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The pace of life for forest trees

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Title: The pace of life for forest trees

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One Sentence Summary: The pace of life for trees varies predictably across biogeographic gradients, with important implications for modeling the forest carbon dynamics in a changing world.

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Keywords: Forest ecology, life history traits, life expectancy, longevity, fast-slow continuum, trade-offs, niche differentiation, demographic diversity, tree growth strategies, demography

26 **Abstract.** Tree growth and longevity trade-offs fundamentally shape the terrestrial carbon
27 balance. Yet, we lack a unified understanding of how such trade-offs vary across the world's
28 forests. By mapping life history traits for a wide range of species across the Americas, we
29 reveal considerable variation in remaining life expectancies from 10 cm in diameter (ranging
30 from 1.3 to 3,195 years) and show that the pace of life for trees can be accurately classified
31 into four demographic functional types. We find emergent patterns in the strength of trade-
32 offs between growth and longevity across a temperature gradient. Furthermore, we show that
33 the diversity of life history traits varies predictably across forest biomes, giving rise to a
34 positive relationship between trait diversity and productivity. Our pan-latitudinal assessment
35 provides new insights into the demographic mechanisms that govern the carbon turnover rate
36 across forest biomes.

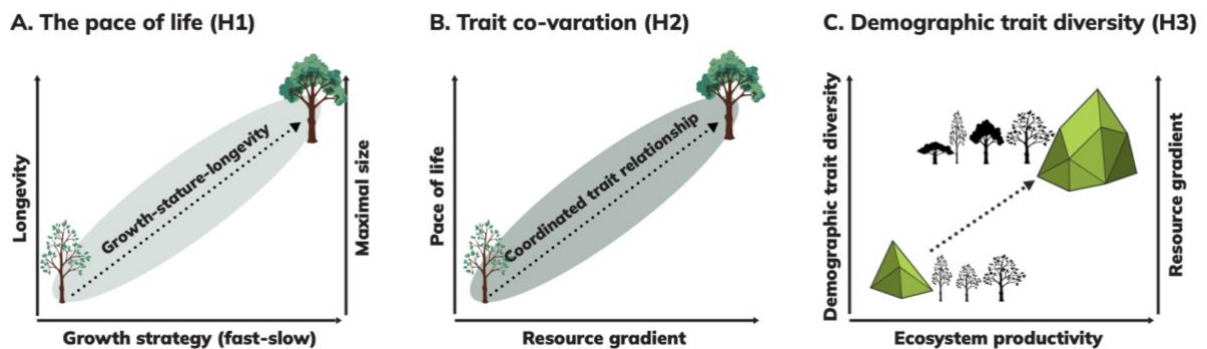
37
38 **Introduction:** The cumulative energetic investment in survival and growth from one year to
39 the next ultimately determines an organism's overarching pace of life, including the time it
40 takes to grow to its maximal size and its life expectancy (1, 2). This fundamental relationship
41 between energetic investments, developmental schedules, and longevity has been extensively
42 studied for animals, showing that high resource allocation toward growth is inversely related
43 to life expectancy and maximal body mass (3, 4). Trees are also assumed to retain tightly
44 coupled relationships between growth strategies, life expectancies, and maximal sizes (Fig.
45 1a) (5), which determine the dynamics and structure of global forests. Yet, although these life
46 history differences fundamentally regulate how fast carbon is sequestered in different regions
47 of the vegetation carbon pool (6–8), we still lack a unified understanding of the range of tree
48 life history strategies that exist across global forests.

49
50 It is widely accepted that tree life history strategies should align along a primary axis of
51 variation in their pace of life, ranging from fast-growing, short-lived species to slow-growing,
52 long-lived species (i.e., fast-slow continuum and r/K selection theory) (Fig. 1a) (5). In this
53 context, high energetic investment of finite resources toward fast growth is expected to come
54 at the cost of reduced survival, which ultimately determines a species' life expectancy and
55 maximal size (Fig. 1a) (9–11). Thus, it is expected that abiotic constraints (e.g. soil nutrients,
56 water, and temperature) should strongly shape the pace of life for trees, giving rise to
57 predictable variation in the strength of life history trade-offs across biogeographic gradients
58 (Fig. 1b) (12). So far, however, the only empirical tests of these trade-offs come from tree
59 ring data and local-scale studies from tropical ecosystems and have produced mixed results
60 (2, 12–14).

61
62 One potential challenge that can obscure predictable patterns in the pace of life for trees is
63 that it is not only the traits that are expected to vary across environmental gradients but also
64 the diversity of those traits. For example, strong biotic competition across tropical forests is
65 thought to have led to high demographic niche differentiation (i.e. high demographic
66 diversity: Fig. 1c, upper right). In contrast, resource limitations in harsh cold/dry regions are
67 assumed to have restricted the species pool to predominantly slow-growing, long-lived
68 species (Fig. 1c, lower left). Yet, these concepts lack empirical evidence because the extreme
69 longevity of trees (which can live for thousands of years) has precluded our capacity to
70 quantify the strength of tree life history trade-offs across a wide range of species, let alone
71 characterize the diversity of life history traits across biogeographic gradients.

72
73 Here, we used the largest dataset of dynamic tree information to date and employed age-
74 from-stage methods to calculate the mean life expectancy and maximal lifespan for a wide
75 range of trees across the Americas (15–17), spanning a latitudinal gradient from Northern

76 Canada to Southern Brazil. This includes long-term records from an international network of
 77 researchers, including members of the Global Forest Dynamics, ForestPlots (18, 19), and
 78 ForestGeo (20–22) networks and the United States and Canadian forest inventory programs
 79 (23–25). To balance this dataset across our biogeographic gradient, we randomly sub-
 80 sampled the North American plots to equal the number of point observations in Central and
 81 South America (see materials and methods), resulting in 3.2 million unique tree
 82 measurements for 1,127 species (i.e., tree size and status). Our big-data approach allowed us
 83 to test for the expectation that trees align along the fast-slow continuum (Fig. 1a, H1) and
 84 quantify if tree growth-longevity-stature relationships co-vary across soil, water, and
 85 temperature gradients (Fig. 1b, H2). Apart from species with low occurrences (< 100
 86 observations, see materials and methods), our systematic sampling allowed us to test for the
 87 expectation that the range of life history strategies occupied by species (i.e., demographic
 88 trait diversity) varies predictably across broadscale biogeographic gradients, with harsh cold
 89 regions in the northern hemisphere restricting trees to a smaller pool of predominantly slow-
 90 growing, long-lived species (Fig. 1c, H3). Based on the well-established diversity-
 91 productivity relationship, we also expected demographic trait diversity to be positively
 92 associated with ecosystem productivity (Fig. 1c, H3).
 93



94
 95 **Fig. 1.** Conceptual diagram of our core aims and associated hypotheses. The expectation is that trees should
 96 align along the fast-slow continuum, with fast-growing short-lived species on one end of the spectrum and slow-
 97 growing long-lived species on the other end (H1, panel A). Life history trait relationships should be
 98 phylogenetically conserved and should co-vary across biogeographic gradients, leading to more conservative
 99 life history strategies in low-resource environments (low soil and nutrient environments and colder
 100 temperatures) (H2, panel B). Lastly, we expect the range of tree life history strategies (i.e., convex-hull volume
 101 in life history trait space that is occupied by species) to vary predictably across biogeographic gradients, with
 102 demographic trait diversity being positively associated with ecosystem productivity (H3, panel C).
 103

104 To quantify tree growth, longevity, and stature for a wide range of species across
 105 biogeographic gradients and test our three core hypotheses, we first grouped the stem-level
 106 tree data into equally sized hexagon grids (size ~ 250,000 km²) and developed species-
 107 specific survival and growth generalized linear mixed effect models that included tree
 108 diameter at breast height (dbh) at the first census interval as a predictor variable and grid cell
 109 as a random effect (see materials and methods). We then used the survival and growth
 110 coefficients to fit size-dependent integral projection models (IPMs) and derive age-related
 111 traits from size-dependent probabilities for each species within each grid cell (see materials
 112 and methods) (15–17, 26–28). IPMs dynamically integrate size-dependent variability in
 113 survival and growth as a continuous process, which allowed us to use cross-sectional data
 114 over discrete time steps to make interspecific comparisons in how many years it takes trees to
 115 attain key milestones in their life cycle. We parameterized our IPMs using methods
 116 specifically developed for trees (27–29). Validations of IPM model outputs, relative to tree

117 ring data, showed this parameterization method can provide realistic estimates of tree age
118 demographics (27).

119

120 We used our species-specific IPMs and employed age-from-stage methods to calculate
121 several quantitative measures of growth, longevity, and stature. Specifically, we calculated
122 the number of years it takes for trees to grow from 10 to 20 cm in diameter (fig. S2, path a.2)
123 and grow from 10 cm to the 70th quantile of their size distribution (fig. S2, path a.1)
124 (hereafter referred to as *growth strategies*). The 10 cm in diameter lower bound threshold was
125 chosen because it was the size at which point trees were consistently monitored across the
126 forest networks and the 70th quantile threshold was chosen because it reflects a mature size at
127 which point trees have approached their ultimate position in the forest. We also calculated
128 two quantitative measures of tree longevity, including their average remaining life
129 expectancy from 10 cm in diameter and their maximal lifespan age (95% cohort mortality
130 from 10 cm), and a measure of maximal tree stature (size at maximal lifespan age) (fig. S2,
131 path b) (15–17). These mean estimates capture the pace of life for trees (growth, longevity,
132 and stature) based on observed climate conditions over the last century (derived from
133 dynamical data collected between 1926–2014, see materials and methods).

134

135 Our estimates of remaining life expectancy from 10 cm dbh range from 1.2 to 3,195 years,
136 with a mean value of 60 years in the tropics and 95 years in the extratropics (Fig 2a). This
137 trend matches our theoretical expectation of broadscale tree life history diversification
138 patterns (Fig. 1b) and confers with known tree longevity hot spots, whereby the oldest
139 recorded species occur in temperate conifer and boreal forests (12, 30). However, there was
140 also considerable overlap in the range of tree life expectancies across biomes (fig S3-S4),
141 table S2) and wide variability in how longevity relates to tree growth strategies and maximal
142 statures (Fig. 2b, fig S3-S4, and table S2). It is important to note that remaining life
143 expectancy from 10 cm dbh is a species-level mean estimate (i.e. is conditional on surviving
144 to 10 cm dbh). A low life expectancy, relative to the mean number of years it takes a species
145 to grow from 10-20 cm dbh, does not imply that no individuals will reach 20 cm dbh. Instead,
146 it implies that less than half of the individuals will survive to that size threshold.

147

148 ***Tree life history strategies do not strictly follow the fast-slow continuum (H1).***

149 To test the expectation that trees align along the fast-slow continuum (Fig. 1a, H1), we first
150 examined univariate trait correlations and found moderate support for trade-offs between tree
151 growth, longevity, and stature (fig. S5). For example, the number of years it takes trees to
152 grow from 10-20 cm in diameter was positively correlated to life expectancy (Pearson
153 correlation = 0.22) and maximal lifespan age (Pearson correlation = 0.21). Similarly,
154 maximal tree size was positively related to life expectancy (Pearson correlation = 0.41).
155 Interestingly, the strength of these pairwise correlations also suggests that tree age
156 demographics do not strictly follow a single axis of variation along the fast-slow continuum
157 (i.e., the assumption that growth is tightly coupled and inversely related to longevity and
158 maximal stature).

159

160 To examine the multidimensionality of tree age demographics (Fig. 1A, H1), we analyzed the
161 variance-covariance matrix of tree growth, longevity, and stature using a principal component
162 analysis (PCA). Highly correlated traits that captured redundant trait information were
163 excluded from the PCA (fig. S5), resulting in the inclusion of tree growth strategies (i.e.,
164 growth from 10 to 20 cm dbh and the 70th quantile of their size distribution), life expectancy
165 from 10 cm dbh, and maximal tree size (fig. S5). The first PC axis captured 46% of the life
166 history trait variation and was heavily weighted by tree growth dynamics (i.e., years to 20 cm

167 dbh and the 70th quantile size) (Fig. 2C). The PC loadings also showed that slow growth was
168 correlated with high life expectancy and large maximal size (table S3). The second axis
169 captured 28% of the trait variation. Interestingly, the directionality between the trait
170 correlations flipped, whereby slow growth was negatively correlated to life expectancy and
171 maximal size (table S3). The third axis was heavily weighted by tree life expectancy, with
172 high life expectancy being positively related to slow growth but negatively related to tree
173 maximal size (table S3). PCA analyses for tropical versus extratropical species retain
174 consistent patterns in the directionality of the trait correlations among the PC axes (table S3),
175 illustrating the modular and flexible nature of tree age demographics beyond the fast-slow
176 continuum within and among the Northern and Southern hemispheres.

177
178 To further contextualize how the variation in tree age demographics among the PC axes
179 shapes the overarching pace of life for trees, we used a K-means clustering algorithm to
180 group species into core demographic functional types (see material and methods subsection 3
181 and fig. S6). Using this clustering algorithm, which reduces the within-group sum of squares,
182 we found that fast-growing species aggregated into a single stature-longevity functional type
183 (Fig. 2C-2D, cluster 1). Conversely, conservative slow-growing species formed three distinct
184 clusters, including low, intermediate, and high stature-longevity functional types (Fig. 2C-
185 2D, clusters 2-4). The fast-growing species cluster matches the theoretical expectation of
186 ubiquitous resource limitations that constrain a species' ability to maintain high growth and
187 high survival simultaneously, leading to low life expectancies and small maximal sizes (Fig.
188 2C-2D, cluster 1). Yet, the emergence of three distinct clusters for slow-growing species
189 suggests conservative trees are less constrained in their pace of life. At one end of these three
190 conservative growth trait clusters were species with high life expectancies but small maximal
191 sizes (Fig. 2C-2D, cluster 4), and at the other end were species with low life expectancies but
192 large maximal sizes (Fig. 2C-2D, cluster 3). Clustering analyses for tropical versus
193 extratropical species indicate that the tropics retain the full range of demographic functional
194 types (fig. S7, four distinct clusters), Conversely, the extratropical species group into two
195 demographic functional types of predominantly slow-growing conservative clusters (fig. S7,
196 two distinct clusters). Together, these results provide key insight into the core groups of
197 demographic functional types that shape the structural complexity and dynamics of tropical
198 versus extratropical forests.

