1	Long-term impacts of wildfire and logging on forest soils
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35 ABSTRACT

Soils are a fundamental component of terrestrial ecosystems, and play key roles in 36 biogeochemical cycles and the ecology of microbial, plant and animal communities. Global 37 increases in the intensity and frequency of ecological disturbances are driving major changes 38 in the structure and function of forest ecosystems, yet little is known about the long-term 39 impacts of disturbance on soils. Here we show that natural disturbance (fire) and human 40 disturbances (clearcut logging and post-fire salvage logging) can significantly alter the 41 42 composition of forest soils for far longer than previously recognized. Using extensive sampling across a multi-century chronosequence in some of the tallest and most carbon-dense 43 44 forests worldwide (southern Australian, mountain ash (Eucalyptus regnans) forests), we provide compelling evidence that disturbance impacts on soils are evident up to least eight 45 decades after disturbance, and potentially much longer. Relative to long-undisturbed forest 46 47 (167 years old), sites subject to multiple fires, clearcut logging or salvage logging were characterized by soils with significantly lower values of a range of ecologically important 48 measures at multiple depths, including available phosphorus and nitrate. Disturbance impacts 49 on soils were most pronounced on sites subject to compounding perturbations, such as 50 multiple fires and clearcut logging. Long-lasting impacts of disturbance on soil can have 51 major ecological and functional implications. 52

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Natural disturbances such as fire are major drivers of the structure and function of terrestrial
ecosystems worldwide, and influence key biotic and abiotic patterns and processes1–4.
Climate change and increases in human disturbances, such as logging, have altered natural
fire regimes, resulting in an increase in large-scale fires across terrestrial ecosystems over the
past few decades1,5,6. These compounding disturbances are driving significant changes in
the structure and function of ecosystems7,8.

While the effects of natural and human disturbances are well characterized for biotic 65 communities, little is known about their long-term impacts on the abiotic components of soil 66 environments, despite their importance for ecosystem function9–11. Soils play key roles in 67 (1) the demography, interspecific interactions and community structure of plant and microbial 68 communities, (2) biogeochemical cycles, (3) biomass production and environmental filtering 69 70 and buffering, and (4) climate change mitigation through the sequestration of carbon and other greenhouse gases12–17. Limited knowledge about the impacts of disturbances on soils 71 hinders the ability to predict the long-term responses of ecosystems to increasing natural and 72 human disturbance10,16,18,19. In a period of rapid, global environmental and climatic 73 change during which disturbances such as fire and anthropogenic landuse changes are 74 75 predicted to increase and intensify, it is critical to quantify their respective impacts on soils to facilitate management and planning3,20,21. 76

Here, we quantify the impact of natural disturbance (fire) and human disturbances (clearcut
and post-fire salvage logging) on soil measures across a multi-century chronosequence in the
mountain ash forests of southeastern Australia. Typical fire regimes in these forests are
characterized by infrequent, high-intensity fires that have historically occurred every 75–150
years22. However, the frequency of these fires has increased and some areas have
experienced multiple high-severity fires over the past century, including those in 1926, 1932,
1939, 1983 and most recently in 20098. Fires in 1939, 1983 and 2009 burned large areas of

mountain ash forest (> 150,000 ha in 1939, 17,250 ha in 1983 and 53,500 ha in 200923). In
addition, these forests have been subject to clearcut logging since the 1970s and post-fire
salvage logging since the late 1930s8,24. Climatic changes within southeastern Australia are
predicted to increase the prevalence of hot and dry conditions over the next few decades25.
These predictions, coupled with the increasing coverage of high-severity- fire-prone logging
regrowth (aged 7–35 years) will potentially increase the frequency of high-intensity standreplacing fires in these forests20,21,25,26.

