Landhäusser, S.M., Tissue,  
679 D.T., Huxman, T.E., Hudson, P.J., Franz, T.E., Allen, C.D. Anderegg, L.D., et al. 2017. A  
680 multi-species synthesis of physiological mechanisms in drought-induced tree  
681 mortality. *Nature Ecology & Evolution*, **1**(9), p.1285.

- 682 75. Gaylord, M. L. et al. Drought predisposes piñon–juniper woodlands to insect attacks and  
683 mortality. *New Phytol.* **198**, 567-578 (2013).
- 684 76. McDowell, N. G. et al. Multi-scale predictions of massive conifer mortality due to chronic  
685 temperature rise. *Nat. Clim. Change* **6**, 295-300 (2016).
- 686 77. Engelbrecht, B. M. J. & Kursar, T. A. Comparative drought-resistance of seedlings of 28  
687 species of co-occurring tropical woody plants. *Oecologia* **136**, 383-393 (2003).
- 688 78. Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., Huasco,  
689 W.H., Silva-Espejo, J.E., Araujo-Murakami, A., Da Costa, M.C., Rocha, W. and  
690 Feldpausch, T.R., 2015. Drought impact on forest carbon dynamics and fluxes in  
691 Amazonia. *Nature*, 519(7541), p.78.
- 692 79. Erb, K. et al. Land management: data availability and process understanding for global  
693 change studies. *Glob. Chang. Biol.* **23**, 512-533 (2017).
- 694 80. Martin, P. A., Newton, A. C., Pfeifer, M., Khoo, M. & Bullock, J. M. Impacts of tropical  
695 selective logging on carbon storage and tree species richness: A meta-analysis. *For. Ecol.*  
696 *and Manage.* **356**, 224-233 (2015).
- 697 81. Chaudhary, A., Burivalova, Z., Koh, L. P. & Hellweg, S. Impact of forest management on  
698 species richness: global meta-analysis and economic trade-offs. *Scientific Reports* **6**  
699 (2016).
- 700 82. Duveneck, M. J., Thompson, J. R., Gustafson, E. J., Liang, Y. & de Bruijn, A. M. G.  
701 Recovery dynamics and climate change effects to future New England forests.  
702 *LandscapeEcol.* **32**, 1385-1397 (2017).
- 703 83. Thom, D., Rammer, W., Garstenauer, R. & Seidl, R. Legacies of past land use have a  
704 stronger effect on forest carbon exchange than future climate change in a temperate forest  
705 landscape. *Biogeosciences* **15**, 5699-5713 (2018).
- 706 84. Vilen, T. et al. Reconstructed forest age structure in Europe 1950-2010. *For. Ecol. and*  
707 *Manage.* **286**, 203-218 (2012).
- 708 85. Jolly, W. M. et al. Climate-induced variations in global wildfire danger from 1979 to 2013.  
709 *Nature Communications* **6**, 7537 (2015).
- 710 86. Andela, N. et al. A human-driven decline in global burned area. *Science* **356**, 1356-1361  
711 (2017).
- 712 87. Abatzoglou, J. T. & Williams, A. P. Impact of anthropogenic climate change on wildfire  
713 across western US forests. *Proc. Natl Acad. Sci.* **113**, 11770-11775 (2016).
- 714 88. Westerling, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H. & Ryan, M. G.  
715 Continued warming could transform Greater Yellowstone fire regimes by mid-21<sup>st</sup> century.  
716 *Proc. Natl Acad. Sci.* **108**, 13165-13170 (2011).
- 717 89. Bowman, D., Williamson, G. J., Prior, L. D. & Murphy, B. P. The relative importance of  
718 intrinsic and extrinsic factors in the decline of obligate seeder forests. *Glob. Ecol. and*  
719 *Biogeography* **25**, 1166-1172 (2016).

