Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming

Ulf Büntgen[1,2,3], Paul J. Krusic[1,4], Alma Piermattei[1], David A. Coomes[5], Jan Esper[6], Vladimir S. Myglan[7], Alexander V. Kirdyanov[1,8,9], J. Julio Camarero[10], Alan Crivellaro[1] & Christian Körner[11]

[1]Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK. [2]Swiss Federal Research Institute (WSL), 8903 Birmensdorf, Switzerland. [3]Global Change Research Centre and Masaryk University, 613 00 Brno, Czech Republic. [4]Department of Physical Geography, Stockholm University, 10691 Stockholm, Sweden. [5]Department of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, UK. [6]Departmemt of Geography, Johannes Gutenberg University, 55099 Mainz, Germany. [7]Institute of Humanities, Siberian Federal University, 660041 Krasnoyarsk, Russia.[8]Sukachev Institute of Forest SB RAS, 660036 Krasnoyarsk, Russia. [9]Institute of Ecology and Geography, Siberian Federal University, 660041 Krasnoyarsk, Russia. [10]Instituto Pirenaico de Ecología (IPE-CSIC), 50059 Zaragoza, Spain. [11]Institute of Botany, University of Basel, 4056 Basel, Switzerland.

Correspondence should be addressed to U.B. (email: ulf.buentgen@geog.cam.ac.uk)

It is generally accepted that animal heartbeat and lifespan are often inversely correlated, however, the relationship between productivity and longevity has not yet been described for trees growing under industrial and pre-industrial climates. Using 1768 annually resolved and absolutely dated ring width measurement series from living and dead conifers that grew in undisturbed, high-elevation sites in the Spanish Pyrenees and the Russian Altai over the past 2000 years, we test the hypothesis of grow fast – die young. We find maximum tree ages are significantly correlated with slow juvenile growth rates. We conclude, the interdependence between higher stem productivity, faster tree turnover, and shorter carbon residence time, reduces the capacity of forest ecosystems to store carbon under a climate warming-induced stimulation of tree growth at policy-relevant timescales.

Introduction

Despite a wide range of recent advancements in tree-ring research[1], including contributions to (paleo)climatology, ecology, plant physiology and wood anatomy, it is still not clear if tree longevity depends on slow growth rates, and whether or not this relationship is species-specific, genetic and/or environmentally controlled. Our lack of understanding has an important bearing on the current debate about carbon sequestration[2], carbon residence time[3], and climate change mitigation[4-7]. This knowledge gap is disconcerting as faster tree growth under future climate change is expected to lead to higher forest carbon stocks, thereby contributing to the mitigation of the anthropogenic greenhouse effect via the biological uptake of carbon dioxide (CO_2). The assumption that a climate warming-induced increase of tree growth translates into large-scale carbon sequestration is a paradigm that has far-reaching political, ecological and economic

2

47   consequences[8,9]. The concept of negative emission, vis-a-vis secondary forests, has generated

48   much governmental and institutional action[8,10]; the Bonn Challenge being one example[11], already

49   causing a multitude of societal and environmental implications[12].

50   The putative tradeoff between the rate of tree growth and achieved tree lifespan is complicated

51   by complex interactions between the composition and density of forest stands and the possibility

52   that trees can switch their growth strategy once they reach a certain size[13]. Accelerated growth

53   rates of juvenile trees in dense forest stands permit individual trees to escape from becoming

54   victims of competitive exclusion, which potentially turns into increased longevity, both within

55   monocultures and mixed populations[14,15]. In more open forests, such as those of the upper alpine

56   and northern boreal treeline ecotones, a distinction between interspecific and intraspecific effects

57   on tree longevity is needed. Though it is generally accepted that fast growing, pioneer tree species

58   exhibit overall lower wood density and a shorter life expectancy[16], which jointly translates into a

59   limited capacity for carbon sequestration, it is still unknown if later successional species growing

60   under cold and temperate climates could live longer if they grew slower during their late

61   adolescence and early adult life. Since this seems to be the case for many humid tropical taxa[17,18],

62   tree mortality rates are often positively correlated with forest net primary productivity[18], whereas

63   our understanding of size-specific tree mortality patterns is challenged by a lack of suitable data[19].

64   Trees that grow fast beyond their juvenile seedling-sapling stage, commonly exhibit an

65   accelerated life cycle[20], whereas slower growing individuals get older and taller[21-23]. This

66   observation resembles the rate of life concept in animal sciences[24], in which high metabolic rates

67   are negatively correlated with longevity. Such a diversity of life histories affects the architecture,

68   age structure, and biomass turnover rates of forest communities[25], and thus, to a large degree, the

69   terrestrial carbon stock[4,9]. On a global scale, the short but fast life of trees is associated with

70   reduced carbon reservoirs (short carbon residence time)[20]. For example, the highly productive

71   southern and western Amazonian forests store less carbon[26] than their less productive eastern

72   counterparts[27], and the same discrepancy is found between temperate and boreal forests[28]. In

73   tropical Borneo, faster growing forests are found to contain less aboveground carbon density

74   compared to slower growing sites simply due to differences in carbon residence time[29]. Although

75   old trees reveal substantial annual biomass increments[22,25,30], relatively little is known about the

76   intraspecific tradeoffs between post-juvenile growth rates, plant height and stem diameter, as well

77   as the lifespan of trees[31]. Are old, high-carbon-stock trees intrinsically slow growers[23]? Though, it

78   has been argued that the tallest trees are also among the oldest[32], it is not known whether this

79   relates to lower growth rates earlier in life. If the size and/or age distribution of forest stands,

80   together with the occurrence of disturbance events[33], determines the extent of forest carbon stock,

81   then the rate of forest carbon turnover (carbon residence time) is of paramount significance for

82   estimating the long-term net CO_2 capture from the Earth's atmosphere[1-3,34,35].