91 From 729 soil cores collected across 81 sites, we used generalized linear models to

92 investigate the influence of nine disturbance history categories varying in stand age (8, 34, 78

and 167 years), fire frequency (0, 1, 2 and 3 fires in recorded history since 1850), clearcut

94 and salvage logging events and environmental variables on measures of organic carbon,

95 macro soil nutrients (ammonium nitrogen (ammonium), nitrate nitrogen (nitrate), available

96 phosphorus, available potassium, sulfur), micronutrients (boron (hot CaCl2), diethylene

97 triamine pentaacetic acid (DTPA) iron, DTPA manganese, DTPA copper, DTPA zinc),

98 exchangeable cations (exc.) (exc. aluminium, exc. calcium, exc. magnesium, exc. Potassium

99 and exc. sodium), soil chemistry (pH(CaCl2), electrical conductivity (conductivity)),

100 sand/silt/clay (%) and soil moisture (% dry mass) (gravimetric moisture content) from two

101 depths of forest soil (0-10 cm and 20-30 cm)27.

102 Multi-decadal disturbance impacts on forest soils

We discovered that fire, clearcut logging and salvage logging significantly influenced soil
measures in the 0–10 cm and 20–30 cmlayers of soil. Significant effects were evident up to at

- least eight decades post-fire and three decades post-clearcut logging (P < 0.001 to P = 0.05)
- 106 (Supplementary Tables 3 and 4). For instance, nitrate and available phosphorus were
- significantly lower across the chronosequence at sites burnt and/or logged and aged 78, 34

and 8 years old, relative to long-undisturbed sites (P < 0.001 to P = 0.05) (Fig. 1,

109 Supplementary Fig. 1 and Supplementary Table 3 and 4).







121 Relative to sites burnt once, forest stands burnt twice in recorded history (since 1850) were characterized by significantly lower levels of ammonium, nitrate, organic carbon, available 122 phosphorus, sulfur, DTPA iron, boron and exchangeable aluminium cations in the 0-10 cm 123 layer of soil (P < 0.001 to P = 0.02), and ammonium, organic carbon, available phosphorus, 124 exchangeable potassium and aluminum cations, and soil moisture in the lower layer of soil 125 (20-30 cm depth) (P < 0.001 to P = 0.04) (Fig. 2 and Supplementary Tables 5 and 6). In 126 contrast, soil pH(CaCl2) was significantly higher in the 0–10 cm layer of soil, relative to sites 127 burnt once (P = 0.01) (Supplementary Table 5). 128

In forest stands burnt three times, ammonium, sulfur, exchangeable aluminium cations and 129 DTPA iron were significantly lower in the top 0-10 cm of soil, relative to sites subject to one 130 fire (P < 0.001 to P = 0.05) (Fig. 2 and Supplementary Tables 5 and 6). In contrast, available 131 potassium and pH(CaCl2) were significantly higher in the 0-10 cm of soil (P < 0.001) and 132 exchangeable cations were significantly higher in the 0-10 cm and 20-30 cm layers of soil, 133 relative to sites burnt once (P < 0.001 to P = 0.02) (Fig. 2 and Supplementary Tables 5 and 6). 134 Sites subject to compounding disturbances, such as multiple fires and clearcut logging or 135 post-fire salvage logging, consistently had the lowest values of soil measures across the 136 chronosequence, relative to long-undisturbed sites (P < 0.05) (Fig. 1 and Supplementary 137 Tables 3 and 4). Specifically, clearcut logging resulted in significantly lower levels of 138 ammonium, nitrate, available phosphorus, available potassium, DTPA zinc, DTPA copper, 139 boron and exchangeable cations in the 0-10 cm of soil (P < 0.001 to P = 0.04), and available 140

141 potassium, ammonium, organic carbon, available phosphorus, exchangeable cations and soil

142 moisture in the lower 20–30 cm layer of soil, relative to unlogged forest (P < 0.001 to P =

143 0.04) (Supplementary Tables 5 and 6). Furthermore, clearcut logged sites had a significantly

higher sand content in the 0-10 cm of soil, compared to unlogged sites (P = 0.01). Salvage