- 720 90. Johnstone, J. F. et al. Changing disturbance regimes, ecological memory, and forest  
721 resilience. *Frontiers in Ecol. and the Environ.* **14**, 369-378 (2016).
- 722 91. Turner, M. G., Braziunas, K. H., Hansen, W. D. & Harvey, B.J. Short-interval severe fire  
723 erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl Acad. Sci.* 201902841  
724 (2019)
- 725 92. Tepley, A. J., Thompson, J. R., Epstein, H. E. & Anderson-Teixeira, K. J. Vulnerability to  
726 forest loss through altered postfire recovery dynamics in a warming climate in the Klamath  
727 Mountains. *Glob. Chang. Biol.* **23**, 4117-4132 (2017).
- 728 93. Kitzberger, T. et al. Fire-vegetation feedbacks and alternative states: common mechanisms of  
729 temperate forest vulnerability to fire in southern South America and New Zealand. *New  
730 Zealand J. of Bot.* **54**, 247-272 (2016).
- 731 94. Lugo, A. E. Visible and invisible effects of hurricanes on forest ecosystems: an international  
732 review. *Austral Ecol.* **33**, 368-398 (2008).
- 733 95. Balaguru, K., Foltz, G. R. & Leung, L. R. Increasing magnitude of hurricane rapid  
734 intensification in the central and eastern tropical Atlantic. *Geophys. Research Lett.* **45**,  
735 4238-4247 (2018).
- 736 96. Diffenbaugh, N. S., Scherer, M. & Trapp, R. J. Robust increases in severe thunderstorm  
737 environments in response to greenhouse forcing. *Proc. Natl Acad. Sci.* **110**, 16361-16366  
738 (2013).
- 739 97. Uriarte, M., Canham, C. D., Thompson, J. & Zimmerman, J. K. A neighborhood analysis of  
740 tree growth and survival in a hurricane-driven tropical forest. *Ecol. Monogr.* **74**, 591-614  
741 (2004).
- 742 98. Gardiner, B., Berry, P. & Moulia, B., Wind impacts on plant growth, mechanics and  
743 damage. *Plant Science*, **245**, 94-118 (2016).
- 744 99. Uriarte, M. et al. Natural disturbances and human land use as determinants of tropical forest  
745 dynamics: results from a forest simulator. *Ecol. Monogr.* **79**, 423-443 (2009).
- 746 100. Comita, L.S. et al. Abiotic and biotic drivers of seedling survival in a hurricane-impacted  
747 tropical forest. *J. Ecol.* **97**, 1346-1359 (2009).
- 748 101. Uriarte, M. et al. Multidimensional trade-offs in species responses to disturbance:  
749 implications for diversity in a subtropical forest. *Ecology* **93**, 191-205 (2012).
- 750 102. Flynn, D. B. F. et al. Hurricane disturbance alters secondary forest recovery and introduced  
751 species dynamics. *Biotropica* **42**, 149-157 (2010).
- 752 103. Yanoviak, S.P., Gora, E.M., Bitzer, P.M., Burchfield, J.C., Muller-Landau, H.C., Detto,  
753 M., Paton, S. and Hubbell, S.P., 2019. Lightning is a major cause of large tree mortality in  
754 a lowland neotropical forest. *New Phytologist*.
- 755 104. Seidl, R., Schelhaas, M. J., Rammer, W. & Verkerk, P. J. Increasing forest disturbances in  
756 Europe and their impact on carbon storage. *Nat. Clim. Change* **4**, 806-810 (2014).

- 757 105. Kautz, M., Meddens, A. J., Hall, R. J. & Arneeth, A. Biotic disturbances in Northern  
758 Hemisphere forests—a synthesis of recent data, uncertainties and implications for forest  
759 monitoring and modelling. *Glob. Ecol. Biogeography* **26**, 533-552 (2017).
- 760 106. Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A. and Kolb, T.E., 2015.  
761 Responses of tree-killing bark beetles to a changing climate. *Climate change and insect*  
762 *pests*, **7**, pp.173-201.
- 763 107. Shurman, J. S. et al. Large-scale disturbance legacies and the climate sensitivity of primary  
764 *Picea abies* forests. *Glob. Chang. Biol.* **24**, 2169-2181 (2018).
- 765 108. Rosenberger, D. W., Venette, R. C. & Aukema, B. H. Development of an aggressive bark  
766 beetle on novel hosts: Implications for outbreaks in an invaded range. *J. Appl. Ecol.* **55**,  
767 1526-1537 (2018).
- 768 109. Seidl, R. et al. Invasive alien pests threaten the carbon stored in Europe's forests. *Nature*  
769 *Communications* **9**, 1626 (2018).
- 770 110. Johnson, D. M. et al. Climatic warming disrupts recurrent Alpine insect outbreaks. *Proc.*  
771 *Natl Acad. Sci.* **107**, 20576-20581 (2010).
- 772 111. di Porcia e Brugnera, M., Meunier, F., Longo, M., Krishna Moorthy, S.M., De  
773 Deurwaerder, H., Schnitzer, S.A., Bonal, D., Faybishenko, B. and Verbeeck, H., 2019.  
774 Modeling the impact of liana infestation on the demography and carbon cycle of tropical  
775 forests. *Global Change Biology*, 25(11), pp.3767-3780.
- 776 112. Pureswaran, D. S., Johns, R., Heard, S. B. & Quiring, D. Paradigms in eastern spruce  
777 budworm (Lepidoptera: Tortricidae) population ecology: a century of debate. *Entomology*  
778 **45**, 1333-1342 (2016).
- 779 113. Virgin, G. V. J. & MacLean, D. A. Five decades of balsam fir stand development after  
780 spruce budworm-related mortality. *For. Ecol. and Manage.* **400**, 129-138, (2017).
- 781 114. Macek, M. et al. Life and death of *Picea abies* after bark-beetle outbreak: ecological  
782 processes driving seedling recruitment. *Ecol. Appl.* **27**, 156-167 (2017).
- 783 115. Laurance, W.F., Delamônica, P., Laurance, S.G., Vasconcelos, H.L. and Lovejoy, T.E.,  
784 2000. Conservation: rainforest fragmentation kills big trees. *Nature*, 404(6780), p.836.
- 785 116. Lindenmayer, D.B., Laurance, W.F. and Franklin, J.F., 2012. Global decline in large old  
786 trees. *Science*, 338(6112), pp.1305-1306.
- 787 117. Peterson, C.J., 2000. Catastrophic wind damage to North American forests and the potential  
788 impact of climate change. *Science of the total Environment*, 262(3), pp.287-311.
- 789 118. Canham, C.D., Papaik, M.J. and Latty, E.F., 2001. Interspecific variation in susceptibility to  
790 windthrow as a function of tree size and storm severity for northern temperate tree  
791 species. *Canadian Journal of Forest Research*, 31(1), pp.1-10.