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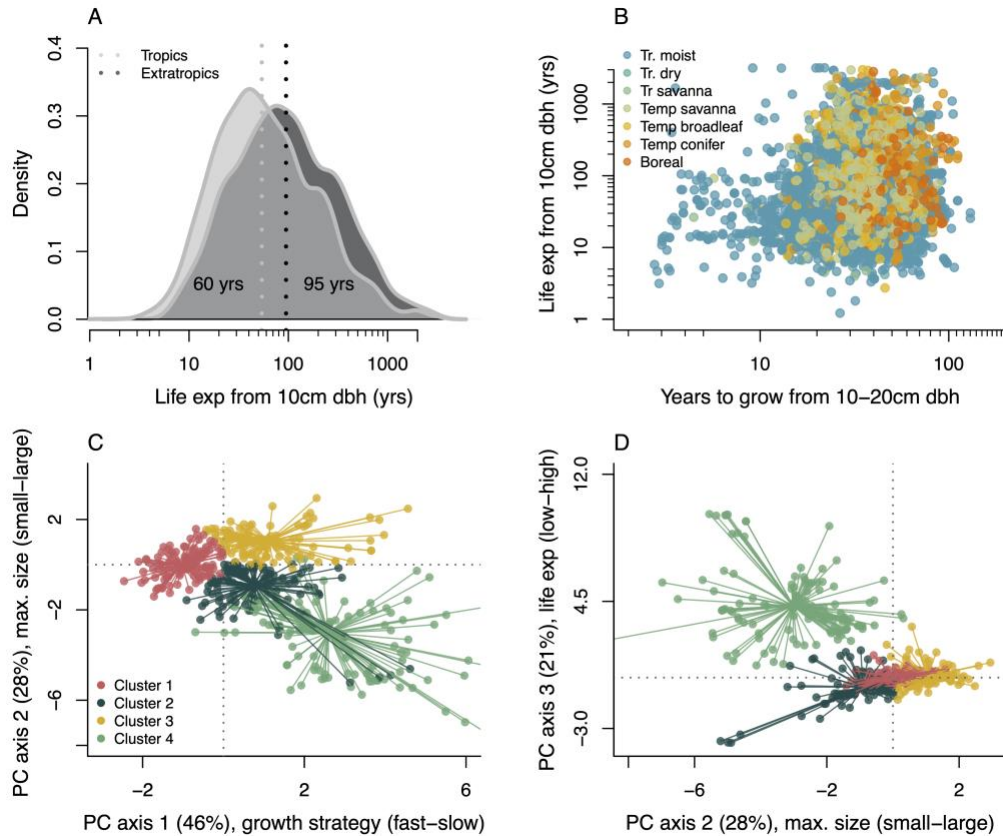


Fig. 2. Visual illustration of tree growth-longevity-stature relationships and core demographic functional types. The mean life expectancy is higher in the extratropics than in the tropics (A), with substantial variation between tree growth strategies and life expectancies (B) (N=6,847 i.e., species X grid ID). The other trait relationships are represented in fig. S8. The core growth-longevity-stature functional types are presented in C-D, which are determined using the K-means clustering algorithm of the life history trait PC scores. PC weights and trait correlations are reported in table S3. The frequency density (A) and the life history traits (B) are scaled by the natural log. The axes for A-D are scaled by the natural log. Data points are species-specific and are calculated using individual tree observations and size-dependent integral projection models (see materials and methods).

Our broadscale assessment of growth-longevity-stature relationships for a wide range of species across the Americas is consistent with trends derived from tropical forest plots, which found survival and growth rates over discrete size ranges differed substantially among species and diminished as trees attained larger sizes (31–37). Similarly, while tree-ring data showed that annual growth rates were negatively correlated with observed maximal ages (12), there was more variation in observed maximal ages for species with fast versus slow growth (12, 14). Together, these emergent patterns illustrate the modular and flexible nature of trees that extend beyond the fast-slow continuum (Fig. 2C-2D, figs. S3-S4) and highlight the tremendous variation in tree life expectancies across forest biomes (Fig 2A and figs. S3-S4), with some of the oldest living species having a remaining life expectancy > 2000 years (such as *Tsuga heterophylla* and *Sequoia sempervirens*).

Building on these foundational insights from predominantly tropical ecosystems, our results provide a novel perspective that contributes to our fundamental understanding of tree age demographics. By converting survival and growth rates over species life cycles to age-based traits, our results provide insight into the time it takes trees to reach their ultimate positions in the forest and their mean age at death (e.g., life expectancy). This allowed us to quantify the pace of life for a wide range of species across the Americas and identify the core demographic functional types more directly linked to carbon turnover. The emergence of the

230 slow-growth short-lifespan functional trait cluster is in line with previous research from
231 tropical forests, which showed that some short-stature trees had slow growth and low survival
232 (31, 32, 34, 38). This emergent trend may be an indication of maladapted species, or a
233 mediated effect of environmental disturbance (10, 32, 33). Conversely, it could be the result
234 of energetic investments in reproduction over species' lifespans (net reproductive rate) that
235 we were not able to capture in our analysis (5, 11, 31, 34). Regardless of the mechanisms,
236 our findings provide a novel perspective on the multidimensionality of tree age demographics
237 for a wide range of phylogenetic and geographical groups. Furthermore, our finding of
238 emergent differences in the number of demographic functional types in the tropics versus
239 extratropics provides novel insight into the mechanisms that shape the dynamics and
240 structure of forests across the Americas.

241 242 ***Weak coordination in the strength of life history trade-offs across biogeographic gradients*** 243 ***(H2).***

244 To test for emergent patterns in the strength of tree life history trade-offs across
245 biogeographic gradients (Fig. 1b, H2), we fit a multi-response Bayesian generalized mixed
246 effect model that included the first PC axis for each of three comprehensive sets of variables
247 related to soil, temperature, and precipitation as fixed effects and the phylogenetic relatedness
248 as a random effect (see materials and methods, table S4, figs S6-S8) (39). These abiotic
249 indexes were selected because they are known to strongly regulate photosynthetic capacity
250 and plant growth and are commonly assumed to induce life history trade-offs. This approach
251 allowed us to test for covariation in life history trait responses across soil, temperature, and
252 precipitation indexes and control for the effects of phylogenetic ancestry (40). These soil,
253 temperature, and precipitation variables were based on mean conditions from 1997-2013 (see
254 materials and methods, table S4), which overlap with the time window that our dynamical
255 tree data were collected. The expectation is that tree life history trade-offs are shaped by the
256 shared influence of abiotic factors and phylogenetic constraints, with colder temperatures and
257 lower resource availability pushing species toward the conservative end of the life history
258 trait spectrum (Fig. 1b, H2).

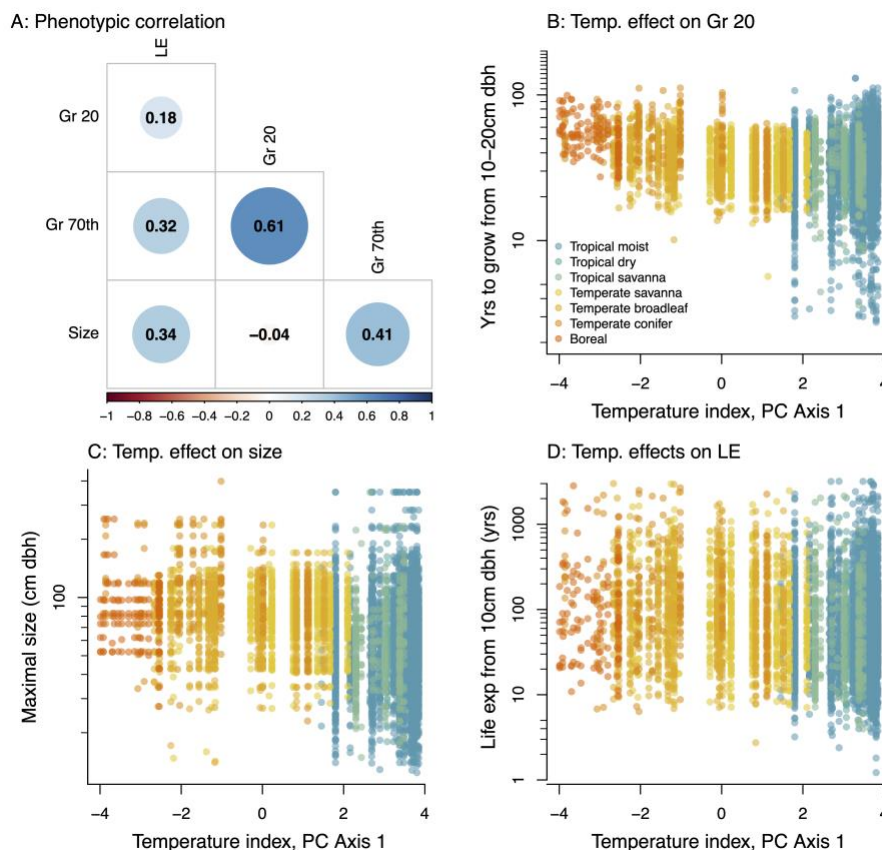
259
260 Our results show that there is a strong relationship between temperature and tree life history
261 traits, with colder temperatures being associated with conservative growth ($\beta = -0.02$, CI = (-
262 0.03, -0.01)) and high life expectancies ($\beta = -0.07$, CI = (-0.05, -0.08)) (Fig. 3 and fig. S12).
263 Conversely, our precipitation and soil indices had a weak effect on life history traits (fig. 12,
264 table S.5). Consistent with Amazon research (41), we found that tree life history traits were
265 phylogenetically conserved (Pagel's λ ranging from 0.88-0.99, fig. S14 and table S6). Yet,
266 we also found low phenotypic correlations among our life history traits, indicating that the
267 strength of trade-offs between tree growth, longevity, and stature do not strongly co-vary
268 across biogeographic gradients (Fig. 1b, H2). For example, the phenotypic correlation
269 between the number of years it takes trees to grow to 20 cm dbh and their life expectancy
270 from 10 cm dbh was 0.18 (Fig. 3a). Together, these results show that, while tree life history
271 traits are phylogenetically conserved (Δ DIC null model versus phylo. model = 76832),
272 growth-longevity-stature relationships are not driven by genetic linkages or shared selective
273 pressures that act on both traits independently over evolutionary time across broad-scale
274 resource gradients (table S6) (42).

275
276 While our results offer the most comprehensive assessment of tree age demographics across
277 broadscale resource gradients, it is important to note the data gap in the subtropics (i.e.,
278 across Mexico and northern Central America, Fig S1). This data gap could help explain the
279 noticeable difference in the range of life history trait strategies between the North American

280 temperate forests (low trait variation) and South American tropical forests (high trait
 281 variation) (Fig 3B-3D and fig S1). This data gap highlights the need for increased sampling
 282 efforts in these understudied regions of the world and should be a priority of future research
 283 and funding.

284
 285 Our findings are in line with trade-offs between physiological and morphological plant
 286 features linked to individual fitness and life history evolution, one reflecting leaf economic
 287 variables related to photosynthetic activity and growth potential and the other associated with
 288 morphological features related to light competition and plant height (43–45). Yet, similar to
 289 our results, the dominant axes of physiological and morphological plant features did not
 290 strongly co-vary across latitudinal gradients (44, 45). Together, our findings and previous
 291 research suggest that organismal function that supports rapid growth is not necessarily linked
 292 to organismal function that results in lower life expectancies and small maximal sizes. These
 293 emergent patterns suggest that rapid shifts in climate conditions may have divergent effects
 294 on the relationship between biomass accumulation in tree growth and biomass retention in
 295 tree longevity, with important implications for modeling the global carbon balance in a
 296 changing world (46).

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 300 **Fig. 3.** Tree life history traits across our temperature index (PC axis 1 for a comprehensive list of temperature
 301 variables, see materials and methods). Overall, we found low phenotypic correlations [variance-covariance of
 302 standardized traits] among tree growth, longevity, and stature, suggesting there is weak support for coordinated
 303 trade-offs over evolutionary time (i.e., organismal function that supports conservative growth does not
 304 necessarily trade-off with organismal function needed to maintain high longevity) (A). We also find a strong
 305 effect of temperature on tree life history traits (panels B–D), with little additional variation explained by soil or
 306 precipitation (see figs. S12-S13 and table S5). The temperature gradient is derived from a principal component
 307 analysis of nine temperature variables and represents a gradient from intermediate temperatures in the tropical
 308 moist forest of the southern hemisphere to colder temperatures in the boreal north (from left to right of the x-

309 axis). The y-axis is scaled by the natural log. Data points are species-specific and are calculated using individual
310 tree observations to fit size-based integral projection models for each species within each grid cell ID (total of
311 1,127 species and 6,847 trait values) (see materials and methods). Model coefficients of the multi-response
312 Bayesian model are reported in fig. S12 and table S5).

313

314 ***Demographic diversity varies predictably across biogeographic gradients (H3).***

315 To characterize the range of life history strategies that are expressed by trees across
316 broadscale biogeographic gradients, we first calculated the convex-hull volume in
317 demographic trait space within each grid cell (see materials and methods) (47) and compared
318 the relationship between the demographic trait diversity of forests and well-established
319 patterns in species richness. The convex-hull volume was calculated using the life history
320 trait PC scores for axes 1-3, which together captured 95% of the life history trait variation.
321 We then tested if the demographic trait diversity of forests varied predictably across
322 biogeographic gradients, and explored potential links between demographic trait diversity
323 and remotely sensed estimates of potential above-ground net primary productivity (NPP)
324 (Fig. 1c, H3, see materials and methods) (48). The expectation is that the diversity of life
325 history trait strategies that are expressed by trees should vary predictably across
326 biogeographic gradients, with higher demographic diversity being positively associated with
327 above-ground productivity.