145 logged sites had significantly lower ammonium, DTPA iron, boron and exchangeable cations

146	in the 0–10 cm layer of soil (P < 0.001 to P = 0.04), and exchangeable sodium and boron in
147	the 20–30 cm layer of soil, relative to unlogged forest (P < 0.001) (Fig. 2 and Supplementary
148	Table 5 and 6) (see Supplementary Information for further details).
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Fig. 2 | The pervasive impacts of multiple fires and logging on soil measures. Coefficients 160 from generalized linear models of each soil measure with respect to disturbance type, 161 parent rock and Australian soil classification, elevation, slope and the abundance of 162 163 dominant plant life forms (parent rock type, Australian soil classification, elevation, slope and the abundance of dominant plant life forms not displayed here). Model factors = 164 165 number of fires, clearcut and salvage logging, parent rock and Australian soil classification; 166 covariates = elevation, slope and the abundance of dominant plant life forms. Note that available phosphorus levels in the 0–10 cm were log-transformed, and in the 20–30 cm were 167 square-root transformed. A complete list of the influence of the factors and covariates 168 169 generated using these models is provided in Supplementary Tables 5 and 6. 170 171

173 Historical impacts on soil measures

By analysing a subset of our data with identical stand age (8 years) but with different prior 174 disturbance histories, we demonstrate that fire and clearcut logging significantly influence 175 key soil measures even when controlling for age/successional effects. Sites clearcut in 2009 176 were characterized by significantly lower concentrations of nitrate, available phosphorus and 177 available potassium in the top 0-10 cm layer of soil (P < 0.001 to P = 0.03), and ammonium, 178 organic carbon, available phosphorus and available potassium in the 20-30 cm of soil, 179 relative to similarly aged unlogged sites (P < 0.001 to P = 0.04). Sites burnt twice (last in 180 2009) resulted in significantly lower levels of available phosphorus and sulfur in the 0–10 cm 181 of soil (P = 0.02 to P = 0.03) and of ammonium, organic carbon and available potassium in 182 the 20–30 cm of soil, relative to similarly aged sites burnt once (P < 0.001 to P = 0.02). Sites 183 184 burnt three times (last in 2009) had significantly lower levels of sulfur in the 0-10 cm of soil (P < 0.01), and higher levels of available potassium, relative to similarly aged sites burnt 185 once (P < 0.001) (Fig. 3 and Supplementary Table 7). 186



Fig. 3 | the impact of fire and logging in similarly aged forests on soil measures. Coefficients 189 from generalized linear models of each soil measure in similarly aged sites (last disturbed in 190 2009) with respect to disturbance type, parent rock and Australian soil classification, 191 elevation, slope and the abundance of dominant plant life forms. Model factors = number of 192 fires, clearcut and salvage logging, parent rock and Australian soil classification; covariates = 193 elevation, slope and the abundance of dominant plant life forms. Note that nitrate levels in 0-194 10 cm were square-root transformed. A complete list of the influence of the factors and 195 covariates generated using these models is provided in Supplementary Table 7. 196

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199 Implications of long-term impacts on forest soils

We discovered that both natural and human disturbances can have long-term effects on forest 200 soils. Soil temperatures can exceed 500 °C during high-intensity fires and result in the loss of 201 soil nutrients, organic carbon and organic matter through volatilization and postfire erosion, 202 which can reduce soil fertility10,18,28,29. Consistent with other studies, we found multiple 203 204 fires resulted in lower levels of soil measures, across both soil depths, relative to longundisturbed forests10. In contrast to our discoveries, the impacts of a single fire on forest 205 soils have been previously found to be short-term, and can result in an increase in plant 206 productivity, decomposition and microbial activity10,18,28. However, we found that a single 207 fire event can result in significantly lower levels of key measures, such as nitrate nitrogen and 208 available phosphorus, that persist for at least eight decades post-fire, relative to long-209 210 undisturbed sites. These long-lasting impacts also were seen in the 20-30 cm soil layer, which indicates that these post-fire effects may not only be attributed to changes in key soil 211 measures, but probably indicate post-fire erosion and nutrient leaching, and reflect changes in 212 biological processes and composition28-30. 213