- 792 119. Boone, Aukema, Bohlmann, Carroll, and Raffa (2011) Efficacy of tree defense physiology  
793 varies with bark beetle population density: a basis for positive feedback in eruptive  
794 species. *Can J Forest Research* 6: 1174-1188.
- 795 120. McDowell, N. G. et al. Predicting chronic climate-driven disturbances and their mitigation.  
796 *Trends Ecol. Evol.* **33**, 15-27 (2018).
- 797 121. Johnson, D.J., et al. Climate sensitive size-dependent survival in tropical trees. *Nature*  
798 *Ecology and Evolution* doi.org/10.1038/s41559-018-0626-z (2018)
- 799 122. Pretzsch, H., Biber, P., Schütze, G., Uhl, E. and Rötzer, T., 2014. Forest stand growth  
800 dynamics in Central Europe have accelerated since 1870. *Nature communications*, 5,  
801 p.4967.
- 802 123. Nicotra, A. B. et al. Plant phenotypic plasticity in a changing climate. *Trends in Plant Sci.*  
803 **15**, 684-692 (2010).
- 804 124. Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. & Curtis-McLane, S. Adaptation,  
805 migration or extirpation: climate change outcomes for tree populations. *Evol. Appl.* **1**, 95-  
806 111 (2008).
- 807 125. Angert, A. L. et al. Do species' traits predict recent shifts at expanding range edges? *Ecol.*  
808 *Lett.* **14**, 677-689 (2011).
- 809 126. Miller, K.M. and McGill, B.J., 2018. Land use and life history limit migration capacity of  
810 eastern tree species. *Glob. Ecol. Biogeog.*, 27(1), pp.57-67  
811
- 812 127. Slot, M. & Katajima, K. General patterns of acclimation of leaf respiration to elevated  
813 temperatures across biomes and plant types. *Oecologia* **177**, 885-900 (2015).
- 814 128. Rieu, P. B., Twell, D. & Frion, N. Pollen development at high temperature: from  
815 acclimation to collapse. *Plant Physiology* **173**, 1967-1976 (2017).
- 816 129. Adams, H. D. et al. Experimental drought and heat can delay phenological development and  
817 reduce foliar and shoot growth in semiarid trees. *Glob. Chang. Biol.* **21**, 4210-4220 (2015).
- 818 130. Grossiord, C. et al. Warming combined with more extreme precipitation regimes modifies  
819 the water sources used by trees. *New Phytol.* **213**, 584-596 (2017).
- 820 131. McLachlan, J. S., Hellmann, J. J. & Schwartz, M. W. A framework for debate of assisted  
821 migration in an era of climate change. *Conservation Biol.* **21**, 297-302 (2007).
- 822 132. Lloret, F., Escudero, A., Iriondo, J. M., Martínez-Vilalta, J. & Valladares, F. Extreme  
823 climatic events and vegetation: the role of stabilizing processes. *Glob. Chang. Biol.* **18**,  
824 797-805 (2012).
- 825 133. Kemp KB, Higuera PE, Morgan P (2015) Fire legacies impact conifer regeneration across  
826 environmental gradients in the U.S. northern Rockies. *Landsc Ecol* 1-18. 133. Isbell, F. et  
827 al. Biodiversity increases the resistance of ecosystem productivity to climate extremes.  
828 *Nature* **526**, 574-577 (2015).