83   While the influence of climate change, nutrient availability and rising CO_2 concentrations on

84   tree growth can be examined experimentally under controlled conditions[34,36], their influence on

85   the lifespan of trees cannot. This is where dendroecology can provide unique insights into extra-

86   tropical, inter-annual tree growth variability at centennial to millennial time-scales[37,38]. However,

87   dendrochronological candidate collections must fulfill numerous criteria that are commonly not

88   addressed in traditional dendroclimatological/ecological tree-ring studies[39,40]. To begin with, a

89   large sample size of several hundreds to thousands of recent (living) and relict (dead) tree stems

90   cross-sections, ideally consisting largely of disc samples that include the innermost ring, or core

91   samples with reliable pith-offset estimates, are needed in order to provide sufficient statistical

92   confidence for precise age and growth rate determinations. In addition, the species- and site-

4

93   specific inventories of annual tree-ring width measurements, preferably from stem discs, rather

94   than increment cores, must be characterized by a homogeneous distribution of the constituent

95   series' start and end dates over past centuries to represent pre-industrial climate conditions. The

96   samples also need to contain a wide range of individual tree ages and growth levels. Moreover, the

97   appropriate datasets should represent trees that grow in open environments, where year-to-year

98   and longer-term ring width variations are largely constrained by growing-season temperatures,

99   rather than between-tree competition. Finally, the collection sites should be free of silvicultural

100   treatments, and minimally affected by natural disturbances[33], such as cyclic insect defoliations

101   and/or stochastic forest fires.

102   This study provides a conceptual framework to examine the growth-lifespan tradeoff in two

103   conifer species and uses tree-ring width measurements from living and relict tree stem cross-

104   sections to address the question: To what extent does the growth rate and lifespan of trees, within

105   given species population, co-vary?

106

107   **Results**

108   *Conceptual tree growth changes under global warming*

109   To meet the aforementioned criteria, and provide a dendroecological perspective on the

110   relationship between plant lifespan and radial stem growth, we use annually resolved and

111   absolutely dated tree-ring information from 1768 conifers that lived during the past two millennia

112   in the Spanish Pyrenees and the Russian Altai. Due to the sites' remote locations, we assume there

113   are no direct anthropogenic disturbances affecting tree growth rates (as opposed to possible

114   indirect affects vis-à-vis climate change). We consider the following three categorical hypotheses

115   (Figure 1), and acknowledge that reality maybe somewhere in between. H1 is the fixed-age

116   hypothesis that states; if mean maximum tree size is reached early (growth has been accelerated

117   for whatever reason), trees will wait to die until they reach a certain age. H2 is the bigger

118   hypothesis that states; faster growing trees will become bigger (taller and greater stem diameter)

119   within a given lifespan, and will die at a species-specific age. H3 is the fixed-size hypothesis that

120   states; when trees grow faster, they will die once they reach a certain size, and that timing will

121   determine the turnover rate. Under H1 and H2 tree growth patterns translate into increasing

122   landscape-wide carbon stocks (sequestration), while the pattern predicted by H3 does not. An

123   extension of H3 could include the possibility of the carbon stock being reduced by virtue of all

124   intermediate responses between H2 and the accelerated turnover hypothesis. Our tests explore the

125   importance of size versus age control on tree lifespan (H2 versus H3). Since neither the fatal

126   consequences of great age or size can be expected to possess sharp thresholds, a large sample size

127   is required to statistically describe tree lifespan (forest demography). Finally, we concede it is

128   impossible to define explicitly the actual causes of tree mortality, because individuals may die due

129   to just age or even age-related susceptibility to disturbance factors and/or post-disturbance

130   pathogens.

131

132   *Grow fast – die young*

133   By analyzing 1108 tree-ring width and basal area increment series from 602 living and 506 dead

134   Mountain pines (*Pinus uncinata* Ramond ex DC.) in the Spanish Pyrenees[41,42], and 660 comparable

135   samples (147 living and 513 relict tree stems) of Siberian larch (*Larix sibirica* Ledeb.) from the

136   Russian Altai[43] (Figure 2), we reconstruct the total lifespan and juvenile growth rates of trees that

137   were growing during both industrial and pre-industrial climate conditions (see Methods). All trees

138   grew under undisturbed and unmanaged, summer temperature limited, high-elevation, climax

139   forests with wide tree spacing in the Pyrenees and the Altai (see Methods). Since the lifespans of

140   these trees from Europe and inner Eurasia are fairly evenly distributed over the past 1000 and 2000

141   years, respectively (Supplementary Figure 1), the timing of each tree's juvenile growth period

142   occurred during different periods of natural climate variability and well before the recent warming.

143   Most samples from the Pyrenees contain between ~100 and 200 growth rings (Figure 2A), with

144   mean ring widths between ~0.5 and 1.0 mm, which translates into a mean annual basal area

145   increment of ~200 to 500 mm^2. The much flatter age distribution of the Altai samples reveals the

146   trees there are generally older and have slightly smaller annual increments (Figure 2B). The Altai

147   mean tree age, ring width and basal area are 355 years, 0.44 mm and 195 mm^2, respectively.

148   The average ring width and basal area increment in the first 25 years of juvenile growth in the

149   1108 Pyrenees pine samples shows a clearly negative relationship with total tree lifespan (Figure

150   3A). Old ages are reached only if juvenile growth is slow. Though less distinct a similar, and

151   statistically significant, relationship can be seen in the 660 Altai larch samples (Figure 3B). While

152   the younger trees exhibit a wide range of growth rates, it is evident from both datasets that low

153   juvenile growth rates are indeed required to reach a great tree age. Considering different periods

154   of juvenile tree growth between 25 and 75 years, does not change this finding (Supplementary

155   Table 1). Moreover, the association between increased juvenile stem growth and reduced total tree

156   age remains statistically significant when calculated separately for the living and relict trees in

157   both regions (Supplementary Table 1 and Supplementary Figures 2-3).