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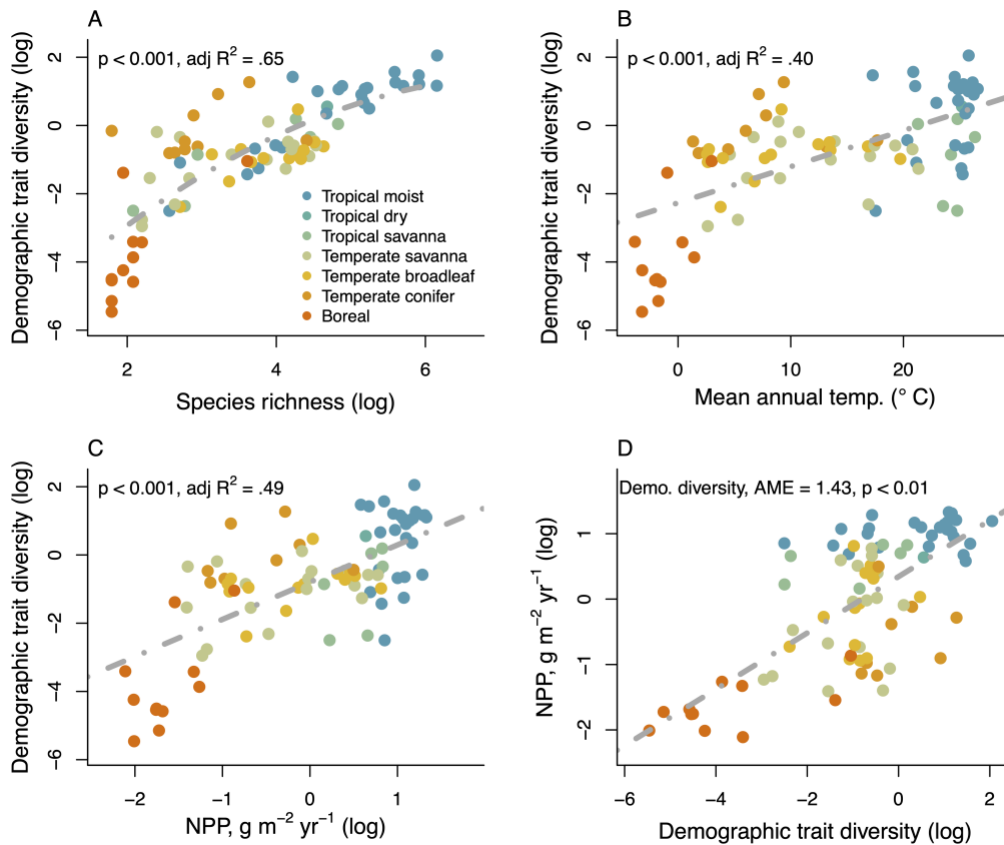
329 Our results illustrate that the demographic trait diversity of forests follows well-established
330 patterns in species richness (Fig. 4a, adj $R^2=0.65$, $p < 0.001$). We also found that the
331 demographic diversity of forests varied predictably across biogeographic gradients, with high
332 demographic trait diversity across warm tropical forests and low diversity of predominantly
333 slow-growing, long-lived species in the cold temperate and boreal forests (adj $R^2=0.40$, $p <$
334 0.001 , Fig. 4b and table S7). Lastly, we found a positive correlation between the demographic
335 diversity of forests and remotely sensed estimates of ecosystem productivity (Pearson
336 correlation = 0.71).

337

338 The emergence of a positive association between the demographic trait diversity and
339 ecosystem productivity is in line with two non-mutually exclusive hypotheses. From an
340 evolutionary perspective, ecosystem productivity is thought to drive species diversification
341 and niche differentiation (49). Conversely, following widely established relationships
342 between biodiversity and ecosystem function, more demographically diverse forests are
343 commonly assumed to have access to a larger resource pool and should thus be more
344 productive (50, 51). Here, we found moderate support for both hypotheses. Specifically, we
345 found that ecosystem productivity was predictive of demographic trait diversity across broad-
346 scale biogeographic gradients (adj $R^2=0.49$, $p < 0.001$, Fig. 4c, table S7). At the same time,
347 ecosystem productivity was jointly influenced by temperature (average marginal effect =
348 0.83, $p =0.04$, Fig. 4d) and demographic trait diversity (average marginal effect = 1.43, $p <$
349 0.001 , Fig. 4d). This positive association was consistent across the tropics (adj $R^2=0.26$, $p <$
350 0.01 , table S7) and extra-tropics (adj $R^2=0.84$, $p < 0.01$, Fig. 4d, table S7). It should be noted
351 that NPP was strongly correlated with mean annual temperature (Pearson correlation = 0.94),
352 which did not allow us to explicitly test for the individual and combined effect of these
353 variables on demographic trait diversity. While our broadscale analysis does not establish
354 causality in the direction of these relationships, it does highlight the inextricable link between
355 demographic trait diversity and ecosystem productivity across forest biomes.

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Fig. 4. The relationship between the demographic trait diversity of forests and ecosystem productivity (H3). We find that the demographic trait diversity is positively related to species richness (A), with increasing demographic trait diversity (i.e., convex-hull volume in life history trait space that is occupied by species) across a mean annual temperature gradient (B). In line with two non-mutually exclusive hypotheses in evolutionary biology and functional ecology, we find a positive association between demographic trait diversity and above-ground net primary productivity (NPP) (C and D). It is important to note that NPP was based on remotely sensed estimates and that these analyses do not establish causality in the directionality of this relationship (C and D). The fully parameterized model in panel D includes the demographic trait diversity and mean annual temperature. Demographic trait diversity and NPP were scaled to a mean of zero and a standard deviation of one. Average marginal effects (AME) represent the response per unit increase for each predictor variable.

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The established association between demographic trait diversity and ecosystem productivity is in line with emergent patterns derived from tropical forest plots, which found that the demographic composition of forests was predictive of empirically derived measures of above-ground carbon dynamics (32). Similarly, our findings match theoretical expectations that the pace of life of organisms within a community (e.g., life expectancy and generation time) should strongly regulate the relationship between carbon turnover (ecosystem fluxes) and carbon retention (ecosystem pools) (52). It is important to note that the association between demographic trait diversity and ecosystem productivity was derived from multi-year averages in remotely sensed NPP from 1997-2013 and mean estimates of tree growth-longevity-stature relationships based on the current distribution of species (i.e., derived from dynamical data collected from the 1900s-2000s). This approach did not allow us to account for potential biogeographic biases in the effects of human disturbance on species diversity (i.e., between boreal and tropical forests). Yet, by quantifying the current distribution of demographic functional types across broad-scale resource gradients, our results provide a powerful backdrop for parameterizing next-generation vegetation models to simulate forest carbon turnover rates across a range of current and future conditions.

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388 More generally, our analysis offers strong empirical support for the expectation of high
389 demographic trait diversity in tropical forests compared to temperate and boreal forests. This
390 multi-biome finding supports the community assembly theory of strong abiotic filtering in
391 boreal regions, resulting in a restricted species pool of predominantly slow-growing, long-
392 lived species (Fig. 1c, H3). This emergent pattern is congruent with known variability in
393 physiological leaf trait characteristics across biogeographic gradients (43–45), with
394 decreasing variation in leaf economic traits from lower to higher latitudes (53). Similarly, our
395 results match well-established species richness–productivity relationships across global
396 forests (51, 54) and community structure-productivity relationships (55). Yet, while it makes
397 intuitive sense that the demographic diversity of forest communities follows well-established
398 patterns in species richness (49, 50), our findings establish a more direct link to the
399 demographic mechanisms that generate global variation in ecosystem carbon turnover.

400

401 **Conclusion:**

402 Our broad-scale analysis reveals the remarkable diversity of life history strategies that exist
403 for tree species across the Americas. Weak trade-offs between tree growth, longevity, and
404 stature across biogeographic gradients demonstrate the modular and flexible nature of trees,
405 highlighting the diversity of evolutionary trajectories that have arisen to address the
406 ecological puzzle of survival. In addition, from a functional perspective, we find that while
407 acquisitive trees sequester carbon at faster rates, they also generally appear constrained to
408 smaller maximum sizes and shorter lifespans that translate to lower carbon storage and faster
409 carbon turnover. More importantly, we find that more demographically diverse forests tend to
410 be more productive at the ecosystem scale across the tropics and extra-tropics. These findings
411 have important implications for informing global restoration and conservation efforts, and for
412 understanding the fundamental feedback between biodiversity and climate change mitigation.

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834 by emailing the following networks: Alberta Agriculture and Forestry Division
835 <https://www.alberta.ca/permanent-sample-plots-program>, email: [af.fmb-](mailto:af.fmb-biometrics@gov.ab.ca)
836 [biometrics@gov.ab.ca](mailto:af.fmb-biometrics@gov.ab.ca), Saskatchewan Minister of Environment Forest Service Branch
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840

841 **Supplementary Materials:**

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876 **Supplementary Materials for**
877 **The pace of life for forest trees**

878
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904 **The PDF file includes:**

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926 **Materials and methods**

927 **1: Forest inventory data**

928 The dataset we used for this project was developed by a global community of network
929 partners, including members of the ForestPlots (18), TreeMort, and ForestGeo networks (20–
930 22), and includes dynamic tree data from thousands of long-term research plots and datasets
931 from National Forest Inventory networks (table S1). Combining and quality controlling this
932 network of dynamic tree data was led by the Global Forest Dynamics team, initiated by the
933 TreeMort project, and the ForestPlots network (18). The compiled dataset includes the
934 following information: tree ID, diameter at breast height (dbh) at 1.3 m of trunk height, status
935 (alive or dead), plot ID, plot coordinates, census year, and management history. Tree species
936 names were standardized across the datasets using The World Consensus on Vascular Plants
937 backbone (57) and the `Treemendous` R package (58). The point of dbh measurement
938 differed by > 30 cm in a few cases for predominantly tropical trees, in which case we
939 excluded the census points. To standardize our life history trait comparisons among species,
940 we excluded tree observation < 10 cm dbh. The time interval between census periods varied
941 from 1 to 36 years, with the highest occurrence of a 5-year census interval. Since time
942 intervals greater than 10 years were not represented across all datasets and were sparse
943 overall, we excluded census intervals >10 years. Thus, we focused on interval lengths that
944 were well-represented across the forest inventory datasets. The plot size ranged from 0.07 ha
945 to 50 ha among forest inventories. Tree observations with ‘unnatural’ modes of death (i.e.,
946 harvest, etc.) were removed from our analysis because they do not reflect ‘ambient’ life
947 history dynamics. We limited our analysis to species with >100 unique observations and
948 excluded species with < 5 observed deaths to maintain a sufficient sample size and excluded
949 tree observations with unknown species identity. We also exclude species that did not have
950 observations across species size ranges (i.e., there were only observations for large-sized
951 individuals, with no information for smaller individuals in the 10 cm dbh size range). To
952 balance our dataset across our biogeographic gradient, we randomly sub-sampled the North
953 American plots to equal the number of point observations in Central and South America (see
954 materials and methods). This allowed us to avoid potential biases due to imbalanced
955 sampling efforts across our biogeographic gradients. These initial filters reduced the dataset
956 from 5.6 million unique observations of 5,612 species to 3.2 million unique tree
957 measurements for 1,127 species (i.e., tree size and status) (Table S1).

958

959 All analyses were conducted in R version 4.2.0 (59). While p-values and R^2 are reported for
960 generalized linear models, we present results in terms of ‘evidence’ versus significance
961 levels, following (60).

962

963 **2: Integral projection models**

964 *2.1 Assigning individual tree observations to hexagon grid IDs*

965 To capture the full range of life history strategies across a latitudinal gradient, we used
966 Google Earth Engine to assign each tree measurement (dbh and status) to equal area hexagon
967 grids (size ~ 250,000 km²) (fig S1). The hexagon grid ID was then included as a categorical
968 random effect in our species-specific survival and growth models. This allowed us to
969 incorporate intra-specific variation in tree life history traits (growth strategies, stature, and
970 longevity) across broadscale biogeographic gradients (see material and methods, subsection
971 2.2-2.5). The unique hexagon grid ID were also used to calculate the demographic trait
972 diversity (convex-hull volume in life history trait space that is occupied by species within
973 each grid) and characterize the relationship between demographic trait diversity and above-
974 ground net primary productivity (see material and methods, subsection 4).

975

976 2.2 Species-specific survival and growth models

977 To estimate size-dependent survival and growth rate coefficients for our integral projection
978 models (IPM), we fit species-specific generalized linear mixed-effect models, using the
979 `glmer` and the `lmer` function in the `lme4` package (61). Here y_{ij} is the response for
980 individual i in grid cell j . The random grid cell effect, μ_j , and error, ϵ_{ij} , are added to the
981 intercept, b_0 . The effect of size, x_{ij} , for individual i in grid cell j is measured by the slope,
982 b_1 . Our survival model included ‘initial tree size’ (dbh) and the square of tree size (centered
983 natural log of dbh) as predictor variables, survival at the second census interval as the
984 response variable, and grid ID as a random effect. Similarly, for our growth model, we
985 included initial tree size (dbh) as a predictor variable, size at the second census interval as the
986 response variable, and grid ID as a random effect. Tree size was natural log-transformed for
987 both models.

988

$$989 y_{ij} = \beta_0 + \beta_1 x_{ij} + \mu_j + \epsilon_{ij}$$

990

991 To account for variation in forest inventory census intervals, we standardized the survival and
992 growth rate estimates to a one-year time-step. This was relatively straightforward for survival
993 but more involved for growth. Specifically, for our survival model, we fit a logistic
994 regression with a complementary log-log link function and included the census interval
995 length as an offset, which effectively standardized the survival rate to a 1-year timestep. To
996 standardize the time step for our growth model, we tested two approaches. First, we
997 calculated the relative growth rate (RGR), which is the geometric mean of the ratio of log tree
998 sizes over the time interval, $rgr = (s_t/s_0)^{1/t}$. Here, rgr is the annualized relative growth
999 rate, s_0 is the log of the initial size, and s_t is the log of size at the end of the time interval, t .
1000 We calculated size in the next year for all initial tree observations by multiplying the initial
1001 size by the annualized growth rate, $s_1 = s_0 rgr$. This method implicitly assumes a zero
1002 intercept in the growth function. To test if the assumption of a zero intercept influenced our
1003 results, we explored a second method that directly computes the annual slope and intercept
1004 for a variable time interval. The algebraic expression that represents the compounding effect
1005 of adding an intercept in each annual estimate within a time series results in a nonlinear
1006 expression. Thus, we employed the nonlinear least squares function to estimate the following
1007 model, $s_t = b_0(1 - b_1^t)/(1 - b_1) + s_0 b_1^t$. Visual inspection of coefficient plots and
1008 model fit plots using both methods showed highly similar results. Due to the extended
1009 computation time for the nonlinear models, we chose the less complex RGR method, and
1010 converted final size, s_t , to size at one year, s_0 , before fitting our growth regressions.

