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TREE TRAITS

The pace of life for forest trees

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Tree growth and longevity trade-offs fundamentally shape the terrestrial carbon balance. Yet, we lack a unified understanding of how such trade-offs vary across the world's forests. By mapping life history traits for a wide range of species across the Americas, we reveal considerable variation in life expectancies from 10 centimeters in diameter (ranging from 1.3 to 3195 years) and show that the pace of life for trees can be accurately classified into four demographic functional types. We found emergent patterns in the strength of trade-offs between growth and longevity across a temperature gradient. Furthermore, we show that the diversity of life history traits varies predictably across forest biomes, giving rise to a positive relationship between trait diversity and productivity. Our pan-latitudinal assessment provides new insights into the demographic mechanisms that govern the carbon turnover rate across forest biomes.

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

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

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

In this study, we used the largest dataset of dynamic tree information to date and used age-from-stage methods to calculate the mean life expectancy and maximal life span for a wide range of trees across the Americas (*15*–*17*), spanning a latitudinal gradient from Northern Canada to Southern Brazil. This includes long-term records from an international network of researchers, including members of the Global Forest Dynamics, ForestPlots.net (*18*, *19*), and ForestGeo (*20*–*22*) networks and the United States and Canadian forest inventory programs (*23*–*25*). To balance this dataset across our biogeographic gradient, we randomly subsampled the North American plots to equal the number of point observations in Central and South America [see supplementary materials (SM), materials and methods], resulting in 3.2 million distinct tree measurements for 1127 species (i.e., tree size and status). Our big-data approach allowed us to test for the expectation that trees align along the fast-slow continuum (Fig. 1A, H1) and to quantify whether tree growth–longevity–stature relationships covary across soil, water, and temperature gradients (Fig. 1B, H2). Apart from species with low occurrences (<100 observations; see SM, materials and methods), our systematic sampling allowed us to test for the expectation that the range of life history strategies occupied by species (i.e., demographic trait diversity) varies predictably across broadscale biogeographic gradients, with harsh cold regions in the Northern Hemisphere restricting trees to a smaller pool of predominantly slow-growing, long-lived species (Fig. 1C, H3). On the basis of the well-established diversity-productivity relationship, we also expected demographic trait diversity to be positively associated with ecosystem productivity (Fig. 1C, H3).

To quantify tree growth, longevity, and stature for a wide range of species across biogeographic gradients and test our three core hypotheses, we first grouped the stem-level tree data into equally sized hexagon grids (size ~250,000 km^2) and developed species-specific survival- and growth-generalized linear mixed-effects models that included tree diameter at breast height (dbh) at the first census interval as a predictor variable

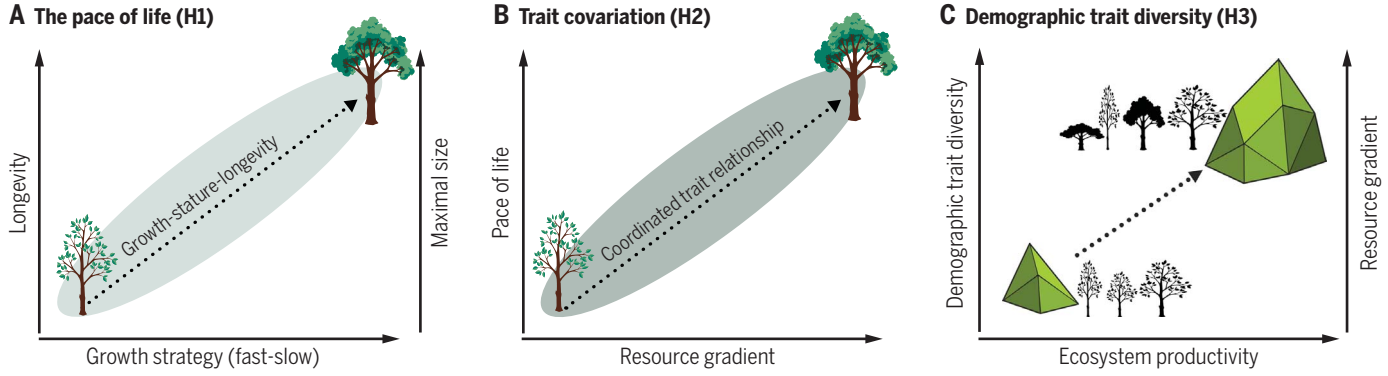

Fig. 1. Conceptual diagram of our core aims and associated hypotheses. (**A**) The expectation is that trees should align along the fast-slow continuum, with fast-growing, short-lived species on one end of the spectrum and slow-growing, long-lived species on the other end (H1). (**B**) Life history trait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