158

159   **Discussion**

160   Based on the evidence of 749 living and 1019 relict tree-ring measurement series, representing

161   species-specific conifer ring widths over the past 1000 and 2000 years at undisturbed high-

162   elevation sites in the Spanish Pyrenees and Russian Altai, this study suggests that accelerated tree

163   growth (past, present and future) is unlikely to translate into enhanced carbon sequestration,

164   thereby mitigating the global greenhouse effect. The data illustrate that increased biomass

165   productivity leads to reduced tree longevity (Figure 1). A faster turnover of individual trees implies

166   a shorter carbon residence time from stand to biome scales[2] (in line with H3).

167   By accepting H3 and rejecting H1 and H2 (Figure 1), we see no evidence for a shift in

168   demography toward higher ages, and thus a greater carbon stock, when trees grow faster. Our data

169   do support a size, rather than an age, control of tree lifespan and thus stand-level turnover, with

170   recorded tree age being a consequence, rather than a cause, of death. Could faster growing trees

171   break the size limit and get larger? This would require anatomical adjustments typically associated

172   with maximum tree size that provide resilience in the face of the many physical disturbance vectors

173   that damage trees[44]. Record tree heights found in both angiosperms (*Eucalyptus regnans* F.Muell.;

174   mountain ash) and gymnosperms (*Sequoia sempervirens* (D.Don) Endl.; coastal redwood), are

175   believed to relate to apical turgor maintenance[31,45] irrespective of whether trees possess vessels or

176   just tracheid cells, and explains why such giants are confined to humid areas[46].

177   Given the data available, our findings are restricted to two conifer species of upper montane

178   forests and the treeline ecotones, and therefore do not contribute to answering the question of how

179   drought stress under predicted climate change will affect the functioning, productivity and carbon

180   stocking of forest ecosystems at lower elevations[47-49]. Future estimates of the amount of stored

181   carbon in arid environments are particularly challenging, as there is a thin line between drought-

182   induced reductions of metabolic activity, which would extend the trees' lifespan in line with our

183   findings and facilitate long-term carbon storage, versus widespread forest dieback that would

184   convert a carbon sink into a source, similar to what happens after large bark-beetle outbreaks and

185   wildfires[50]. Any model-based predictions of how forest regrowth across different parts of the

186   Earth's landmass will affect global carbon dynamics are, however, associated with great

187   uncertainties in the lights of demography[51] and mortality[52].

188   Although site- and species-specific, our results warn against scaling from growth rates to

189   carbon stocking without accounting for tree lifespan and stand turnover (shifts in demography)[35].

190   The data presented here suggest that faster growth does not permit one to infer levels of carbon

191   sequestration at the landscape scale. Such an inference would require responses closer to H1 and

192   H2, which we did not find. Our data rather suggest that accelerated growth is associated with faster

193   ontogeny, as was demonstrated by plantation trees exposed to elevated CO_2 (53), and a higher

194   likelihood of tree death as a function of tree size. The idea that global warming, artificial nitrogen

195   deposition, or atmospheric CO_2 enrichment will rise carbon stocks in forests, the size control of

196   turnover hypothesis (extension of H3) must be rejected.

197

198   **Methods**

199   **Tree-ring sampling.** During several field campaigns since 2004, disc and core samples from 1108

200   living and dead Mountain pine (*Pinus uncinata* Ramond ex DC.) trees were collected at two upper

201   treeline sites in the most northern part of the Aigüestortes i Estany de Sant Maurici National Park

202   in the central Spanish Pyrenees[41,42]. This region is characterized by undisturbed, open ecotone

203   habitats between around 2300 and 2600m asl.

204   Over the past decade, stem discs and a few increment cores from 660 living and dead Siberian

205   larch (*Larix sibirica* Ledeb.) trees were collected at five upper treeline sites across the Russian

206   Altai-Sayan Mountains[43]. This region also is characterized by undisturbed, open forests around

207   2000-2400m asl. High-elevation tree growth in both regions is predominantly controlled by

208   summer temperature conditions. Individual trees at all sites can reach ages of up to 1000 years.

209   The abundance of dead wood in the Altai and Pyrenees is indicative of remote locations with little

210   to no modification by humans, or disturbance due to grazing by wild or domestic animals.

211   **Tree-ring analyses.** All disc and core samples were air-dried and polished with sand paper of

212   progressively finer grain size down to 800 grit. Tree-ring width (TRW) was measured at a

213   resolution of 0.001 mm using LINTAB measuring systems, and cross-dated via TSAP-win and

214   PAST4 software. All dating was verified with COFECHA (Version 6.02P). The germination year

215   (birth) of each tree was defined by the calendar date of its pith. In those cases where samples had

216   no pith, pith-offset estimates were calculated, by fitting a geometric pith locator to the innermost

217   rings and converting this distance into the number of missing rings. The dated TRW measurements

218   were transformed into basal area increments (BAI) to account for the geometric constraints of

219   adding incremental growth to an ever-increasing surface area.

220   Linear functions fitted to the log-transformed data of the first 25, 50 or 75 years of juvenile

221   tree growth in all 1108 and 660 individual series of TRW and BAI from the Pyrenees and Altai,

222   and plotted against total tree age, describe the overall tradeoff between the productivity (growth)

223   and longevity (lifespan) of trees. Mean TRW and BAI of the juvenile tree growth of all samples

224   ≤200 and ≥400 years further emphasize the tendency of younger trees to grow faster and older

225   trees to grow slower. Finally, we performed the same analysis on the 506 and 513 relict (602 and

226   147 living) trees from the Pyrenees and Altai to test for the temporal stability in our results.

227

228   **Data availability**

229 All source data underlying this study are provided as two separate Source Data files, for the

230 Spanish Pyrenees (SourceDataPyrenees.txt) and the Russian Altai (SourceDataAltai.txt). All

231 calculations were performed with the open access software R.

232

233 **References**

234 1. Büntgen, U. Re-thinking the boundaries of dendrochronology. *Dendrochronologia* **53**, 1–4

235   (2019).

236 2. Körner, C. A matter of tree longevity. *Science* **355**, 130–131 (2017).

237 3. Friend, A. et al. Carbon residence time dominates uncertainty in terrestrial vegetation

238   responses to future climate and atmospheric CO_2. *Proc. Natl. Acad. Sci. USA* **111**, 3280–3285

239   (2014).