Logging impacts observed in this study were highly significant in both the short and mid term 214 215 (8 and 34 years), and result from the high-intensity combination of physical disturbance (clearing of forest with machinery) and post-logging 'slash' burning (of remaining 216 vegetation)31. These disturbances can expose the forest floor18, compact the soil32, volatilize 217 soil nutrients28 and redistribute organic matter28,33, resulting in the release of large amounts 218 of CO2 into the atmosphere (Fig. 4)33. These impacts can alter plant-soil-microbial 219 dynamics and subsequently decomposition rates and carbon storage, and result in the 220 leaching of dissolved organic carbon and nitrogen, and the depletion of base cations, reducing 221 overall site productivity3,18,28,34. Given the long-lasting impacts of fire, we suggest that the 222 logging-related depletion of key soil measures may act as a precursor for longer-term, and 223

224	potentially severe changes in soil composition33. Multi-decadal logging impacts occur in
225	other large-tree, slow turnover forests, such as boreal forests (which experience losses in soil
226	carbon and nitrogen), and can take up to a century to recover3,9,18,19,28,33,35. The long-
227	lasting impacts of both fire and clearcut logging in mountain ash ecosystems indicate that the
228	abiotic soil environments of this (and possibly other) forest ecosystems may be maladapted to
229	frequent, high-intensity disturbances that exceed natural disturbance return intervals3,28.
230	Therefore, predicted changes to global disturbance patterns, such as increasing fire intensity
231	and frequency, could result in severe declines in key soil measures in the long term, with
232	major ecological and functional implications3.
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247	Fig. 4 Post-disturbance processes and pathways that influence and impact abiotic soil
248	environments. White arrows indicate influential relationships and flow-on effects associated
249	with disturbance in soil environments. For example, fire and clearcut logging can alter the
250	structural integrity of soils, which can impede the water and nutrient holding capacity of soils
251	and subsequently result in nutrient leaching and erosion, potentially impacting plant
252	productivity. Credit: images provided by Elle Bowd, David Lindenmayer and David Blair.
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259 In mountain ash forests and other slow-turnover forests, vegetation rapidly regenerates after stand-replacing disturbances36,37. This growth is supported by an increase in light and the 260 availability of phosphorus and nitrogen from surface ash deposits 38. Further inputs of these 261 key nutrients are a product of self-thinning and litterfall39, microbial activity40 and above-262 ground biological fixation from species such as Acacias, which can dominate post-263 disturbance regrowth and offset losses in nitrogen within nine years post-disturbance41. 264 Despite these biochemical inputs, our results demonstrate that significantly lower 265 concentrations of key nutrients such as nitrate and available phosphorus are still evident up to 266 267 eight decades post-fire and three decades post logging, with the lowest measures found in highly disturbed forests subject to compounding disturbances. We did not measure the uptake 268 rate of nutrients in the surrounding vegetation, which may explain some deficits within the 269 270 soil in some ecosystems42. However, when controlling for successional stage, we found 271 unlogged sites burnt in 2009 consistently had higher estimates of key soil measures relative to similarly aged sites logged in 2009. This comparison indicates that disturbance intensityand 272 frequency is a major factor in determining the composition of forest soils, regardless of stand 273 age and nutrient uptake (Fig. 3). 274

275 Recommendations for forest management

We have empirically demonstrated long-term natural and human disturbance impacts on 276 forest soils. Climate change and human disturbances are projected to increase large stand-277 replacing fires globally3,43,44. This will probably result in substantial long-term losses of 278 crucial soil measures, which can effect ecosystem function and forest productivity and 279 growth over the medium to long term18,45–47. To maintain vital soil nutrient pools and 280 preserve the key functions that soils have in ecosystems, such as carbon sequestration and the 281 regulation of plant and microbial community productivity, land managers should consider the 282 impacts of current and future disturbances on soils in ecosystem assessments and land-use 283