- 829 134. Thom, D., Rammer, W. & Seidl, R. The impact of future forest dynamics on climate:  
830 interactive effects of changing vegetation and disturbance regimes. *Ecol. Monogr.* **87**, 665-  
831 684 (2017).
- 832 135. Powell, T. L. et al. Variation in hydroclimate sustains tropical forest biomass and promotes  
833 functional diversity. *New Phytol.* **219**, 932-946 (2018).
- 834 136. Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of  
835 forests. *Science* **320**, 1444-1449 (2008).
- 836 137. Luysaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P.  
837 and Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature*, 455(7210), p.213.
- 838 138. Harmon, M.E., 2001. Carbon sequestration in forests: addressing the scale question. *Journal*  
839 *of Forestry*, 99(4), pp.24-29.
- 840 139. Pretzsch, H., Biber, P., Schütze, G., Uhl, E. and Rötzer, T., 2014. Forest stand growth  
841 dynamics in Central Europe have accelerated since 1870. *Nature Communications*, 5,  
842 p.4967.
- 843 140. Campbell, J.E., Berry, J.A., Seibt, U., Smith, S.J., Montzka, S.A., Launois, T., Belviso, S.,  
844 Bopp, L. and Laine, M., 2017. Large historical growth in global terrestrial gross primary  
845 production. *Nature*, 544(7648), pp.84-87.
- 846 141. Randerson, J. T. et al. The impact of boreal forest fire on climate warming. *Science* **314**,  
847 1130-1132 (2006).
- 848 142. Lee, X., et al. Observed increase in local cooling effect of deforestation at higher latitudes.  
849 *Science* **479**, 384-387 (2011).
- 850 143. Devaraju, N., Bala, G. & Modak, A. *Effects of large-scale deforestation on precipitation in*  
851 *the monsoon regions: Remote versus local effects. Proceedings of the National Academy of*  
852 *Sciences* **112**, 201423439 (2015).
- 853 144. Lejeune, Q., Davin, E. L., Guillod, B. P. & Seneviratne, S. I. *Influence of Amazonian*  
854 *deforestation on the future evolution of regional surface fluxes, circulation, surface*  
855 *temperature and precipitation. Climate Dynamics* **44**, 2769–2786 (2015).
- 856 145. Le Page, Y., Morton, D., Bond-Lamberty, B., Pereira, J.M.C. and Hurtt, G., 2015.  
857 HESFIRE: a global fire model to explore the role of anthropogenic and weather  
858 drivers. *Biogeosciences*
- 859 146. McDowell, N. G. et al. Evaluating theories of drought-induced vegetation mortality using a  
860 multimodel–experiment framework. *New Phytol.* **200**, 304-321 (2013).
- 861 147. Lawrence, D., Hurtt, G., Arneth, A., Brovkin, V., Calvin, K., Jones, A., Jones, C.,  
862 Lawrence, P., Noblet-Ducoudré, N., Pongratz, J., Seneviratne, S., Shevliakova,  
863 E. (2016). The Land Use Model Intercomparison Project (LUMIP) contribution to CMIP6:  
864 rationale and experimental design. *Geoscientific Model Development* 9(9), 2973 - 2998.
- 865 148. Simard, M., Pinto, N., Fisher, J. B. & Baccini, A. Mapping forest canopy height globally  
866 with spaceborne lidar. *J. Geophys. Research: Biogeosciences* **116**, G4 (2011).

- 867 149. Lehsten, V., Mischurow, M., Lindström, E., Lehsten, D. & Lischke, H. LPJ-GM 1.0:  
868 simulating migration efficiently in a dynamic vegetation model. *Geosci. Model Dev.* **12**,  
869 893-908 (2019).
- 870 150. Smith, B., Prentice, I. C. & Sykes, M. T. Representation of vegetation dynamics in the  
871 modelling of terrestrial ecosystems: comparing two contrasting approaches within  
872 European climate space. *Glob. Ecol. Biogeog.* **10**, 621-637 (2001).
- 873 151. Fisher, R. A. et al. Taking off the training wheels: the properties of a dynamic vegetation  
874 model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development* **8**,  
875 3593-3619 (2015).
- 876 152. Chen, Y. et al. Simulating Damage for Wind Storms in the Land Surface Model  
877 ORCHIDEE-CAN (Revision 4262). *Geosci. Model Dev.* **8**, 3593-3619 (2018).
- 878 153. Henkel, T. K., Chambers, J. Q. & Baker, D. A. Delayed tree mortality and Chinese tallow  
879 (*Triadica sebifera*) population explosion in a Louisiana bottomland hardwood forest  
880 following Hurricane Katrina. *For. Ecol. Manage.* **378**, 222-232 (2016).
- 881 154. Roccaforte, J. P. et al. Delayed tree mortality, bark beetle activity, and regeneration  
882 dynamics five years following the Wallow Fire, Arizona, USA: Assessing trajectories  
883 towards resiliency. *For. Ecol. Manage.* **428**, 20-26 (2018).
- 884 155. Kennedy, D. et al. Implementing plant hydraulics in the Community Land Model, version 5.  
885 *J. Adv. Modeling Earth Systems* **11**, 485-513 (2019).
- 886 156. Grubb, P.J. The maintenance of species-richness in plant communities: the importance of  
887 the regeneration niche. *Biol. Rev.* **52**, 107-145 (1977).
- 888 157. Amiro, B. D. et al. Ecosystem carbon dioxide fluxes after disturbance in forests of North  
889 America. *J. Geophys. Research: Biogeosciences* **115**, G4 (2010).
- 890 158. Hicke, J. A. et al. Effects of biotic disturbances on forest carbon cycling in the United States  
891 and Canada. *Glob. Chang. Biol.* **18**, 7-34 (2012).
- 892 159. Grime, J. P. *Plant strategies and vegetation processes* (University of Michigan, Ann Arbor,  
893 1979) .
- 894 160. Jentsch, A. and White, P. A theory of pulse dynamics and disturbance in ecology. *Ecol.*  
895 100(7) p.e02734.
- 896 161. Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N.,  
897 Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J.,  
898 Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P.,  
899 Kassem, K. R. 2001. Terrestrial ecoregions of the world: a new map of life on Earth.  
900 *Bioscience* 51(11):933-938.