240 4. Canadell, J.G. & Schulze, E.D. Global potential of biospheric carbon management for climate

241   mitigation. *Nature Com.* **5**, 5282 (2014).

242 5. Johnson, M.E. et al. Variation in stem mortality rates determines patterns of above-ground

243   biomass in Amazonian forests: implications for dynamic global vegetation models. *Glob.*

244   *Change Biol.* **22**, 3996–4013 (2016).

245 6. Johnson, D.J. et al. Climate sensitive size-dependent survival in tropical trees. *Nature Eco.*

246   *Evo.* **2**, 1436–1442 (2018).

247 7. Rödig, E. et al. The importance of forest structure for carbon fluxes of the Amazon rainforest.

248   *Env. Res. Let.* **13**, 054013 (2018).

249 8. Geden, O., Scott, V. & Palmer, J. Integrating carbon dioxide removal into EU climate policy:

250   Prospects for a paradigm shift. *WIREs Clim. Change* **2018**, e521 (2018).

251 9. Smith, P. et al. Biophysical and economic limits to negative CO_2 emissions. *Nature Clim.*
252   *Change* **6**, 42–50 (2016).

253 10. IPPC, Cambridge University Press, Cambridge, UK and New York, NY, USA (2014).

254 11. http://www.bonnchallenge.org/ (04th October 2018).

255 12. Global Forest Coalition. *The risks of large-scale biosequestration in the context of carbon*
256   *dioxide removal.* Asunción, Paraguay: Heinrich Boell Foundation (2017).

257 13. Grubb, P.J. A reassessment of the strategies of plants which cope with shortages of resources.
258   *Perspec. Plant Ecol. Evo. System.* **1**, 3–31 (1998).

259 14. Gilbert, B., Wright, S.J., Muller-Landau, H.C., Kitajima, K. & Hernandéz, A. Life history
260   trade-offs in tropical trees and lianas. *Ecology* **87**, 1281–1288 (2006).

261 15. Iida, Y., Poorter, L., Sterck, F., Kassim, A.R., Potts, M.D., Kubo, T. & Kohyama, T.S. Linking
262   size-dependent growth and mortality with architectural traits across 145 co-occurring tropical
263   tree species. *Ecology* **95**, 353–363 (2014).

264 16. Zuidema, P.A., Brienen, R.J.W., During, H.J. & Güneralp, B. Do persistently fast-growing
265   juveniles contribute disproportionately to population growth? A new analysis tool for matrix
266   models and its application to rainforest trees. *Am. Nat.* **174**, 709–719 (2009).

267 17. Wright, S.J. et al. Functional traits and the growth-mortality tradeoff in tropical trees. *Ecology*
268   **91**, 3664–3674 (2010).

269 18. Stephenson, N.L. et al. Causes and implications of the correlation between forest productivity
270   and tree mortality rates. *Ecol. Mono.* **81**, 527-555 (2011).

271 19. Hurst, J.M., Allen, R.B., Coomes, D.A. & Duncan, R.P. Size-specific tree mortality varies
272   with neighbourhood crowding and disturbance in a montane *Nothofagus* forest. *PLoS ONE* **6**,
273   e26670 (2011).

274   20. Erb, K.H. et al. Bias in the attribution of forest carbon sinks. *Nature Geosci.* **9**, 674–678

275   (2016).

276   21. Vieira, S. et al. Forest structure and carbon dynamics in Amazonian tropical rain forest.

277   *Oecologia* **140**, 468–479 (2004).

278   22. Bigler, C. & Veblen, T.T. Increased early growth rates decrease longevities of conifers in

279   subalpine forests. *Oikos* **118**, 1130–1138 (2009).

280   23. Issartel, J. & Coiffard, C. Extreme longevity in trees: live slow, die old? *Oecologia* **165**, 1-5

281   (2011).

282   24. Hulbert, A.J., Pamplona, R., Buffenstein, R. & Buttemer, W.A. Life and death: metabolic rate,

283   membrane composition, and life span of animals. *Physiol. Rev.* **87**, 1175–1213 (2007).

284   25. Luyssaert, S. et al. Old-growth forests as global carbon sinks. *Nature* **455**, 213–215 (2008).

285   26. Brienen, R.J.W. et al. Long-term decline of the Amazon carbon sink. *Nature* **519**, 344–348

286   (2015).

287   27. Philipps, O.L. et al. Pattern and process in Amazon tree turnover 1976-2001. *Phil. Trans. R.*

288   *Soc. Lond. B* **359**, 381–407 (2004).

289   28. Stephenson, N.L. & van Mantgem, P.J. Forest turnover rates follow global and regional

290   patterns of productivity. *Ecol. Lett.* **8**, 524–531 (2005).

291   29. Jucker, T. et al. Topography shapes the structure, composition and function of tropical forest

292   landscapes. *Ecol. Let.* **21**, 989–1000 (2018).

293   30. Bugmann, H. & Bigler, C. Will the CO_2 fertilization effect in forests be offset by reduced tree

294   longevity? *Oecologia* **165**, 533–544 (2011).

295   31. Di Filippo, A. et al. The longevity of broadleaf deciduous trees in Northern Hemisphere

296   temperate forests: insights from tree-ring series. *Front. Ecol. Evol.* **3**, 46 (2015).

297   32. Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. The limits to tree height. *Nature* **428**,

298   851–854 (2004).

299   33. Coomes, D.A., Holdaway, R.J., Kobe, R.K., Lines, E.R. & Allen, R.B. A general integrative

300   framework for modelling woody biomass production and carbon sequestration rates in forests.

301   *J. Ecol.* **100**, 42–64 (2012).

302   34. Körner, C. Biosphere responses to CO_2 enrichment. *Ecol. Appl.* **10**, 1590–1619 (2000).

303   35. Bigler, C. Trade-offs between growth rate, tree size and lifespan of Mountain Pine (*Pinus*

304   *montana*) in the Swiss National Park. *PLoS ONE* **11**, e0150402 (2016).