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and grid cell as a random effect (SM, materials and methods). We then used the survival and growth coefficients to fit size-dependent integral projection models (IPMs) and derive age-related traits from size-dependent probabilities for each species within each grid cell (SM, materials and methods) (*15–17*, *26–28*). IPMs dynamically integrate size-dependent variability in survival and growth as a continuous process, which allowed us to use cross-sectional data over discrete time steps to make interspecific comparisons of how many years it takes trees to attain key milestones in their life cycle. We parameterized our IPMs using methods specifically developed for trees (*27–29*). Validations of IPM model outputs, relative to tree ring data, showed that this parameterization method can provide realistic estimates of tree age demographics (*27*).

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

Our estimates of remaining life expectancy from 10 cm dbh range from 1.2 to 3195 years, with a mean value of 60 years in the tropics and 95 years in the extratropics (Fig. 2A). This trend matches our theoretical expectation of broadscale tree life history diversification patterns (Fig. 1B) and confers with known tree longevity hotspots, in which the oldest recorded species occur in temperate conifer and boreal forests (*12*, *30*). However, there was also considerable overlap in the range of tree life expectancies across biomes (figs. S3 and S4, and table S2) and wide variability in how longevity relates to tree growth strategies and maximal statures (Fig. 2B, figs. S3 and S4, and table S2). It is important to note that remaining life expectancy from 10 cm dbh is a species-level mean estimate (i.e., is conditional on surviving to 10 cm dbh). A low life expectancy, relative to the mean number of years it takes a species to grow from 10 to 20 cm dbh, does not imply that no individuals will reach 20 cm dbh. Instead, it implies that less than half of the individuals will survive to that size threshold.

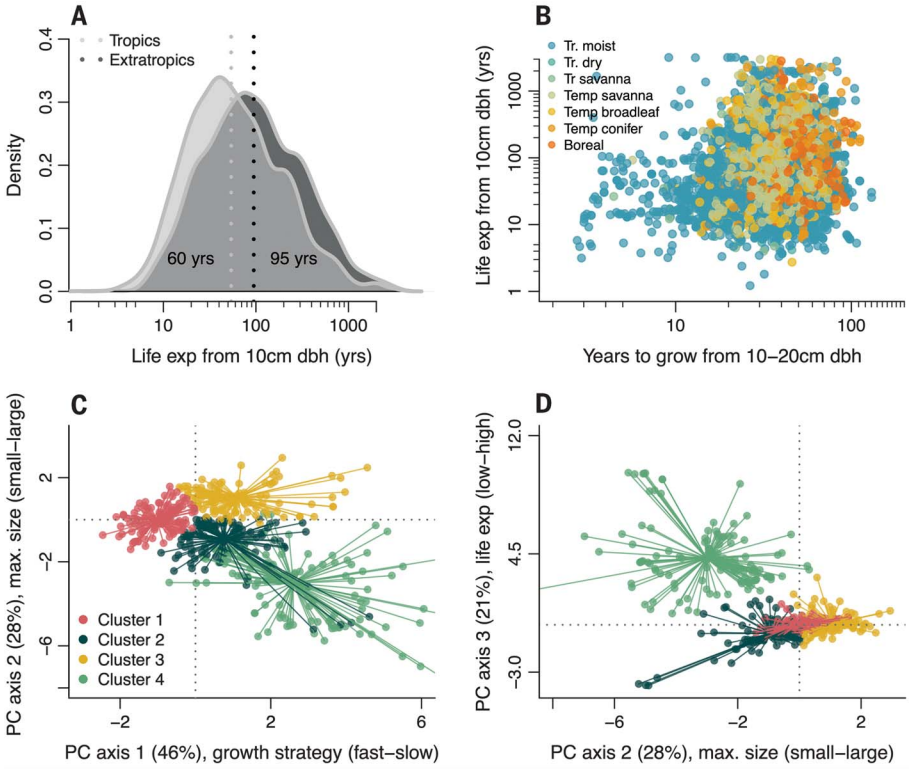

Fig. 2. Visual illustration of tree growth-longevity-stature relationships and core demographic functional types. The mean life expectancy is higher in the extratropics than in the tropics (**A**), with substantial variation between tree growth strategies and life expectancies (**B**) (N = 6847, i.e., species X grid ID). The other trait relationships are represented in fig. S8. The core growth-longevity-stature functional types are presented in (**C** and **D**), which are determined using the k-means clustering algorithm of the life history trait principal components analysis (PCA) 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. Data points are species-specific and are calculated using individual tree observations and size-dependent integral projection models (SM, materials and methods).