901

902

903 **Acknowledgements:** This manuscript was derived from the Department of Energy  
904 Workshop “Disturbance and vegetation dynamics in Earth System Models” held in March  
905 2018 in Washington DC. Support was provided as follows: **NGM** the Department of  
906 Energy’s Next Generation Ecosystem Experiment-Tropics (NGEE-Tropics) and Pacific  
907 Northwest National Lab’s LDRD program, BA McIntire-Stennis MIN-17-095, **CDA** the U.S.  
908 Geological Survey’s Ecosystems and Land Resources mission areas, **MGT** the Joint Fire Science  
909 Program (16-3-01-4) and the University of Wisconsin-Madison Vilas Trust, **JL** sabbatical  
910 fellowship support from sDiv, the Synthesis Centre of iDiv (DFG FZT 118), **CX** DOE's NGEE-  
911 Tropics and the University of California’s Laboratory Fees Research Program (grant no. LFR-  
912 18-542511), **TP** the European Research Council (ERC) under the European Union’s Horizon  
913 2020 research and innovation programme (grant agreement no. 758873, TreeMort), Paper  
914 number 43 of the Birmingham Institute of Forest Research, **BBL** PNNL’s LDRD program, **GH**  
915 **and BP** the NASA Carbon Monitoring System and NASA Interdisciplinary Science Programs.  
916 Oak Ridge National Laboratory is operated by UT-Battelle, LLC, under contract DE-AC05-  
917 00OR22725 to the United States Department of Energy. NM conceived of the manuscript layout;  
918 all authors contributed to the literature survey and writing, TP with BP and GH conducted the  
919 global analyses. All data are available 10.5281/zenodo.3698178

920

921

922 **Box 1 Vegetation dynamics definitions**

923 We focus on three main plant demographic processes: recruitment, growth, and mortality.

924 Recruitment (including reproduction) results in the seedling and sapling composition of a plant  
925 community following disturbance (156). Growth from sapling to mature plants results in  
926 development of mature forests and includes competitive processes. Mortality is a key rate  
927 controlling carbon storage and species composition in a plant community and is a dominant  
928 demographic rate during a pulse-disturbance (157,158).

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

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

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

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

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

940 **Disturbance.** The destruction of live plant biomass in a discrete event (159,160).

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

943 **Growth.** The rate of biomass production over time at the individual or ecosystem scale (i.e. Net  
944 Primary Production grams C m<sup>-2</sup> yr<sup>-1</sup>).

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

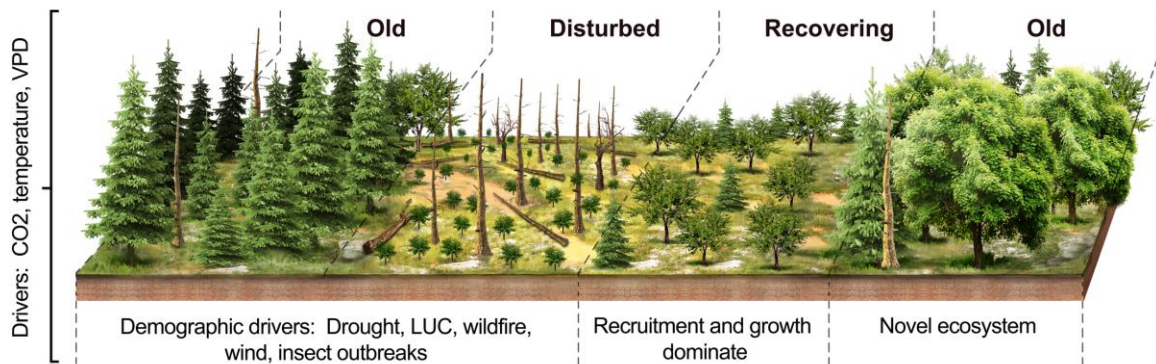
947 **Mortality.** Defined herein as the complete loss of a plants' ability to reproduce and ultimately  
948 loss of cellular metabolism.

949 **Recruitment.** The rates of transition of plants from one size class into another (typically in units  
950 of individuals m<sup>-2</sup> yr<sup>-1</sup>). Recruitment results from the birth and growth of individuals. Herein we  
951 consider recruitment from the stage of seed dispersal through seedling growth into the sapling  
952 stage.