305   36. Klein, T., Bader, M.K.F., Leuzinger, S., Mildner, M., Schleppi, P., Siegwolf, R.T.W. &

306   Körner, C. Growth and carbon relations of mature Picea abies trees under 5years of free-air

307   CO2 enrichment. *J. Ecol.* **104**, 1720–1733 (2016).

308   37. St. George, S. An overview of tree-ring width records across the Northern Hemisphere. *Quat.*

309   *Sci. Rev.* **95**, 132–150 (2014).

310   38. Babst, F., Poulter, B., Bodesheim, P., Mahecha, M.D. & Frank, D.C., Improved tree ring

311   archives will support earth-system science. *Nature Ecol. Evo.* **1**, 0008 (2017).

312   39. Babst, F. et al. When tree rings go global: Challenges and opportunities for retro- and

313   prospective insight. *Quat. Sci. Rev.* **197**, 1–20 (2018).

314   40. Nehrbass-Ahles, C. et al. The influence of sampling design on tree-ring based quantification

315   of forest growth. *Glob. Change Biol.* **20**, 2867–2885 (2014).

316   41. Büntgen, U. et al. New tree-ring evidence from the Pyrenees reveals western Mediterranean

317   climate variability since medieval times. *J. Clim.* **30**, 5295–5318 (2017).

318   42. Sangüesa-Barreda, G., Camarero, J.J., Esper, J., Galván, J.D. & Büntgen, U. A millennium-
319   long perspective on high-elevation pine recruitment in the Spanish central Pyrenees. *Canadian*
320   *J. Forest Res.* **48**, 1108–1113 (2018).

321   43. Büntgen, U. et al. Cooling and societal change during the Late Antique Little Ice Age from
322   536 to around 660 AD. *Nature Geosci.* **9**, 231–236 (2016).

323   44. Meyer, F.D., Paulsen, J. & Körner, C. Windthrow damage in *Picea abies* is associated with
324   physical and chemical stem wood properties. *Trees* **22**, 463–473 (2008).

325   45. Sala, A. & Hoch, G. Height-related growth declines in ponderosa pine are not due to carbon
326   limitation. *Plant Cell Environ.* **32**, 22–30 (2009).

327   46. Klein, T., Randin, C. & Körner, C. Water availability predicts forest canopy height at the
328   globalscale. *Ecol. Lett.* **18**, 1311–1320 (2015).

329   47. Choat, B. et al. Global convergence in the vulnerability of forests to drought. *Nature* **491**, 752–
330   755 (2012).

331   48. Anderegg, W.R.L. et al. Pervasive drought legacies in forest ecosystems and their implications
332   for carbon cycle models. *Science* **349**, 528–532 (2015).

333   49. Schwalm, C.R. et al. Global patterns of drought recovery. *Nature* **548**, 202–205 (2017).

334   50. Williams, A.P. et al. Temperature as a potent driver of regional forest drought stress and tree
335   mortality. *Nature Clim. Change* **3**, 292–297 (2012).

336   51. Pugh, T.A.M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V. & Calle L. Role
337   of forest regrowth in global carbon sink dynamics *Proc. Natl. Acad. Sci. USA* **116**, 4382–4387
338   (2019).

339   52. Bugmann, H. et al. Tree mortality submodels drive simulated long-term forest dynamics:
340   assessing 15 models from the stand to global scale. *Ecosphere* **10**, e02616 (2019).

341 53. LaDeau, S.L. & Clark, J.S. Rising CO_2 levels and the fecundity of forest trees. *Science* **292**,

342   95–98 (2001).

343

350

351 **Authors contributions**

352 U.B. and C.K. designed the study. C.K. developed the theories with input from D.A.C. and U.B.

353 U.B., J.E., V.S.M., A.V.K., and J.J.C. collected data, and A.P. and A.C. performed statistical

354 analyses. U.B, C.K. and P.J.K. wrote the paper with input from all others. Each author was

355 involved in revision and approved resubmission.