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

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

To examine the multidimensionality of tree age demographics (Fig. 1A, H1), we analyzed the variance-covariance matrix of tree growth, longevity, and stature using a principal components analysis (PCA). Highly correlated traits that captured redundant trait information were excluded from the PCA (fig. S5), resulting in the inclusion of tree growth strategies (i.e., growth from 10 to 20 cm dbh and the 70th quantile of their size distribution), life expectancy from 10 cm dbh, and maximal tree size (fig. S5). The first PC axis captured 46% of the life history trait variation and was heavily weighted by tree growth dynamics (i.e., years to 20 cm dbh and the 70th quantile size) (Fig. 2C). The PC loadings also showed that slow growth was correlated with high life expectancy and large maximal size (table S3). The second axis captured 28% of the trait variation. The directionality between the trait correlations flipped, whereby slow growth was negatively correlated to life expectancy and maximal size (table

S3). The third axis was heavily weighted by tree life expectancy, with high life expectancy being positively related to slow growth but negatively related to tree maximal size (table S3). PCA analyses for tropical versus extratropical species retained consistent patterns in the directionality of the trait correlations among the PC axes (table S3), illustrating the modular and flexible nature of tree age demographics beyond the fast-slow continuum within and among the Northern and Southern hemispheres.

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

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 that survival and growth rates over discrete size ranges differed substantially among species and diminished as trees attained larger sizes (*31*–*37*). Similarly, although 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