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

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

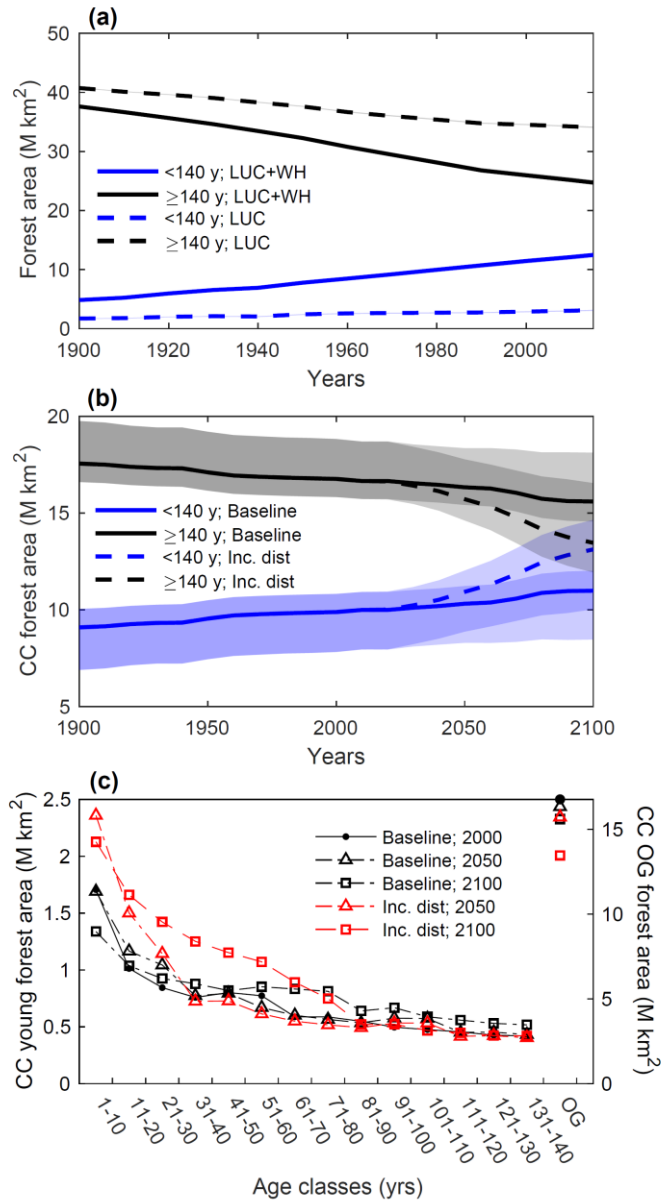
957



959

960 **Figure 1. A conceptual diagram of the components of forest dynamics and disturbances**  
 961 **that drive them.** In the far-left panel, a mature ecosystem is responsive primarily to localized  
 962 mortality, and the primary drivers of demography are chronically changing variables such as  
 963 CO<sub>2</sub>, temperature, and *VPD*. The system is disturbed in the second panel, due to fire, insect  
 964 outbreak, or another large-scale perturbation that removes much of the overstory trees, and  
 965 species adapted to rapid post-disturbance recruitment become established. In the third panel  
 966 recruitment and growth dominate demographic processes, with mortality increasing over time as  
 967 competition leads to self-thinning. In the last panel, a mature ecosystem is dominated by species  
 968 that have replaced the original community in response to chronic environmental changes, leading  
 969 to a novel ecosystem.

970



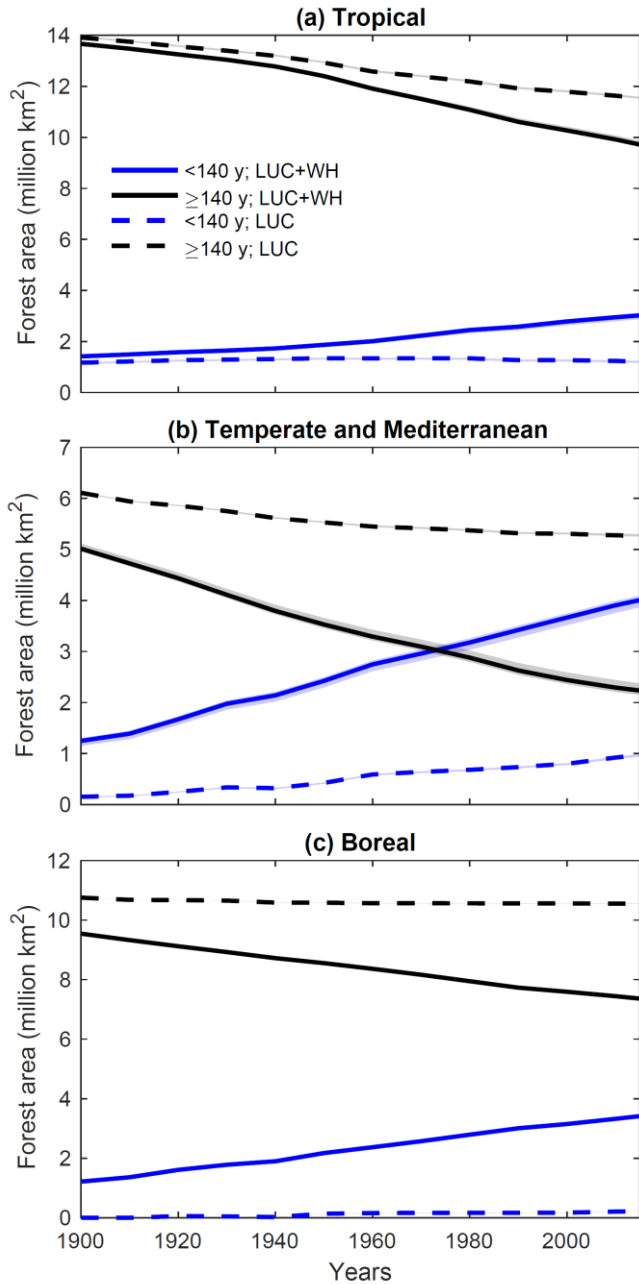
**Figure 2. (a) Human activities have increased the amount of young forest area (stands < 140 years old) over the 20<sup>th</sup> century as a result of both land-use change (LUC) and wood harvest (WH). Forest stand age distribution was reconstructed using forest-cover transitions from LUHv2, initialized using forest cover fractions in 1750 and incrementing forest cover each year, tracking the age of forest up to 140 years. Solid lines show the effect of LUC and WH, dashed lines 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 constant at observed 2001-2014 values throughout. In the *Inc. dist* scenario (dashed lines), disturbance rates are incremented linearly to 200% of the 2001-2014 values over the period 2015 to 2050 and held constant at that level thereafter. The underlying LUC scenario is GCAM RCP 3.4 that includes land-based mitigation for CO<sub>2</sub> emissions. Results are presented for closed-canopy forests only (25), which is why total forest area is lower between (a) and (b), as non-LUC disturbance rate information is not currently available for**