356

357 **Competing interests**

358 The authors declare no competing interests.

359

360
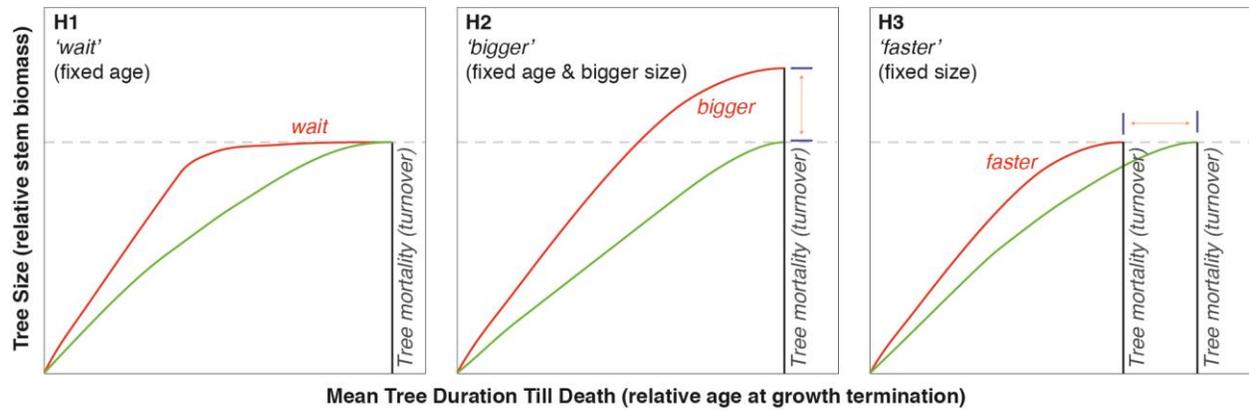
Fig. 1 Conceptual diagram of tree growth under global warming. Three alternative hypotheses of how the relationship between the longevity (age) and growth rate (size) of trees may change under predicted global warming (red lines). H1 shows faster initial growth rates that are, however, not sustained until tree death. H2 shows faster growth rates throughout the entire lifetime that is, however, not affected. H3 shows faster growth rates together with a shorter lifespan.
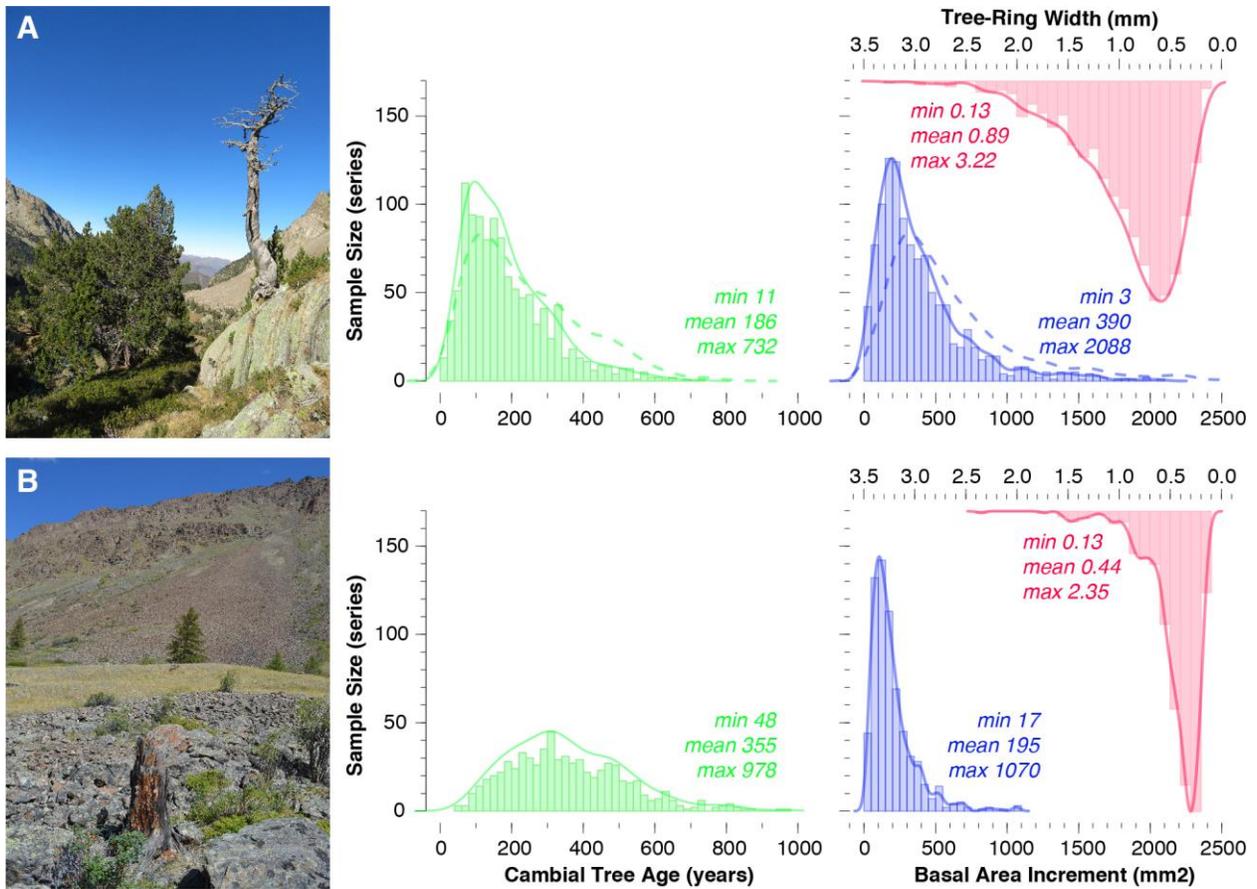
Fig. 2 Tree growth characteristics. (**a**) Spanish Pyrenees and (**b**) Russian Altai where 1108 and 660 disc and core samples were collected from recent (602 and 147) and relict (506 and 513) Mountain pines (*Pinus uncinata*) and Siberian larch (*Larix sibirica*), respectively. Histograms show different distributions of tree age (green), as well as annual tree-ring width and basal area increment (red and blue). Dashed lines represent the contribution made when considering pith-offset estimates (the number of missing rings between the innermost annual increment and the pith). Colored numbers show the minimum, mean and maximum (min, mean, max) values of cambial tree age, tree-ring width and basal area increment (green, red, blue).
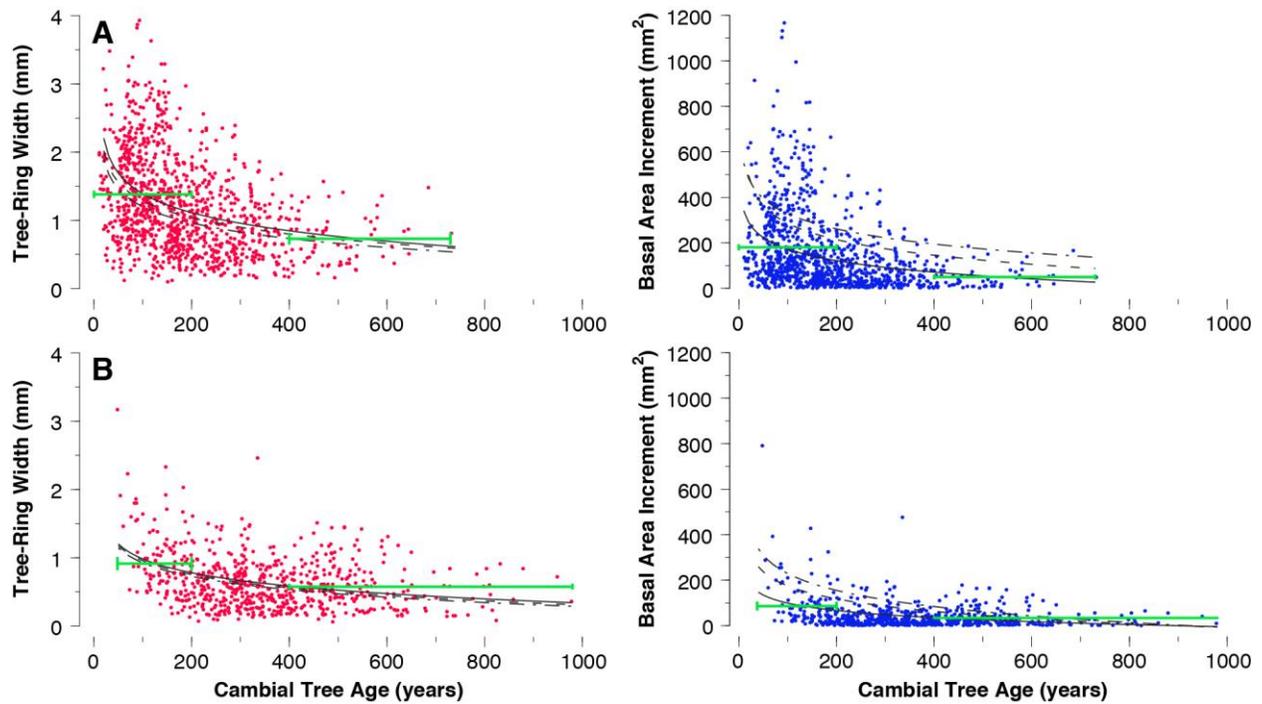
Fig. 3 Tree growth rates and mortality. Annual tree-ring width and basal area increment averaged over the first 25 years of juvenile growth (red and blue) from the (**a**) Spanish Pyrenees and (**b**) Russian Altai. Green lines are the mean value of samples aged ≤200 and ≥400 years, with their vertical bars indicating the corresponding standard error. Logarithmic functions consider the first 25, 50 or 75 years of juvenile tree growth (solid, regular dashed, irregular dashed).