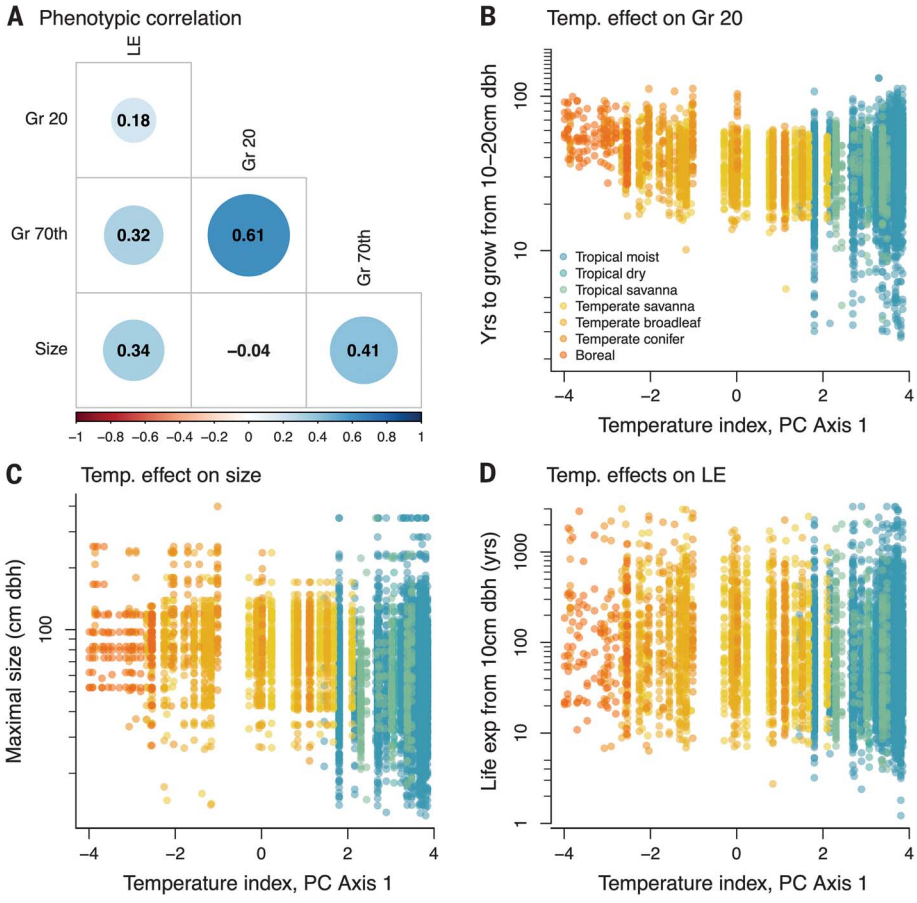

Fig. 3. Tree life history traits across our temperature index. (PC axis 1; for a comprehensive list of temperature variables, see SM, materials and methods). (**A**) Overall, we found low phenotypic correlations (variance-covariance of standardized traits) among tree growth, longevity, and stature across our biogeographic indexes, suggesting that there is weak support for coordinated trade-offs over evolutionary time (i.e., organismal function that supports conservative growth does not necessarily trade off with organismal function needed to maintain high longevity). (**B** to **D**) We also find a strong effect of temperature on tree life history traits, with little additional variation explained by soil or precipitation (figs. S12 and S13 and table S5). The temperature gradient is derived from a PCA of nine temperature variables and represents a gradient from intermediate temperatures in the tropical moist forest of the Southern Hemisphere to colder temperatures in the boreal north (from left to right of the *x* axis). The *y* axes are scaled by the natural log and the *x* axes are scaled to a mean of zero and a SD of 1. Data points are species-specific and are calculated using individual tree observations to fit size-based integral projection models for each species within each grid cell ID (total of 1127 species and 6847 trait values) (SM, materials and methods). Model coefficients of the multiresponse Bayesian model are reported in fig. S12 and table S5.

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. 2, C and D, and figs. S3 and S4) and highlight the tremendous variation in tree life expectancies across forest biomes (Fig. 2A and figs. S3 and 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 slow-growth short–life span functional trait cluster is in line with previous research from tropical forests, which showed that some short-stature trees had slow growth and low survival (*31*, *32*, *34*, *38*). This emergent trend may be an indication of maladapted species or a mediated effect of environmental disturbance (*10*, *32*, *33*). Conversely, it could be the result of energetic investments in