1007 open-canopy forests. The shaded areas in panels **a** and **b** indicate the effect of assuming that disturbances  
 1008 are five times more likely to affect the youngest forests versus old-growth, or vice versa, as opposed to an  
 1009 even probability across ages (solid lines). The apparent large dampening of this assumption in **a** vs **b** is  
 1010 primarily due to the different y-scales. **(c) Changes in the disturbance regime propagate through**  
 1011 **forest age structure at decadal time scales.** Closed-canopy young (<140 years old) forest area is  
 1012 shown on the left-hand y-axis. Old-growth (>140 years old; OG) forest area is shown on the right axis  
 1013 (same units) and refers to the data points in the upper right-hand of the panel. Scripts used and additional  
 1014 methods can be accessed at [https://github.com/pughtam/AgeClassReconst\\_rel.git](https://github.com/pughtam/AgeClassReconst_rel.git).

1015

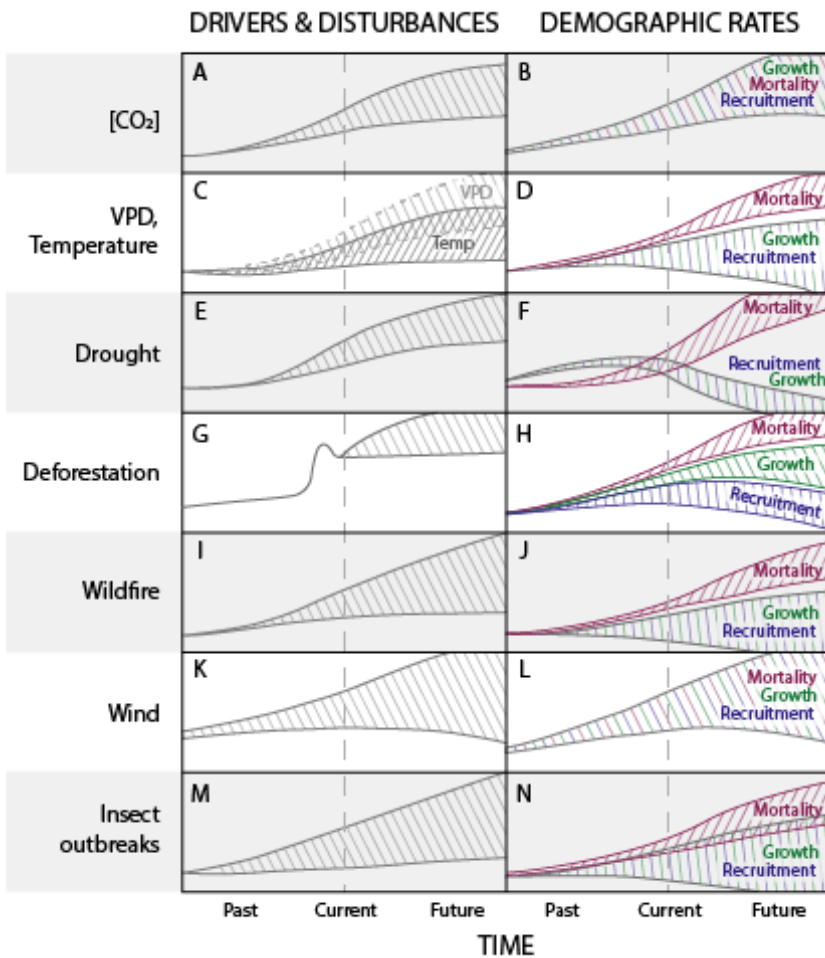
1016

1017 Figure 3. **Human activities have increased the amount of young forest area irrespective of biome.**  
 1018 As for Figure 2a, but broken down by biome<sup>161</sup>.  
 1019