Supplementary Figures

396
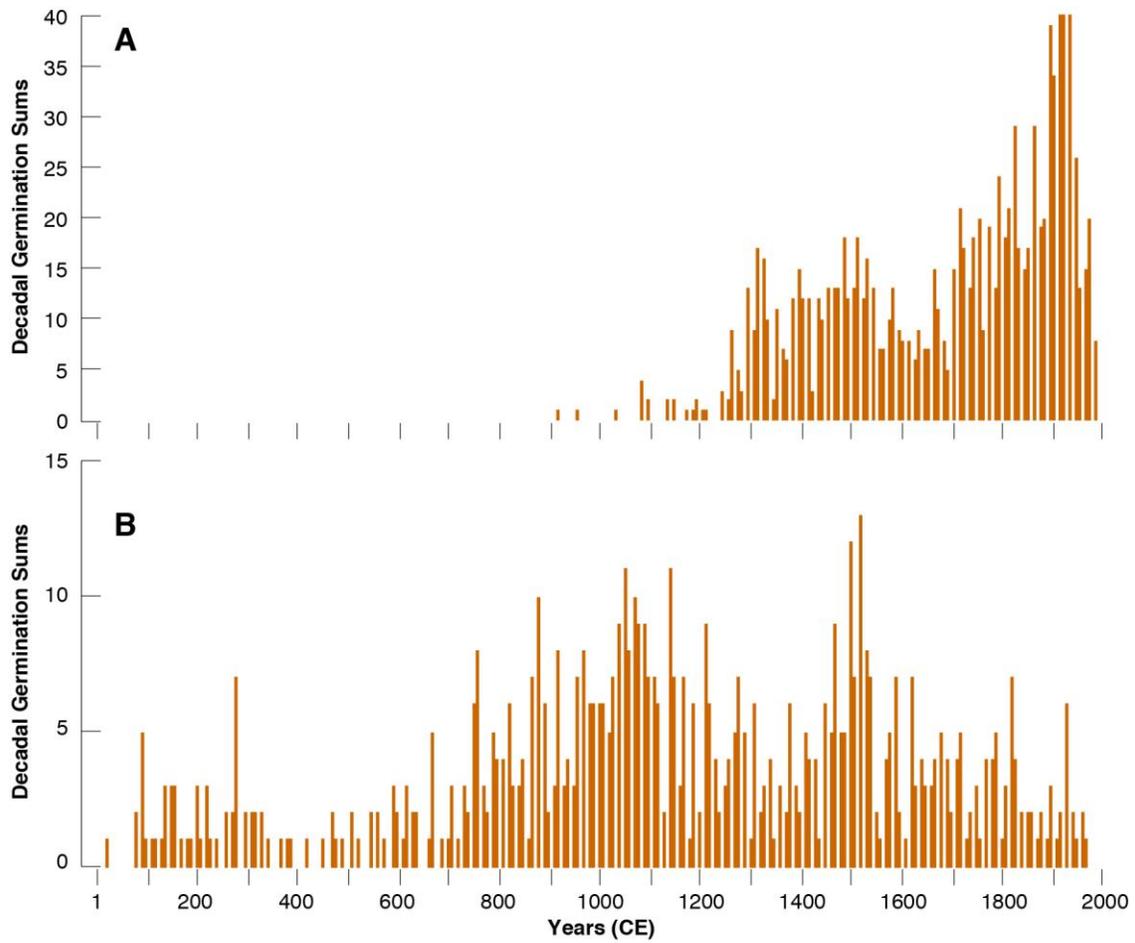
Fig. 1 Decadal-sums of the germination dates of (**a**) 1108 pine and (**b**) 660 larch trees

from the Spanish Pyrenees and the Russian Altai.