1011

1012 Model evaluation of our vital rate regressions showed that initial tree size captured a high
1013 amount of variance for our growth models and was a significant predictor of tree size in the
1014 following timestep ($R^2=0.83-0.99$, and $p < 0.001$). Similarly, initial size was a significant
1015 predictor of survival ($p < 0.001$). It is important to note that, for nonlinear regression models,
1016 the R^2 does not represent the proportion of variance explained by the predictor variable and is
1017 thus not a useful metric for evaluating the goodness of fit for logistic regression. For this
1018 reason, we did not report this value for our survival models.

1019

1020 2.3 Size-dependent integral projection model

1021 An integral projection model (IPM) is a tractable way to derive life history traits, using
1022 continuous size-based survival and growth rates. To calculate age-related traits from size-
1023 dependent probabilities, we used a key component of an IPM, the survival-growth kernel, \mathbf{P} ,
1024 and with methods developed by (26), we projected the future fate of living individuals. By

1025 excluding reproduction, this model captures cohort dynamics based on survival and growth
1026 rates. A change in the size-specific density of trees, $n(t)$, is projected using the following
1027 equation:

$$1028$$
$$1029 \quad n(y, t + 1) = \int_L^U \mathbf{P}(y, x)n(x, t)dx$$
$$1030$$

1031 where the kernel $\mathbf{P}(y, x)$ is a non-negative surface of survival and growth transition
1032 probabilities of individual plants from size x at time t to size y at time $t+1$. L and U represent
1033 the minimum and maximum plant size thresholds respectively, with the lower threshold L
1034 being set to 10 cm dbh and the upper size threshold being set to the species maximal tree size.
1035 \mathbf{P} is composed of two functions,

$$1036$$
$$1037 \quad \mathbf{P}(y, x) = s(x)g(y, x)$$
$$1038$$

1039 where $s(x)$ represents the survival rate of an x -sized individual and growth $g(y, x)$ is the
1040 probability density for individuals of size x transitioning to size y over a 1-year timestep.
1041 These parameters are derived from the species- and grid-cell-specific survival and growth
1042 regression models that we parameterized with empirical field data (see materials and
1043 methods, subsection 2.2).

1044

1045 Our species- and grid cell-specific IPMs were informed by hundreds to thousands of unique
1046 tree measurements across a large portion of a species life cycle (from 10 cm dbh to their
1047 maximal size) and across a wide range of local conditions (light and nutrient conditions,
1048 varying levels of density dependence, etc.). This framework allowed us to explicitly account
1049 for survival-growth trade-offs that operate across species life cycles and thus provide a
1050 tractable way to calculate robust species-level mean life history trait estimates (passage time
1051 and life expectancy) across broadscale biogeographic gradients (i.e., for each species by grid
1052 cell combination).

1053

1054 *2.4 IPM kernel integration and diagnostic checks*

1055 The relatively slow incremental growth of trees can create a sharp ridge along the diagonal of
1056 the probability surface, \mathbf{P} . Defining this ridge with sufficiently high resolution becomes
1057 computationally expensive when numerically integrating the kernel, \mathbf{P} , and failing to do so
1058 can lead to biologically unreasonable column sums, which theoretically equal the survival
1059 rate for each size class. Previous work indicates that IPM model outputs for trees (first
1060 passage times, etc.) are sensitive to the dimension used for kernel integration, whereby a
1061 small kernel size (i.e., 10 size categories) can underestimate tree age demographics and a
1062 large kernel size (i.e., 1,000 size categories) can overestimate tree age demographics. Thus,
1063 previous works show that a kernel dimension equivalent to a tree size transition rate between
1064 0.1-1 cm in diameter is needed to produce realistic tree age demographics for trees (27).
1065 Thus, to balance the need for high biological resolution and reduced computation time and
1066 memory, a mixed kernel integration approach has been established for trees (27–29).
1067 Following this mixed kernel integration approach, we selected a moderately large resolution
1068 for the overall kernel, 600×600 , and used the standard mid-bin integration for most of these
1069 cells. Along the growth ridge, we used a Gaussian-Legendre quadrature integration, whereby
1070 each cell was divided into 420 sub-rows (i.e., along the size-dependent growth probability
1071 density) and 3 sub-columns. The result was a 600×600 kernel with a well-defined ridge and
1072 biologically reasonable column sums and element values.

1073

1074 *2.5 Life history trait calculations and age-from-stage methods*

1075 Following numerical integration, the survival-growth kernel, \mathbf{P} , was used to calculate a series
 1076 of life history traits, including first passage time, life expectancy from 10 cm dbh, and
 1077 maximal lifespan. These life history traits were derived from survival and growth data that
 1078 were collected between 1926 and 2014. These life history traits are thus representative of tree
 1079 age demographics based on observed climate conditions over the last century.

1080

1081 Passage time: First passage time captures the number of years it takes for an x -sized
 1082 individual to reach a predetermined size threshold for the first time. Using the kernel, \mathbf{P} , we
 1083 calculated passage time τ_{ij} from initial size class j to the target size class i , following (15–
 1084 17) :

1085

1086

$$\tau_{ij} = \frac{(\mathbf{I} - \mathbf{P}')^{-2}(i, j)}{(\mathbf{I} - \mathbf{P}')^{-1}(i, j)}$$

1087

1088 where \mathbf{I} is an identity matrix and \mathbf{P}' is identical to \mathbf{P} except for column j , which is replaced
 1089 with zeros in all cells. The initial size for all passage time calculations was 10 cm dbh
 1090 because this is the size when all species were tagged in our standardized dataset. Throughout
 1091 the main text, we refer to our passage time to target size thresholds as tree *growth strategies*.

1092

1093 To make biologically reasonable comparisons in growth strategies among species, we
 1094 calculated first passage times to 20 cm dbh (fig. S2, path a.2) and the 70% quantile of
 1095 observed maximal size (fig. S2, path a.1). The 20 cm target size threshold serves as a time-
 1096 standardized rate of growth for all species in our dataset. However, the passage time from 10
 1097 to 20 cm dbh may represent the time to max size for the smallest statured species in our
 1098 dataset (i.e., 20 cm size is the 95% quantile of maximum size for small trees). Conversely,
 1099 this target threshold captures early life growth dynamics for larger tree species. To capture
 1100 growth dynamics over a wider range of a species life cycle, we also calculated the first
 1101 passage time from 10 cm DHB to the 70% quantile of the observed size distribution for each
 1102 species across the full dataset. This quantile-based target size varied among species and
 1103 represented an above-average size at which point a tree has approached its ultimate position
 1104 in the canopy, whether that be a short-statured understory tree that reaches its maximal height
 1105 in 5-years or a tall dominant canopy tree that grows for decades before reaching their ultimate
 1106 position in the canopy.

1107

1108 Life expectancy: To examine differences in early-life tree mortality patterns and survivorship
 1109 trajectories over species lifespans, we calculated life expectancy from size class i to size class
 1110 j using (fig. S2, path b) (1, 15–17):

1111

1112

$$\eta_j = \sum_{i=1}^n (\mathbf{I} - \mathbf{P})^{-1}(i, j)$$

1113

1114 where \mathbf{I} is an identity matrix. Life expectancy from 10 cm dbh was calculated using the
 1115 equation above with $j = 1$. For total life expectancy conditional on reaching the target size
 1116 classes (either 20cm dbh or the 70th quantile of a species size distribution), we determined
 1117 which column, j , corresponded to the target class and then added the time to reach size class j
 1118 to the remaining life expectancy for size class j , i.e., $\tau_{ij} + \eta_j$. It is important to note that life
 1119 expectancy is highly left skewed by early life mortality, with smaller individuals having
 1120 higher mortality than larger individuals. A low life expectancy to a given size (e.g., 20 cm
 1121 dbh) does not imply that no individuals of a given species will survive to that size threshold

1122 (i.e., it is not a maximal). It simply means that individuals that do live longer represent the
1123 lucky few, resulting in a higher proportion of smaller individuals within a population.

1124

1125 Maximal lifespan: We calculated the maximal lifespan as the age at which the cumulative
1126 mortality was 95%. Starting with a cohort composed exclusively of 10 cm dbh individuals,
1127 we projected the cohort through time using the recursion equation $n(t + 1) = \mathbf{P}n(t)$. The
1128 simulation limit was set to 10,000, which resulted in the exclusion of 38 species. We
1129 normalized the initial cohort to sum to one and identified the time step, x , where the sum of
1130 $n(x)$ was less than 0.05. The number of years, x , is thereby the age at which less than 5% of
1131 the initial cohort is still alive. At this maximal age, x , we also calculated the mean size from
1132 the population density, $n(x)$, which we refer to in the main text as *size at maximal age*.

1133

1134 Model valuation: We parameterized our IPMs using methods that were specifically
1135 developed for cross-sectional tree data (see materials and methods, subsection 2.4) (27–29)
1136 and used age-from-stage methods to calculate age-related demographics (15–17). Validation
1137 of age-related outputs would require an extensive longitudinal dataset that tracks the fate of
1138 individual trees over their life cycle (which would require decades to millennia of
1139 longitudinal data for long-lived trees). This level of longitudinal data is rarely available and is
1140 also why cross-sectional forest inventory data and age-from-stage estimates are so valuable.
1141 The next best validation method relies on tree ring data. Previous validations of IPM model
1142 outputs for trees with paired tree ring data showed that IPMs can produce realistic estimates
1143 of tree age demographics (27). Similarly, IPM model validations, using 34-year time series
1144 data, showed that IPM outputs match time series data over snapshots of species life cycles
1145 (62). Together, previous validation efforts for IPMs using time series and tree ring data
1146 suggest model outputs can accurately capture the age dynamics for long-lived species with
1147 slow growth and low mortality. We did not have such paired time series or tree ring data to
1148 compare with the wide range of species included in our analysis. Yet, while not directly
1149 comparable, the directionality of our biome-level comparisons in tree longevity was
1150 congruent with longevity estimates from tree ring data (12). Specifically, that assessment
1151 showed that the mean longevity for trees in the tropics and extratropics were 186 ± 138 and
1152 322 ± 201 years respectively (12). In our study, we found that the mean life expectancy for
1153 trees in the tropics and extratropics were 60 and 95 years respectively (see Figure 2).

1154

1155 While the directionality of our biome-level patterns in tree longevity is in line with
1156 broadscale trends derived from tree ring studies, there are several reasons why it does not
1157 make conceptual sense to make one-to-one comparisons in measures of tree longevity
1158 derived from IPMs from that of tree ring-studies that differ in temporal times scales and
1159 geographical scope. First, age estimates from tree-ring studies can be heavily influenced by
1160 anthropogenic disturbance and climate-induced shifts in tree growth-longevity trade-offs.
1161 Second, the sampling framework used for tree ring studies tends to target the largest trees in
1162 areas of low anthropogenic disturbance. Yet, considering that the oldest trees can be up to
1163 half the size of the largest trees (30), it is impossible to derive standardized metrics of tree
1164 age (e.g., mean life expectancy) from tree ring studies and thus they serve as a coarse
1165 estimate of tree longevity.

1166

1167 **3: Tree life history trade-offs and core demographic functional types**

1168 To test for broadscale tree growth- longevity-stature trade-offs, we conducted a correlation
1169 analysis, using the `cor` function in the `stats` package (59). To further contextualize the full
1170 dimensionality of growth- longevity-stature trait constellations, we conducted a standard
1171 principal component analysis (PCA) of the life history traits, using the `princomp` function

1172 in the `stats` package (59). All traits included in the PCA were scaled to have a mean of
1173 zero and a standard deviation of one. Highly correlated traits that captured redundant trait
1174 information were dropped from the PC analysis to avoid issues of multicollinearity, resulting
1175 in the inclusion of passage time to 20 cm dbh, passage time to 70th quantile size range, size at
1176 maximal age, and life expectancy from 10 cm dbh (fig. S3). We then used the K-means
1177 machine learning algorithm to identify the core growth- longevity- stature groupings, setting
1178 the maximum number of iterations to 15 and the number of random starting points to 50,
1179 using the `kmeans` function in the R `stats` package. To identify the optimal number of
1180 clusters, we calculated the coefficient scores and the total within sum of squares across
1181 cluster sizes, using the `silhouette` and `wss` functions in the R `cluster` package (63).
1182 The sum of squares elbow method (`wss`) and the silhouette method both indicated that 4 was
1183 the optimal number of clusters, and the silhouette method identified 3 as the second optimal
1184 number of clusters (fig. S5).

1185

1186 **4: The strength of tree life history trade-offs across biogeographic gradients:**

1187 To examine the independent and joint effects of soil, precipitation, and temperature on tree
1188 life history traits we used a multivariate Bayesian generalized mixed effect model, using the
1189 `MCMCglmm` package in R (39). We included the same four life history traits used in S3 as
1190 response variables (i.e., time to 20cm, time to 70th percentile of size, size at maximal age, and
1191 life expectancy from 10cm dbh) and soil, precipitation, and temperature indexes as fixed
1192 effects (described below). To account for the signature of phylogenetic ancestry on tree life
1193 history traits, we included the phylogenetic distances between species as a random effect (39,
1194 42). We also controlled for the covariation between our life history traits and the residual
1195 variation within each trait response to account for potential trade-offs among life history traits
1196 (39). To meet model assumptions, we scaled our life history traits and climate variables to a
1197 mean of zero standard deviation of one.

1198

1199 Biogeographic indexes: We included soil, precipitation, and temperature indexes in our
1200 Bayesian model because they are known to strongly regulate photosynthetic capacity and
1201 plant growth and are commonly assumed to induce life history trade-offs. To avoid issues
1202 with multicollinearity and reduce model complexity, we first extracted a comprehensive set
1203 of variables related to soil, temperature, and precipitation from WorldClim and SoilGrids
1204 (64) and calculated the mean of these variables for each grid cell, using Google Earth Engine
1205 (see fig. S1 and table S4). We then assigned each variable to a categorical soil, climate, or
1206 precipitation grouping (table S4) and conducted a principal component analysis for the list of
1207 variables within each group. The first PC axis for each group (e.g., soil, precipitation, and
1208 temperature indexes) were then included as fixed effects in our Bayesian generalized mixed
1209 effect model. These soil, temperature, and precipitation indexes represent multi-year mean
1210 conditions from 1997-2013. These multi-year averages capture the mean conditions that
1211 correspond with the dynamical data used to calculate our age-related demographic traits (e.g.,
1212 mean life expectancy of trees based on observation data from the 1900s-2000s).