284	management and planning. Specifically, perturbations such as fire (outside the historical fire
285	return interval of 75–150 years22) and clearcut and post-fire salvage logging should be
286	limited wherever possible, especially in areas previously subject to these disturbances.
287	Aboveground ecosystem legacies that occur in highly fertile, long-undisturbed sites, such as
288	large old trees, are diminishing globally, and can take over a century to recover from the
289	impacts of disturbance48. Our findings suggest that below-ground abiotic soil environments
290	may take a similar amount of time to recover.
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313 **REFERENCES**

- 314
- 1. Bowman, D. M. et al. Fire in the Earth system. *Science* **324**, 481–484 (2009).
- 316 2. Fraver, S. et al. Forest structure following tornado damage and salvage
- 317 logging in northern Maine, USA. Can. J. For. Res. 47, 560–564 (2017).
- 318 3. Seidl, R., Schelhaas, M. J., Rammer, W. & Verkerk, P. J. Increasing forest
- 319 disturbances in Europe and their impact on carbon storage. *Nat. Clim.*
- 320 *Change* **4**, 806–610 (2014).
- 4. Bond, W. J. J., Woodward, F. I. I. & Midgley, G. F. F. The global distribution
- of ecosystems in a world without fire. *New Phytol.* **165**, 525–537 (2005).
- 5. Giglio, L., Randerson, J. T. & van der Werf, G. R. Analysis of daily, monthly,
- and annual burned area using the fourth-generation global fire emissions
- database (GFED4). J. Geophys. Res. Biogeosci. 118, 317–328 (2013).
- 6. Van Der Werf, G. R. et al. Global fire emissions estimates during 1997–2016.
- 327 Earth Syst. Sci. Data 9, 697–720 (2017).
- 328 7. Cochrane, M. A. & Laurance, W. F. Synergisms among fire, land use, and
- climate change in the Amazon. *Fire Ecol. Manag.* **37**, 522–527 (2008).
- 8. Lindenmayer, D. B., Hobbs, R. J., Likens, G. E., Krebs, C. J. & Banks, S. C.
- 331 Newly discovered landscape traps produce regime shifts in wet forests.
- 332 *Proc. Natl Acad. Sci. USA* **108**, 15887–15891 (2011).
- 333 9. Diochon, A., Kellman, L. & Beltrami, H. Looking deeper: an investigation of
- soil carbon losses following harvesting from a managed northeastern red
- 335 spruce (*Picea rubens* Sarg.) forest chronosequence. *For. Ecol. Manage.* 257,
- 336 413–420 (2009).
- 10. Pellegrini, A. F. A. et al. Fire frequency drives decadal changes in soil carbon
- and nitrogen and ecosystem productivity. *Nature* **553**, 194–198 (2018).
- 11. Watson, J. E. M. et al. The exceptional value of intact forest ecosystems.
- 340 *Nat. Ecol. Evol.* **2**, 599–610 (2018).
- 12. De Deyn, G. B., Raaijmakers, C. E. & Van Der Putten, W. H. Plant
- community development is affected by nutrients and soil biota. J. Ecol. 92,
 824–834 (2004).
- 13. Mckenzie, N., Jacquier, D., Isbell, R. & Brown, K. Australian Soils and
- *Landscapes: An Illustrated Compendium* (CSIRO Publishing, Collingwood,
 2004).
- 14. Blum, W. E. H. Functions of soil for society and the environment.
- 348 Rev. Environ. Sci. Bio/Technol. 4, 75–79 (2005).
- 15. Tedersoo, L. et al. Global diversity and geography of soil fungi. *Science* **346**, 1052, 1052, (2014)
- 350 1052–1053 (2014).
- 351 16. Paustian, K. et al. Climate-smart soils. *Nature* **532**, 49–57 (2016).
- 352 17. van der Putten, W. H. et al. Plant-soil feedbacks: the past, the present and
- 353 future challenges. J. Ecol. 101, 265–276 (2013).
- 18. Hume, A. M., Han Chen, Y. H., Taylor, A. R. & Han, C. Intensive forest
- harvesting increases susceptibility of northern forest soils to carbon, nitrogen
 and phosphorus loss. J. Appl. Ecol. 55, 246–255 (2018).
- 19. Prest, D., Kellman, L. & Lavigne, M. B. Mineral soil carbon and nitrogen still
- 358 low three decades following clearcut harvesting in a typical acadian forest
- 359 stand. *Geoderma* **214-215**, 62–69 (2014).
- 20. Bowman, D. M. J. S., Murphy, B. P., Neyland, D. L. J., Williamson, G. J. &
- 361 Prior, L. D. Abrupt fire regime change may cause landscape-wide loss of
- mature obligate seeder forests. *Glob. Change Biol.* **20**, 1008–1015 (2014).