399
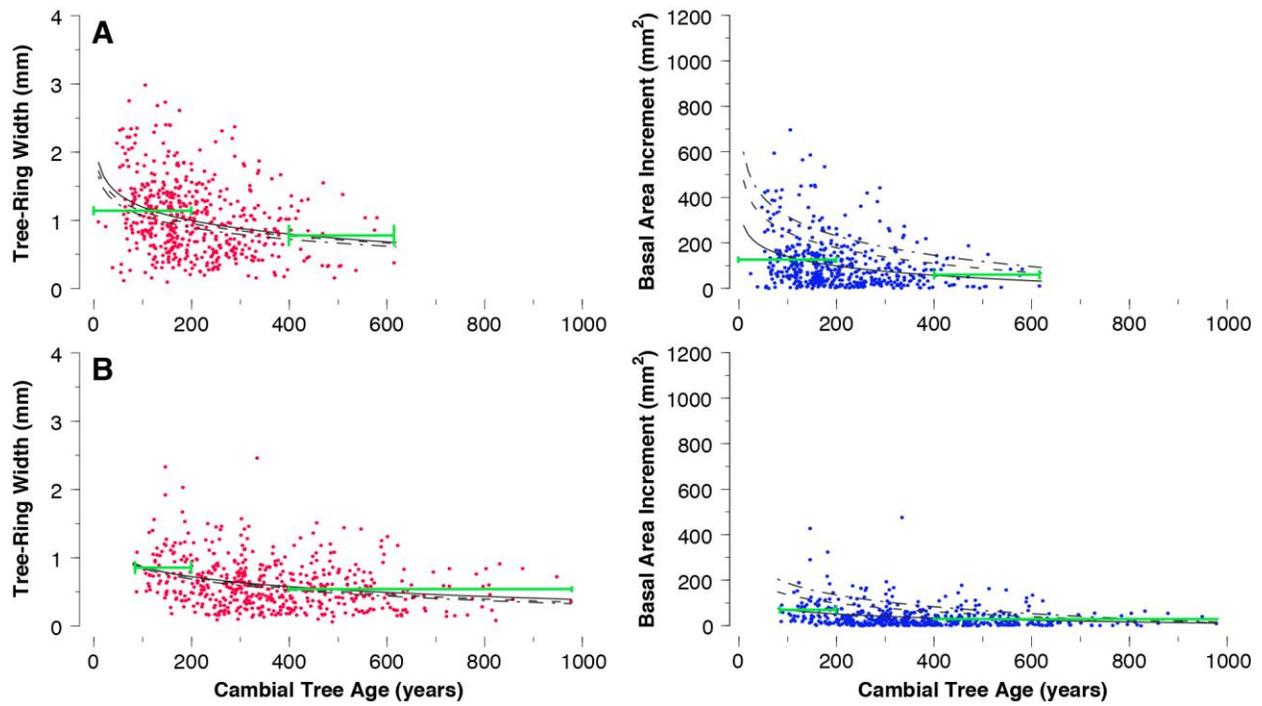
Fig. 2 Similar to Figure 2 though restricted to the 506 and 513 relict samples from the (**a**) Spanish Pyrenees and (**b**) Russian Altai, respectively, which were growing under natural, pre-industrial climate conditions.
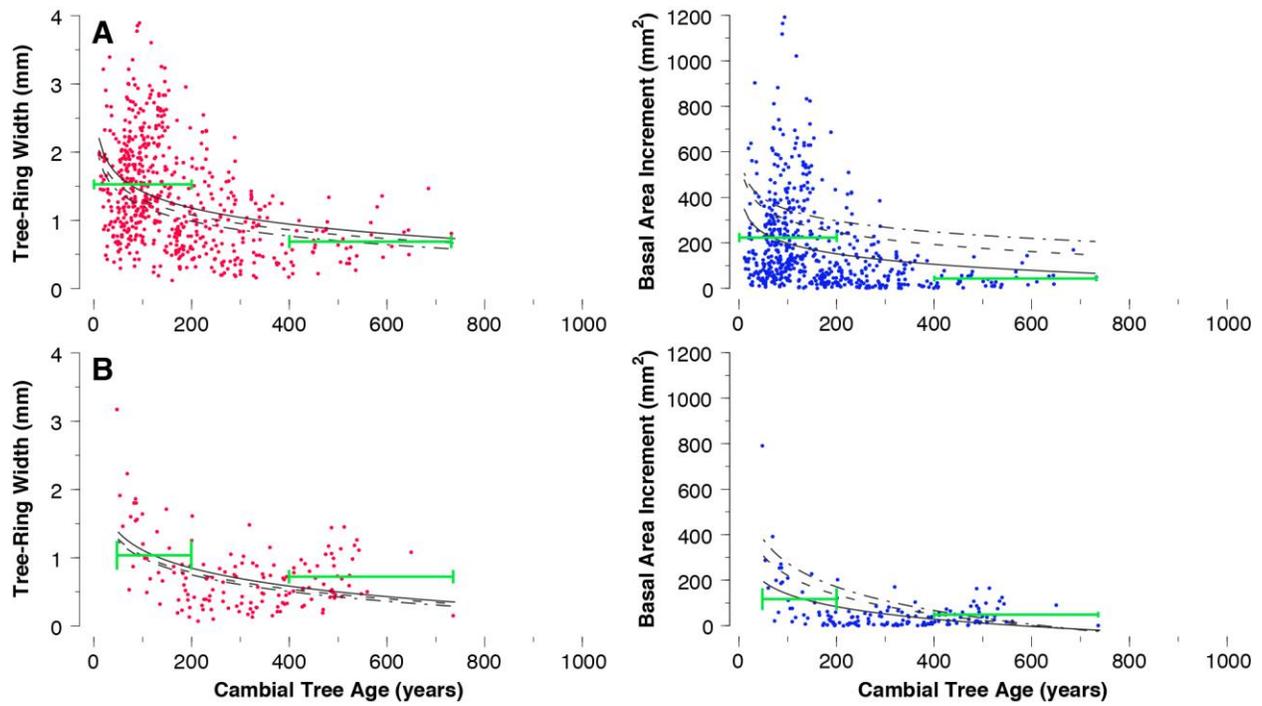
Fig. 3 Similar to Figure 2 though restricted to the 602 and 147 recent samples from the (**a**) Spanish Pyrenees and (**b**) Russian Altai, respectively, which were growing under anthropogenic, industrial climate conditions.