1213

1214 Phylogenetic tree: We constructed the time-calibrated phylogeny for all tree species using the
1215 Qian and Jin 2016 megaphylogeny (65) for plants and the `V. Phylomaker2` (66) package
1216 in R. The three species that were missing from the phylogenetic backbone were added to the
1217 tree using the most closely related species within the same genus, following Cardoso et. Al
1218 2013 (67).

1219

1220 Bayesian model construction and validation: The multivariate Bayesian models were run with
1221 15,000 iterations, a burnin of 5,000, and a thinning rate of 10, with an effective sample size

1222 of 1000 MCMC samples. Model convergence was assessed via inspection of trace and
1223 density plots. Posterior means and upper and lower credible intervals for the fixed and
1224 random effects were used to examine the shared influence of phylogenetic ancestry and soil,
1225 temperature, and precipitation variables on mean life history trait differences across our
1226 biogeographic gradient (figs. S9 and S11, table S5-S9). The estimated variance coefficients
1227 for the fixed and random effects are reported in figs. S9 and S11, Table S5-S9. Credible
1228 intervals that do not overlap with zero are suggestive of mean trait differences across
1229 broadscale soil, temperature, and precipitation gradients. The phenotypic variance-
1230 covariance, genetic variance-covariance and residual variance-covariance, and Pagels lambda
1231 (i.e., phylogenetic heritability) are reported in Table S6.

1232

1233 **5: Demographic trait diversity across biogeographic gradients**

1234 To characterize the range of life history strategies that were occupied by species across
1235 broadscale biogeographic gradients, we first calculated the 3-dimensional convex-hull
1236 volume of tree growth-longevity-stature strategies (i.e., demographic trait diversity) using the
1237 life history trait PC scores for axes 1-3 within each grid cell (47). The convex-hull volume is
1238 a widely used method to test for macroevolutionary signatures of trait diversity and habitat
1239 filtering (47). To avoid known effects of variable plot sizes between North and South
1240 America (see table S1) and minimize the potential effects of local scale disturbance events on
1241 broadscale diversity patterns, we balanced the number of individual tree observations across
1242 our biogeographic gradient (see materials and methods, section 1) and calculated the convex
1243 hull volume across equal sized hexagon grids. Four of our grid cells did not meet the
1244 minimum number of species that were needed to calculate the convex-hull volume (i.e.,
1245 included < 4) and were thus excluded from our analysis.

1246

1247 The convex hull volume of each grid cell was then used to test for predictable variation in
1248 demographic trait diversity across biogeographic gradients, using a generalized linear model
1249 (Fig 1c, H3). We used mean annual temperature as our predictor variable because it was
1250 found to have the strongest effect on our univariate traits (see Figs. 3 and S9). We also tested
1251 for two non-mutually exclusive expectations of a positive relationship between demographic
1252 diversity and ecosystem productivity, including the expectation from an evolutionary theory
1253 perspective (i.e., productivity should drive diversification) and functional perspective (i.e.,
1254 more diverse systems should be more productive). To test these non-mutually exclusive
1255 hypotheses (Fig 1c, H3), we used linear and generalized linear models. The predictor
1256 variables were scaled to a mean of zero and a standard deviation of one. We assessed the
1257 normality of the residuals and, when needed, we transformed the variable by the natural log.
1258 It is important to note that mean annual temperature and our remotely sensed estimate of
1259 above-ground net primary productivity (NPP) were based on multi-year mean conditions
1260 from 1997-2013 (48). These multi-year averages serve as coarse proxies of the conditions
1261 related to the mean pace of life for trees over the last century (life expectancies, etc.), which
1262 were derived from dynamical data collected from 1926 to 2014.

Supplementary Figures:

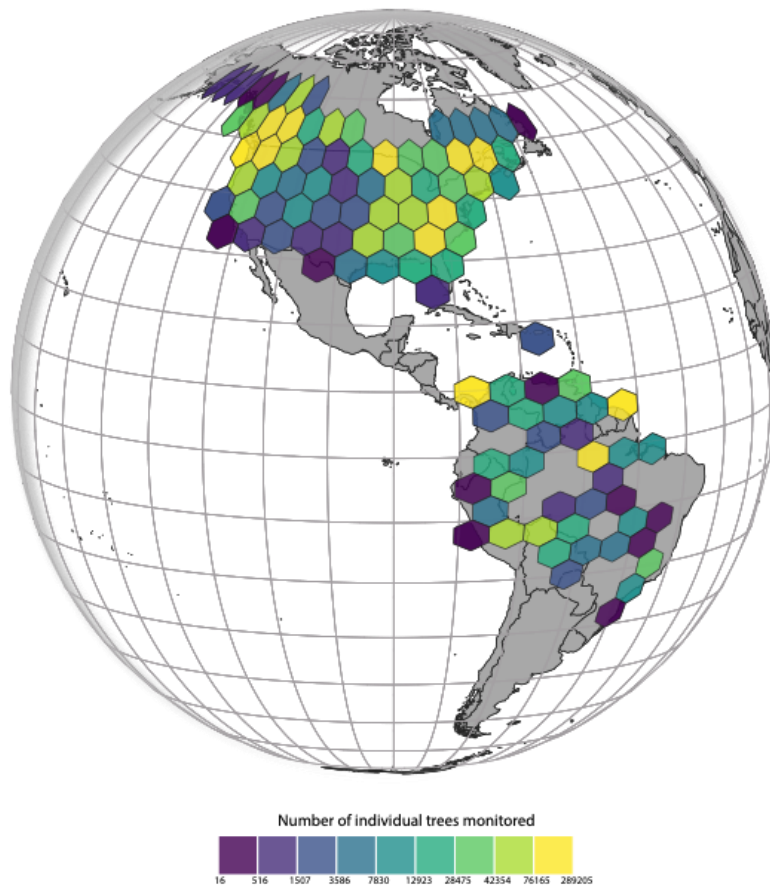


Figure S1. Map of equal area hexagon grids (size ~ 250,000 km²) that were used to calculate our species by grid ID life history traits. The heatmap represents the total number of tree observations within each grid cell.

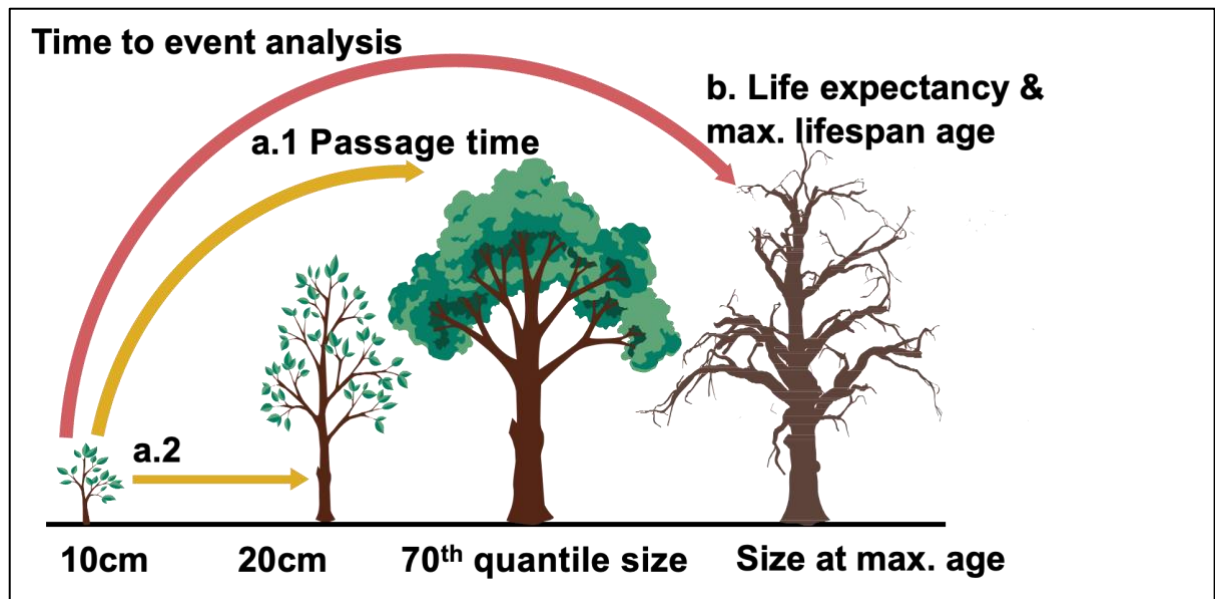


Figure S2. Visual illustration of life-history traits, including first passage times from 10 to 20 cm dbh and the 70% quantile of the observed size distribution, the life expectancy from 10 cm dbh, and the maximal lifespan age and size.

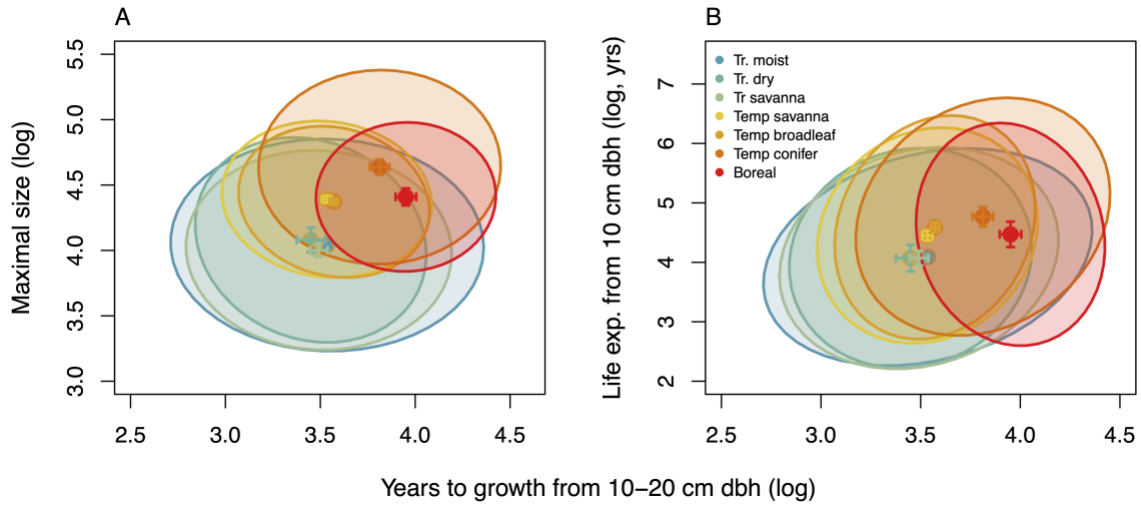


Figure S3. The relationship between growth-longevity-stature relationships across forest biomes, with means and 95% CI values. Ellipses capture the 70th quartile of trait variation among biomes (i.e., range of life history trait occupied by species across biomes).

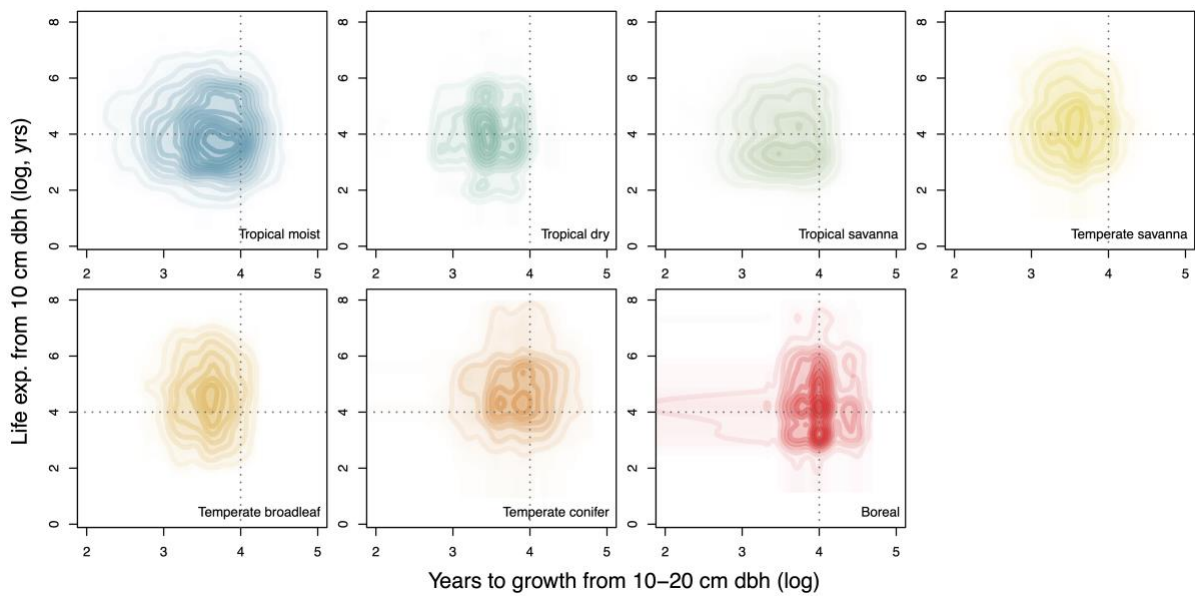


Figure S4. Heatmaps across biomes that show the relationship between tree growth strategies and the remaining life expectancies from 10 cm dbh. Color transparency represents the concentration of species with similar trait values, with less transparent colors representing a high concentration of species with similar trait values within biome.