- 263 21. Clarke, H. G., Smith, P. L. & Pitman, A. J. Regional signatures of future fire
- weather over eastern Australia from global climate models. *Int. J. Wildl. Fire*20, 550–562 (2011).
- 22. McCarthy, M. A., Malcolm Gill, A. & Lindenmayer, D. B. Fire regimes in
- 367 mountain ash forest: evidence from forest age structure, extinction models
- and wildlife habitat. For. Ecol. Manage. 124, 193–203 (1999).
- 369 23. Burns, E. L. et al. Ecosystem assessment of mountain ash forest in the
- 370 Central Highlands of Victoria, south-eastern Australia. *Austral. Ecol.* 40,
- **371 386–399** (2015).
- 372 24. Florence, R. *Ecology and Silviculture of Eucalypt Forests* (CSIRO Publishing,
 373 Collingwood, 1996).
- 25. Commonwealth Scientific and Industrial Research Organisation (CSIRO)
- 375 Climate Variability and Change in South-eastern Australia: A Synthesis of
- 376 Findings from Phase 1 of the South Eastern Australian Climate Initiative
- 377 *(SEACI)* (CSIRO Publishing, 2010).
- 26. Taylor, C., Mccarthy, M. A. & Lindenmayer, D. B. Nonlinear effects of stand
- age on fire severity. *Conserv. Lett.* 7, 355–370 (2014).
- 27. Bissett, A. et al. Introducing BASE: the Biomes of Australian Soil
- Environments soil microbial diversity database. *Gigascience* **5**, 21 (2016).
- 28. Certini, G. Effects of fire on properties of forest soils: a review. *Oecologia* 143, 1–10 (2005).
- 29. Malvar, M. C. et al. Short-term effects of post-fire salvage logging on runoff
- and soil erosion. For. Ecol. Manage. 400, 555–567 (2017).
- 386 30. Wilson, C. J. Effects of logging and fire on runoff and erosion on highly
- erodible granitic soils in Tasmania. *Water Resour. Res.* **35**, 3531–3546 (1999).
- 388 31. Bowd, E. J., Lindenmayer, D. B., Banks, S. C. & Blair, D. P. Logging and fire
- regimes alter plant communities. *Ecol. Appl.* **28**, 826–841 (2018).
- 390 32. Rab, M. A. Recovery of soil physical properties from compaction and soil
- 391 profile disturbance caused by logging of native forest in Victorian Central
- 392 Highlands, Australia. For. Ecol. Manage. 191, 329–340 (2004).
- 393 33. Zummo, L. M. & Friedland, A. J. Soil carbon release along a gradient of
- 394 physical disturbance in a harvested northern hardwood forest. For. Ecol.
- 395 *Manage.* **261**, 1016–1026 (2011).
- 396 34. Simard, D. G., Fyles, J. W., Paré, D., Nguyen, T. & Nguyen, D. Impacts of
- clearcut harvesting and wildfire on soil nutrient status in the Quebec boreal
- 398 forest. Can. J. Soil Sci. 81, 229–237 (2001).
- 399 35. Menge, D. N. L., Pacala, S. W. & Hedin, L. O. Emergence and maintenance of
- 400 nutrient limitation over multiple timescales in terrestrial emergence and
- 401 maintenance of nutrient limitation over multiple timescales in terrestrial
- 402 ecosystems. *Source Am. Nat.* **173**, 164–175 (2009).
- 403 36. Ashton, D. H. in *Fire and the Australian Biota* (eds Gill, A. M., Groves, R. H.
- 404 & Noble, I. R.) 339–366 (Australian Academy of Science, Canberra, 1981).
- 405 37. Bélanger, N., Côté, B., Fyles, J. W., Courchesne, F. & Hendershot, W. L. H. Forest
- 406 regrowth as the controlling factor of soil nutrient availability 75 years after fire
- 407 in a deciduous forest of Southern Quebec. *Plant Soil* **262**, 363–372 (2004).
- 408 38. Chambers, A. B. & Attiwill, P. The ash-bed effect in Eucalyptus regnans
- 409 forest: chemical, physical and microbiological changes in soil after heating or
- 410 partial sterilisation. *Austral. J. Bot.* **42**, 739–749 (1994).
- 411 39. Polglase, P. J. & Attiwill, P. M. Nitrogen and phosphorus cycling in relation to
- 412 stand age of *Eucalyptus regnans* F. Muell. I. Return from plant to soil in