1020

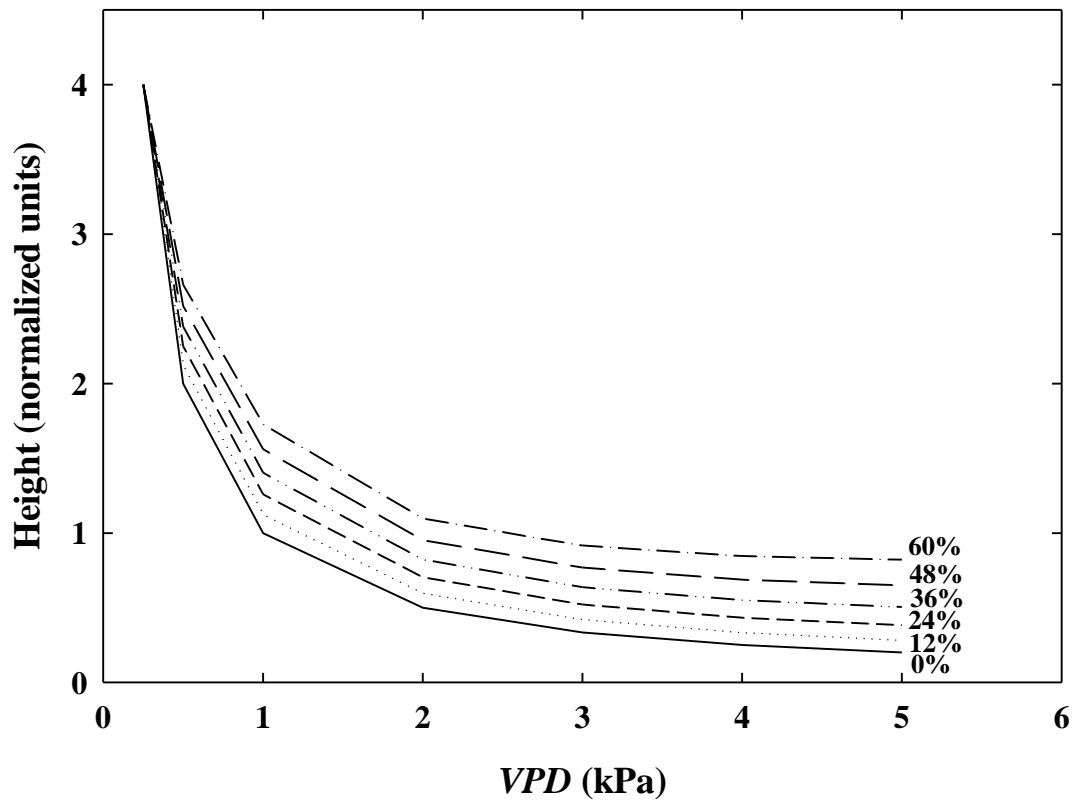
1021



1022

1023 **Figure 4. Drivers, disturbances, and demographics are changing both historically and into**  
1024 **the future.** A graphical summary of the literature evidence of changing drivers and disturbances  
1025 (left-hand column) and subsequent demographic rates (right-hand column). Shown are the  
1026 chronically changing drivers A) CO<sub>2</sub>, C) VPD and temperature and the more transient  
1027 disturbances of E) drought (low precipitation), G) deforestation, I) wildfire, K) wind, and M)  
1028 insect outbreaks. Each driver or disturbances' corresponding demographic responses (shown as  
1029 carbon fluxes per area<sup>-1</sup> time<sup>-1</sup>) are shown on the right-hand panels.  
1030





1031

1032 **Figure 5. Rising VPD forces declines in potential plant stature.** Predictions of plant height in  
 1033 response to rising VPD from the hydraulic corollary to Darcy's law. The equation is  $h =$   
 1034  $A_s * k_s * (\Delta\Psi) / G * A_l * VPD$ , where  $h$  is height,  $A_s$  is sapwood area,  $k_s$  is specific conductivity,  $\Delta\Psi$  is  
 1035 the leaf to soil water potential gradient,  $G$  is stomatal conductance, and  $A_l$  is leaf area<sup>53</sup>. The  
 1036 different lines represent different levels of acclimation of  $A_s$ ,  $k_s$ ,  $\Delta\Psi$ ,  $G$ , and  $A_l$ , all allowed to  
 1037 adjust simultaneously from 0 to 60% from their initial values. In the case of  $G$  it is assumed to  
 1038 decrease due to rising atmospheric CO<sub>2</sub>. Acclimation can help, but not completely mitigate, the  
 1039 impacts of rising VPD on plant size.

1040

1041