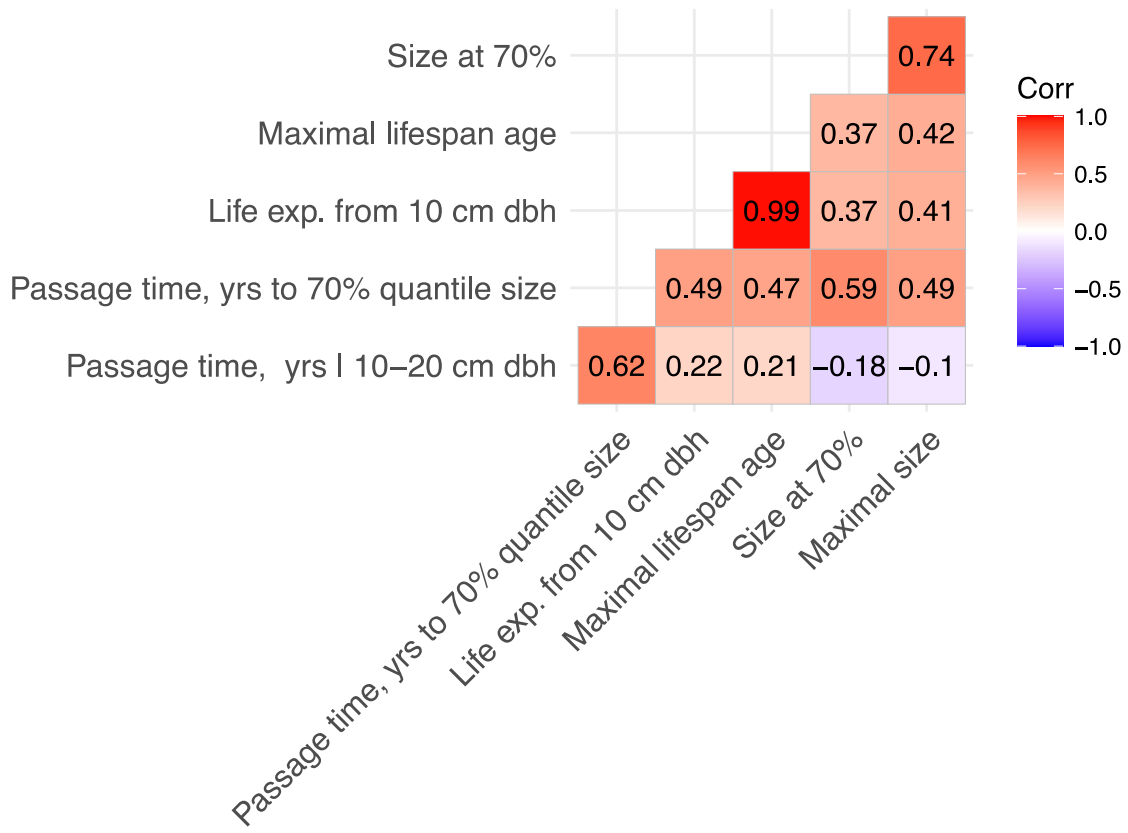


Figure S5. Life history trait correlations.

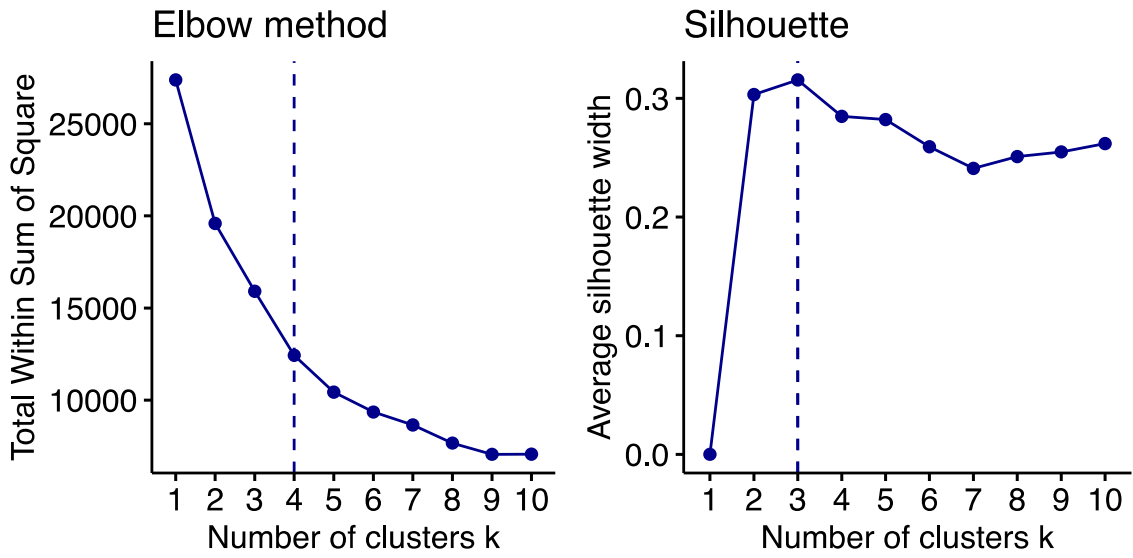


Figure S6. Optimal number of clusters using the elbow total within sum of square and Silhouette methods, including all species.

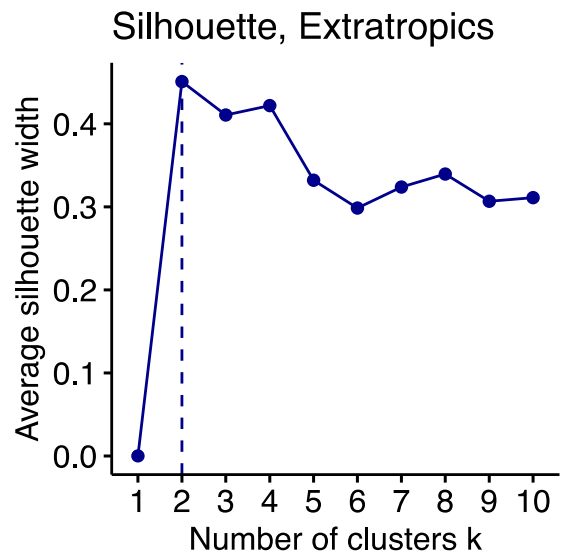
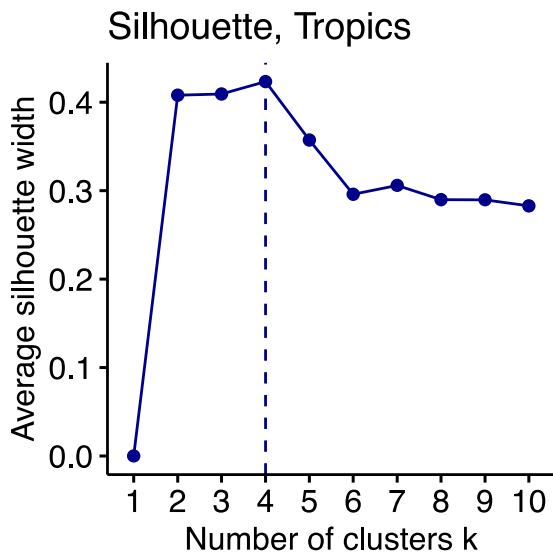
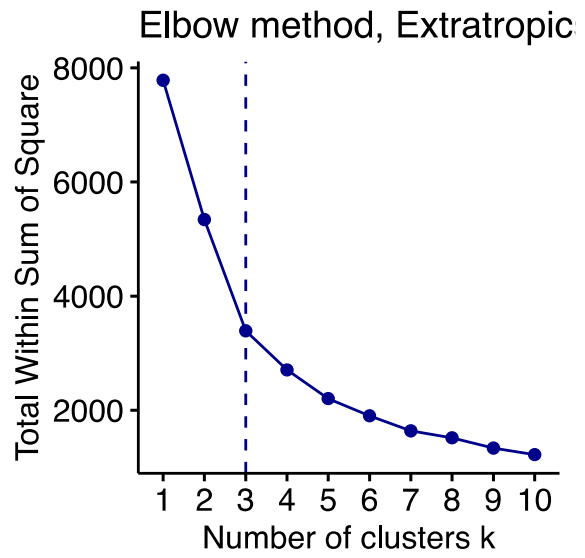
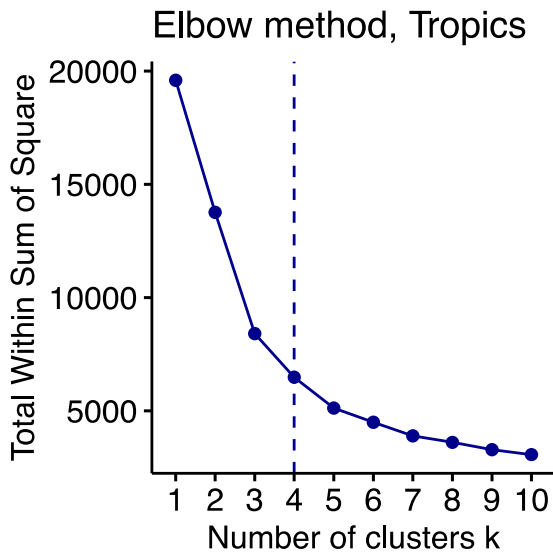


Figure S7. Optimal number of clusters using the elbow total within sum of square and silhouette methods for species in the tropics and extratropics.

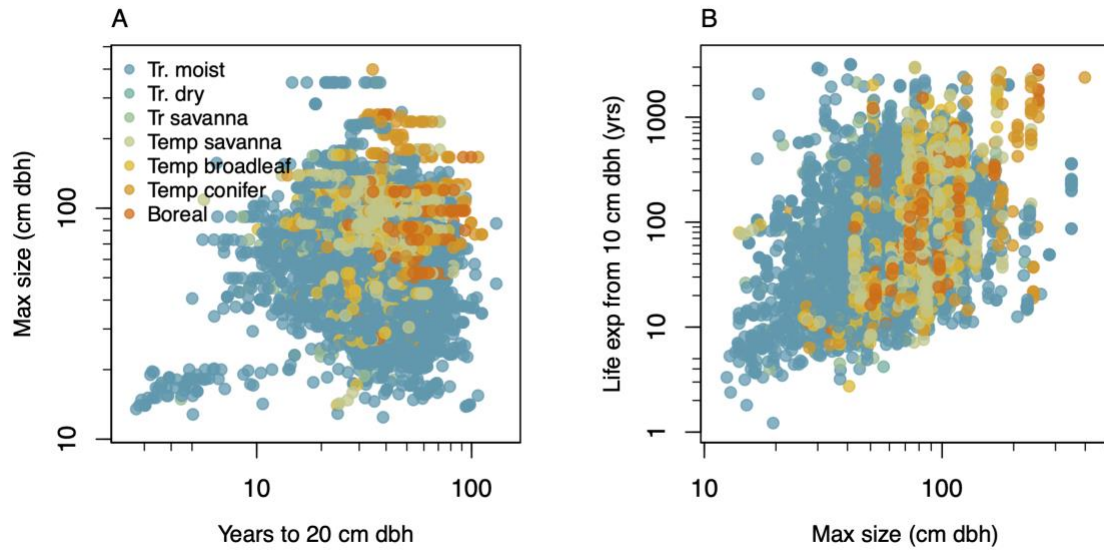


Figure S8. Visual illustration of tree growth- longevity-stature relationships for all species within each grid cell (total of 1,127 species and 6,847 trait values, i.e., species \times grid).

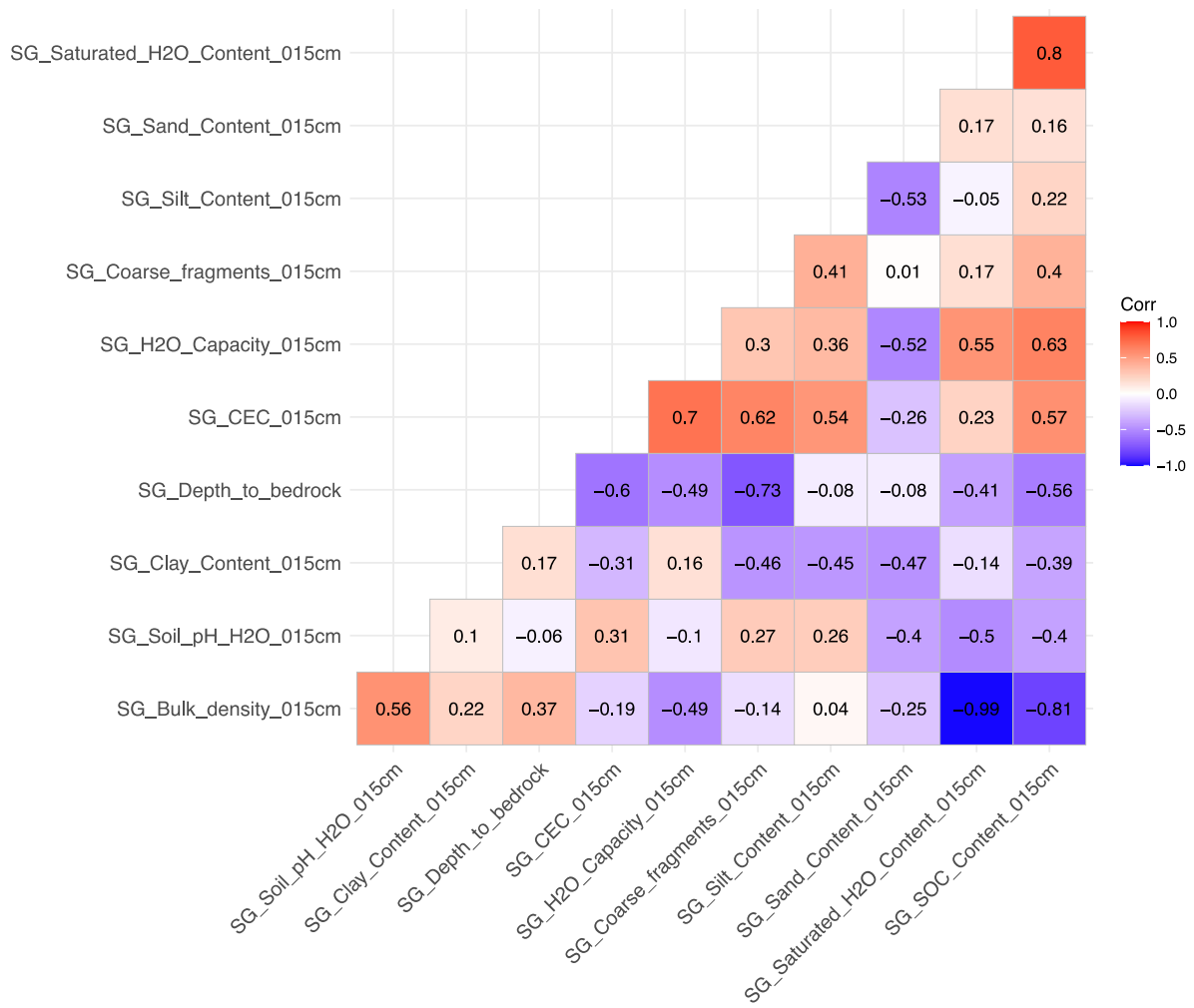


Figure S9. Correlations among soil variables, extracted from soil grids (GS)(64).