- 413 litterfall. *Plant Soil* **142**, 157–166 (1992).
- 414 40. Dijkstra, F. A. et al. Enhanced decomposition and nitrogen mineralization sustain
- 415 rapid growth of *Eucalyptus regnans* after wildfire. J. Ecol. **105**, 229–236 (2017).
- 41. May, B. M. M. & Attiwill, P. M. M. Nitrogen-fixation by Acacia dealbata and
- 417 changes in soil properties 5 years after mechanical disturbance or slashburning
- following timber harvest. For. Ecol. Manage. 181, 339–355 (2003).
- 419 42. Russell, A. E. & Raich, J. W. Rapidly growing tropical trees mobilize
- 420 remarkable amounts of nitrogen, in ways that differ surprisingly among
- 421 species. Proc. Natl Acad. Sci. USA 109, 10398–10402 (2012).
- 42. 43. Moritz, M. A. et al. Climate Change and disruptions to global fire activity.
 423 *Ecosphere* 3, 49 (2012).
- 424 44. Bowman, D. M. J. S. et al. The human dimension of fire regimes on Earth.
- 425 *J. Biogeogr.* **38**, 2223–2236 (2011).
- 426 45. Kishchuk, B. E. et al. Decadal soil and stand response to fire, harvest, and
- 427 salvage-logging disturbances in the western boreal mixedwood forest of
- 428 Alberta, Canada. Can. J. For. Res. 45, 141–152 (2015).
- 429 46. Turner, B. L., Brenes-Arguedas, T. & Condit, R. Pervasive phosphorus
- 430 limitation of tree species but not communities in tropical forests. *Nature* **555**,
- 431 367–370 (2018).
- 432 47. Alvarez-Clare, S., Mack, M. C. & Brooks, M. A direct test of nitrogen and
- 433 phosphorus limitation to net primary productivity in a lowland tropical wet 424 forest Easler: 04, 1540, 1551 (2012)
- 434 forest. *Ecology* **94**, 1540–1551 (2013).
- 435 48. Lindenmayer, D. B. & Laurance, W. F. The ecology, distribution, conservation
- 436 and management of large old trees. *Biol. Rev.* **92**, 1434–1458 (2017).
- 437 438

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