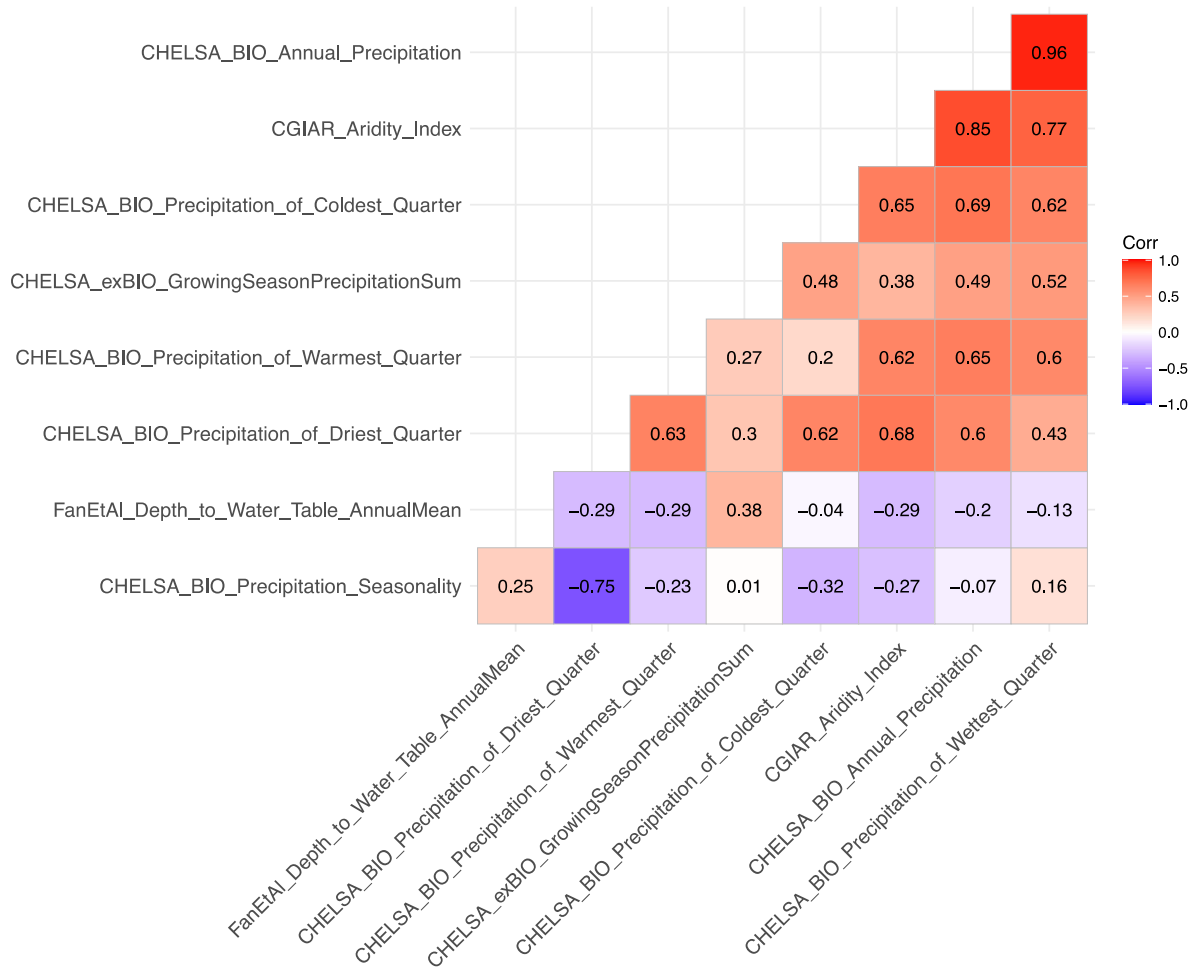


Figure S10. Correlations among precipitation variables.

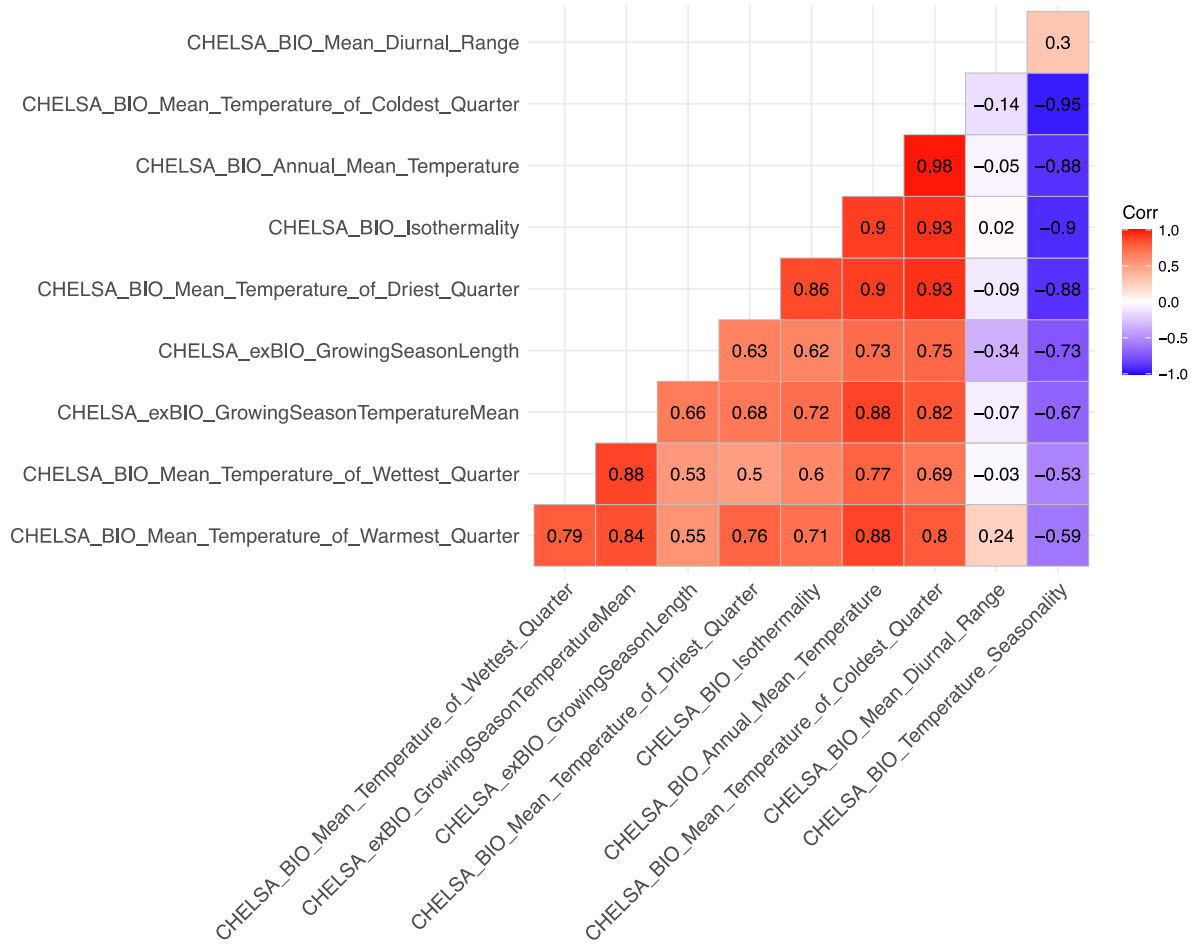


Figure S11. Correlations among temperature variables.

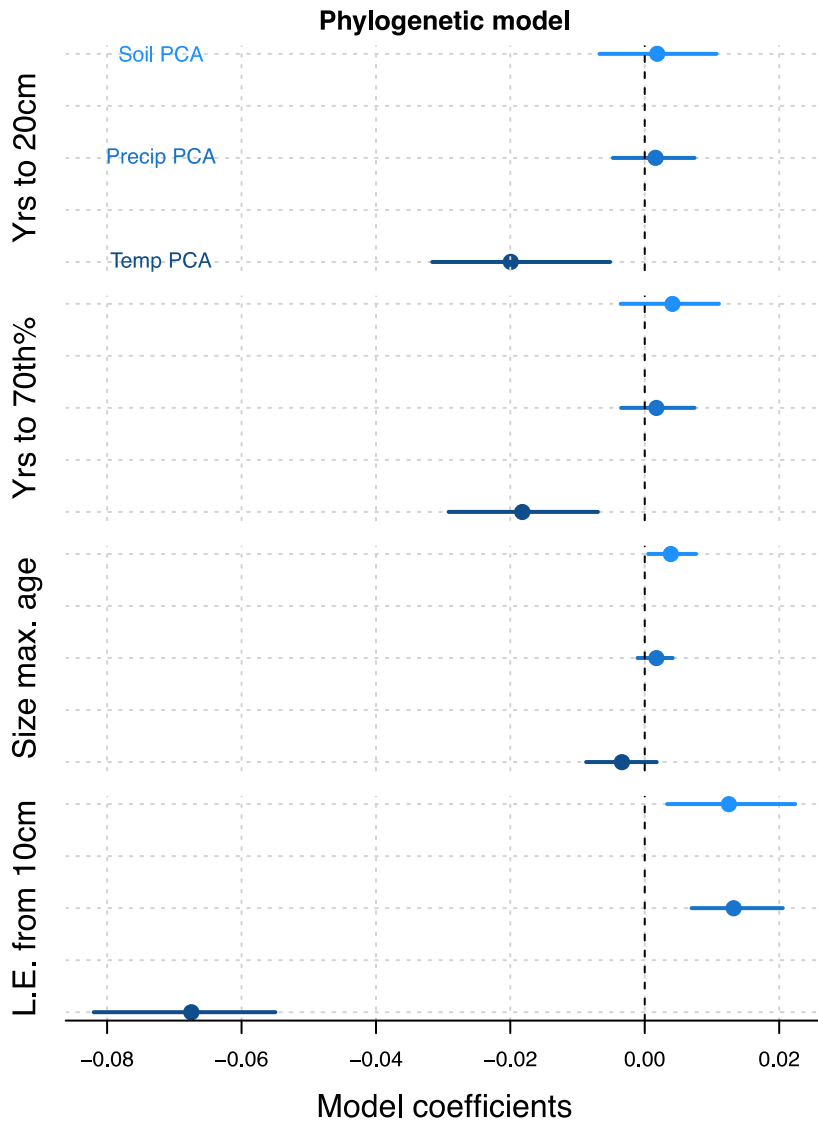


Figure S12. Estimated coefficients, with posterior mean and 95% credible intervals, for life history traits across broadscale soil, temperature, and precipitation gradients, using a multi-response Bayesian generalized mixed effect model.

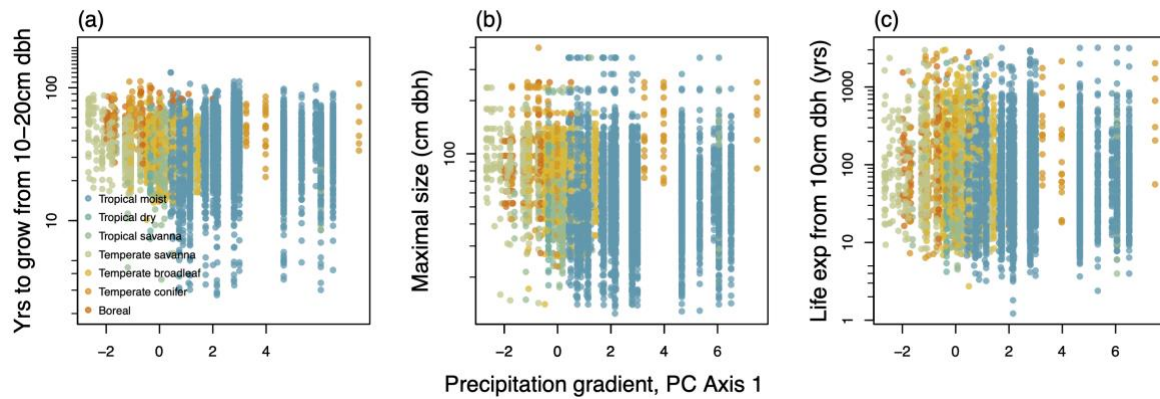


Figure S13. Life history trait variation across a precipitation gradient, which represents the first PC axis of 8 precipitation variables that we derived from WorldClim(48) and SoilGrids and span a latitudinal gradient from southern Brazil to northern Canada. The Y-axis is scaled by the natural log. Data points are species- and grid-specific and are calculated using individual tree observations to fit size-based integral projection models for each species within each grid cell ID. Model coefficients of the multi-response Bayesian model are reported in Fig. SI.10).

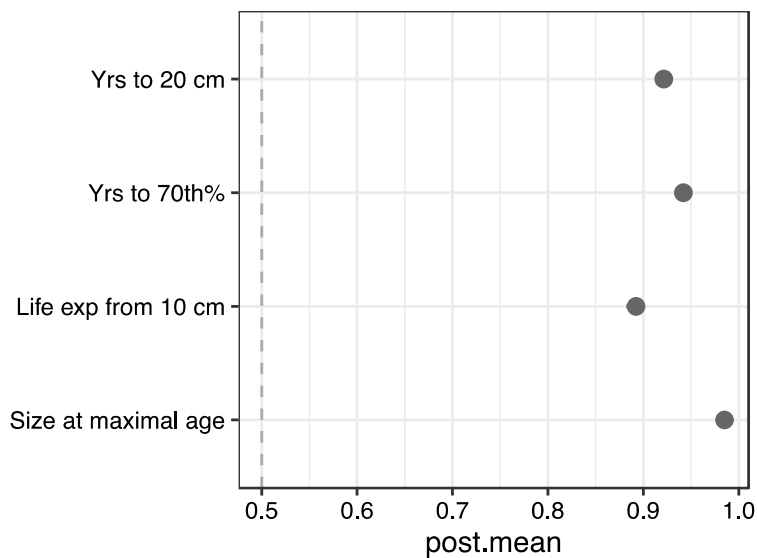


Figure S14. Estimated phylogenetic heritability from the Bayesian multiple-response mixed effect model, with posterior mean and 95% credible intervals.

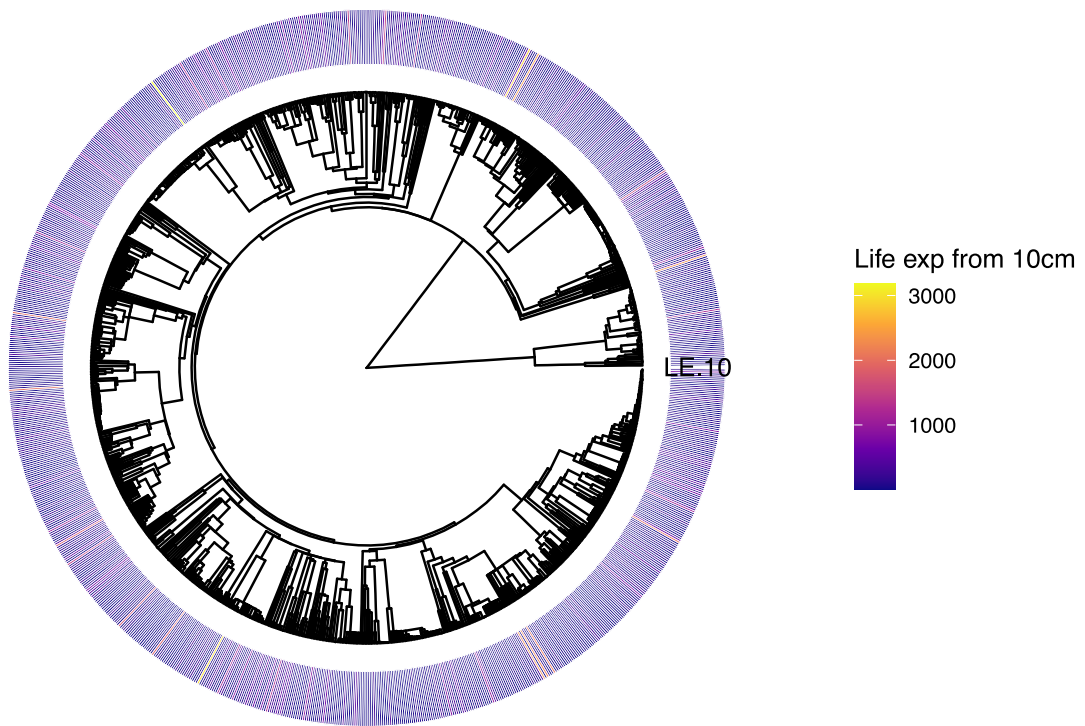


Figure S15. The phylogenetic tree for species included in our study, with a heatmap of tree life expectancies from 10 cm dbh.

Supplementary Tables:

S1. Forest inventory network datasets used in this study.

Network name	Network regional code	# of unique tree measurements	# of species	Min census year	Max census year	Countries
ForestGeo	FGE	180,002	216	1982	2013	Panama and United States of America
ForestPlots	FPN	633,406	921	1961	2013	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela
NFI	NAL	313,091	13	1960	2007	Canada (Alberta)
NFI	NBC	702,018	28	1926	2012	Canada (British Columbia)
NFI	NQU	252,176	34	1970	2014	Canada (Quebec)
NFI	NSA	84,207	9	1958	1999	Canada (Saskatchewan)
SYN	SYN	24,070	13	1982	2014	United States of America
FIA	FIAN	303,264	130	1999	2013	United States of America
FIA	FIANE	170,424	102	2001	2013	United States of America
FIA	FIANW	96,804	52	1995	2007	United States of America
FIA	FIARM	63,917	30	2000	2008	United States of America
FIA	FIAS	374,777	154	2000	2013	United States of America

Table S2. Mean and CI values in the number of years it takes trees to go to 20 cm in diameter across biomes. The history-history traits were scaled by the natural log before calculating the mean traits and back-transformed for reporting purposes.

Life expectancy from 10 cm in diameter						
Biome	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Boreal	10	35	73	87	186	2825
Temperate conifer	6	48	108	118	245	2674
Temperate broadleaf	3	39	100	98	253	3005
Temperate savanna	7	36	79	86	189	2976
Tropical dry	4	27	54	59	112	2037
Tropical moist	1	25	54	60	129	3195
Tropical savanna	4	23	56	59	129	2143

Growth strategy, years to grow from 10-20 cm in diameter						
Biome	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Boreal	27	42	53	52	62	99
Temperate conifer	14	35	48	45	61	112
Temperate broadleaf	10	29	36	36	45	83
Temperate savanna	4	25	35	33	46	85
Tropical dry	7	26	32	31	41	82
Tropical moist	3	26	37	34	50	130
Tropical savanna	4	25	35	33	46	85

S3. Principal component analysis loadings of the life history traits.

ALL species	PC 1	PC 2	PC 3	PC 4
Yrs to 20 cm dbh	0.513	0.616	0.12	0.585
Yrs to 70th max size	0.68	0.129	-0.227	-0.685
Life exp. From 10 cm dbh	0.344	-0.433	0.833	
Max size	0.395	-0.645	-0.49	0.433

Tropical species

Yrs to 20 cm dbh	0.55	0.591		0.586
Yrs to 70th max size	0.702		0.216	-0.679
Life exp. From 10 cm dbh	0.306	-0.214	-0.928	
Max size	0.333	-0.777	0.299	0.442

Extratropical species

Yrs to 20 cm dbh	0.481	0.603	0.227	0.594
Yrs to 70th max size	0.64	0.252	-0.192	-0.7
Life exp. From 10 cm dbh	0.388	-0.545	0.742	
Max size	0.456	-0.526	-0.601	0.393

S4. List of the environmental variables included in the soil, temperature, and precipitation variables used in the multi-response Bayesian generalized mixed effect model.

Env. group	Variable name	Data source	Unit	Resolution
Soil	Bulk density 015cm	Soilgrids(64)		≈250m
Soil	Soil pH H2O 15cm	Soilgrids(64)		≈250m
Soil	Clay content 15cm	Soilgrids(64)		≈250m
Soil	Saturated H2O content 15cm	Soilgrids(64)		≈250m
Soil	Silt content 15cm	Soilgrids(64)		≈250m
Soil	CEC 15cm	Soilgrids(64)		≈250m
Soil	SOC content 15cm	Soilgrids(64)		≈250m
Soil	Sand content 15cm	Soilgrids(64)		≈250m
Soil	Coarse fragments 15cm	Soilgrids(64)		≈250m
Soil	Depth to bedrock	Soilgrids(64)		≈250m
Soil	H2O capacity 15cm	Soilgrids(64)		≈250m
Soil	Sand content 15cm	Soilgrids(64)		≈250m
Precipitation	Aridity index	CGIAR (48)	AI value	1km
Precipitation	Annual precipitation	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Precipitation of coldest quarter	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Precipitation of driest quarter	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Precipitation of warmest quarter	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Precipitation of wettest quarter	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Precipitation seasonality	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Growing season precipitation sum	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Precipitation	Depth to water table annual mean	CHELSA(68)	mm	30 arcsec (≈900m at equator)
Temperature	Isothermality	CHELSA(68)	Unitless	30 arcsec (≈900m at equator)

Temperature	Mean diurnal range	CHELSA(68)	°C	30 arcsec (≈900m at equator)
Temperature	Mean temperature of coldest quarter	CHELSA	°C	30 arcsec (≈900m at equator)
Temperature	Mean temperature of coldest quarter	CHELSA	°C	30 arcsec (≈900m at equator)
Temperature	Mean temperature of coldest quarter	CHELSA	°C	30 arcsec (≈900m at equator)
Temperature	Mean temperature of coldest quarter	CHELSA	°C	30 arcsec (≈900m at equator)
Temperature	Temperature seasonality	CHELSA	°C	30 arcsec (≈900m at equator)
Temperature	Growing season length	CHELSA	Number of days	30 arcsec (≈900m at equator)
Temperature	Growing season temperature mean	CHELSA	°C	30 arcsec (≈900m at equator)

Table S5. Results of Bayesian generalized mixed effect model, with estimates of posterior means, upper and lower credible intervals.

Life history trait	Env. variable	post.mean	lower-95% CI	upper-95% CI	eff.samp	p value MCMC	
Life exp. From 10 cm dbh	--	0.055	-0.030	0.134	1000.0	0.218	
Yrs to 20 cm dbh	--	0.160	0.082	0.256	1000.0	0.001	**
Yrs to 70th max size	--	0.106	0.022	0.193	1000.0	0.020	*
Max size	--	-0.273	-0.357	-0.191	1000.0	0.001	***
Life exp. From 10 cm dbh	Soil PCA	0.012	0.003	0.022	1115.9	0.016	*
Yrs to 20 cm dbh	Soil PCA	0.002	-0.007	0.011	1000.0	0.686	
Yrs to 70th max size	Soil PCA	0.004	-0.004	0.011	1000.0	0.316	
Max size	Soil PCA	0.004	0.000	0.008	1117.3	0.040	*
Life exp. From 10 cm dbh	Precipitation PCA	0.013	0.007	0.021	1000.0	0.001	**
Yrs to 20 cm dbh	Precipitation PCA	0.002	-0.005	0.007	1000.0	0.620	
Yrs to 70th max size	Precipitation PCA	0.002	-0.004	0.007	1000.0	0.544	
Max size	Precipitation PCA	0.002	-0.001	0.004	1000.0	0.196	
Life exp. From 10 cm dbh	Temperature PCA	-0.067	-0.082	-0.055	1000.0	0.001	***
Yrs to 20 cm dbh	Temperature PCA	-0.020	-0.032	-0.005	1000.0	0.002	**
Yrs to 70th max size	Temperature PCA	-0.018	-0.029	-0.007	1000.0	0.002	**
Max size	Temperature PCA	-0.003	-0.009	0.002	1000.0	0.200	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table S6. Phylogenetic variance-covariance of the Bayesian generalized mixed effect model, with the genetic and residual correlations for each life history trait and Pagel's lambda.

Phenotypic correlations [variance-covariance of standardized traits]

	Life exp. From 10 cm dbh	Yrs to 20 cm dbh	yrs to 70th max size	Max size
Life exp. From 10 cm dbh	1	0.18	0.32	0.34
Yrs to 20 cm dbh	0.18	1	0.61	-0.04
Yrs to 70th max size	0.32	0.61	1	0.41
Max size	0.34	-0.04	0.41	1

Genetic variance-covariance

	Life exp. From 10 cm dbh	Yrs to 20 cm dbh	yrs to 70th max size	Max size
Life exp. From 10 cm dbh	0.94	0.21	0.36	0.35
Yrs to 20 cm dbh	0.21	1.14	0.67	-0.05
Yrs to 70th max size	0.36	0.67	1.15	0.48
Max size	0.35	-0.05	0.48	1.09

Residual variance-covariance

	Life exp. From 10 cm dbh	Yrs to 20 cm dbh	yrs to 70th max size	Max size
Life exp. From 10 cm dbh	0.12	0.00	0.00	0.01
Yrs to 20 cm dbh	0.00	0.10	0.08	0.00
Yrs to 70th max size	0.00	0.08	0.07	0.00
Max size	0.01	0.00	0.00	0.02

Genetic correlations

	Life exp. From 10 cm dbh	Yrs to 20 cm dbh	yrs to 70th max size	Max size
Life exp. From 10 cm dbh	1	0.20	0.35	0.35
Yrs to 20 cm dbh	0.20	1	0.59	-0.05
Yrs to 70th max size	0.35	0.59	1	0.43
Max size	0.35	-0.05	0.43	1

Residual correlations

	Life exp. From 10 cm dbh	Yrs to 20 cm dbh	yrs to 70th max size	Max size
Life exp. From 10 cm dbh	1	-0.04	-0.01	0.28
Yrs to 20 cm dbh	-0.04	1	0.93	0.08
Yrs to 70th max size	-0.01	0.93	1	0.08
Max size	0.28	0.08	0.08	1

Pagel's lambda

	lambda	Lower CI	Upper CI
Life exp. From 10 cm dbh	0.89	0.88	0.90
Yrs to 20 cm dbh	0.92	0.92	0.93
Yrs to 70th max size	0.94	0.94	0.95
Max size	0.99	0.98	0.99

Table S7. Linear model coefficients and summary statistics associated with Fig 4, including species richness and demographic trait diversity (**A**), mean annual temperature and demographic trait diversity (**B**), net primary productivity and demographic trait diversity table (**C**), and the combined effect of demographic trait diversity and mean annual temperature on net primary productivity (**D**).

Species richness on demo. diversity (Fig 4.A)

Term	Estimate	Std error	Statistic	P value
(Intercept)	-6.732	0.984	-6.840	<0.01
Species richness (log)	2.193	0.554	3.959	0.000
Species.richness^2 (log)	-0.146	0.073	-2.006	0.048

Adj R² = 0.65, F_{2,82} = 79, p < 0.01

Mean annual temp on demo diversity (Fig 4.B)

Term	Estimate	Std error	Statistic	P value
(Intercept)	-2.267	0.2376	-9.541	<0.01
Mean annual temp (scaled)	0.106	0.0139	7.593	<0.01

Adj R² = 0.40, F_{1,83} = 58, p < 0.01

NPP on demo diversity (Fig 4.C)

Term	Estimate	Std error	Statistic	P value
NPP (scaled and log)	0.708	0.077	9.182	<0.01

Adj R² = 0.49, F_{1,84} = 84.32, p < 0.01

Demographic diversity on NPP (Fig 4.D)

Term	Estimate	Std error	Statistic	P value
Demo. diversity (scaled and log)	0.178	0.0441	4.041	<0.01
Mean annual temp. (scaled and log)	0.827	0.044	18.777	<0.01

Adj R² = 0.90, F_{2,83} = 394.9, p < 0.01

The effect of demographic diversity on NPP, tropics

Term	Estimate	Std error	Statistic	P value
Temp (scaled)	0.308	0.152	2.030	0.051
Demo diversity (log and scaled)	0.412	0.152	2.716	0.011

Adj R² = 0.26, F_{2,31} = 6.912, p = 0.003

The effect of demographic diversity on NPP, extra-tropics

Term	Estimate	Std error	Statistic	P value
Temp (scaled)	0.790	0.068	11.611	<0.001
Demo diversity (log and scaled)	0.199	0.068	2.917	0.005

Adj R² = 0.840, F_{2,50} = 136.6, p < 0.01