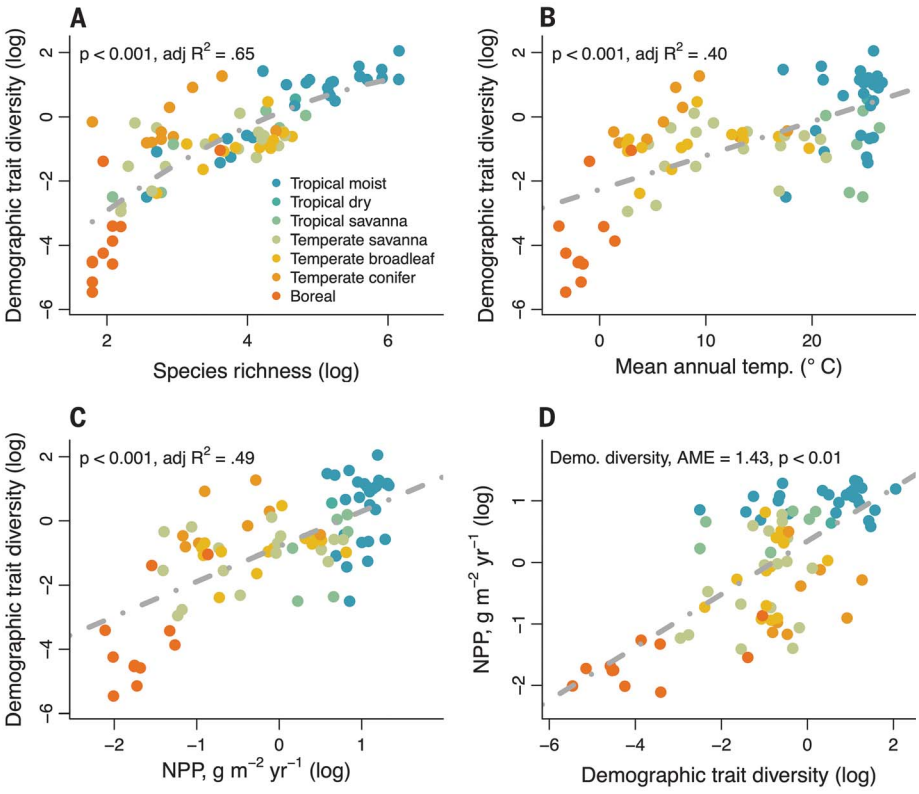

Fig. 4. The relationship between the demographic trait diversity of forests and ecosystem productivity (H3). We find that the demographic trait diversity is positively related to species richness (**A**), with increasing demographic trait diversity (i.e., convex-hull volume in life history trait space that is occupied by species) across a mean annual temperature gradient (**B**). In line with two nonmutually exclusive hypotheses in evolutionary biology and functional ecology, we find a positive association between demographic trait diversity and aboveground 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 (D) includes the demographic trait diversity and mean annual temperature. Demographic trait diversity and NPP were scaled to a mean of zero and a SD of 1. Average marginal effects (AME) represent the response per unit increase for each predictor variable.

reproduction over species' life spans (net reproductive rate) that we were not able to capture in our analysis (*5*, *11*, *31*, *34*). Regardless of the mechanisms, our findings provide a novel perspective on the multidimensionality of tree age demographics for a wide range of phylogenetic and geographical groups. Furthermore, our finding of emergent differences in the number of demographic functional types in the tropics versus extratropics offers novel insight into the mechanisms that shape the dynamics and structure of forests across the Americas.

Weak coordination in the strength of life history trade-offs across biogeographic gradients (H2)

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

Our results show that there is a strong relationship between temperature and tree life history traits, with colder temperatures being associated with conservative growth [$\beta = -0.02$, confidence interval (CI) = (-0.03, -0.01)] and high life expectancies [$\beta = -0.07$, CI = (-0.05, -0.08)] (Fig. 3 and fig. S12). Conversely, our precipitation and soil indices had a weak effect on life history traits (fig. S12 and table S5). Consistent with Amazon research (*41*), we found that tree life history traits were phylogenetically conserved (Pagel's λ ranging from 0.88 to 0.99; fig. S14 and table S6). Yet, we also found low phenotypic correlations among our life history traits, indicating that the strength of trade-offs between tree growth, longevity, and stature do not strongly covary across biogeographic gradients (Fig. 1B, H2). For example, the phenotypic correlation between the number of years it takes trees to grow to 20 cm dbh and their life expectancy from 10 cm dbh was 0.18 (Fig. 3A). Together, these results show that, although tree life history traits are phylogenetically conserved [Δ deviance information criterion (DIC) null model versus phylogenetic model = 76832], growth-longevity-stature relationships are not driven by genetic linkages or shared selective pressures that act on both traits independently over evolutionary time across broadscale resource gradients (table S6) (*42*).

Although our results offer the most comprehensive assessment of tree age demographics across broadscale resource gradients, it is important to note the data gap in the subtropics (i.e., across Mexico and northern Central America; fig. S1). This data gap could help explain the noticeable difference in the range of life history trait strategies between the North American temperate forests (low trait variation) and South American tropical forests (high trait variation) (Fig. 3, B to D, and fig. S1). This data gap highlights the need for increased sampling efforts in these understudied regions of the world and should be a priority of future research and funding.

Our findings are in line with trade-offs between physiological and morphological plant features linked to individual fitness and life history evolution, one reflecting leaf economic variables related to photosynthetic activity and growth potential and the other associated with morphological features related to light competition and plant height (*43*–*45*). Yet, similarly to our results, the dominant axes of physiological and morphological plant features did not strongly covary across latitudinal gradients (*44*, *45*). Together, our findings and previous research suggest that organismal function that supports rapid growth is not necessarily linked to organismal function that results in lower life expectancies and small maximal sizes. These emergent patterns suggest that rapid shifts in climate conditions may have divergent effects on the relationship between biomass accumulation in tree

growth and biomass retention in tree longevity, with important implications for modeling the global carbon balance in a changing world (*46*).

Demographic diversity varies predictably across biogeographic gradients (H3)

To characterize the range of life history strategies that are expressed by trees across broadscale biogeographic gradients, we first calculated the convex-hull volume in demographic trait space within each grid cell (SM, materials and methods) (*47*) and compared the relationship between the demographic trait diversity of forests and well-established patterns in species richness. The convex-hull volume was calculated by using the life history trait PC scores for axes 1 to 3, which together captured 95% of the life history trait variation. We then tested whether the demographic trait diversity of forests varied predictably across biogeographic gradients and explored potential links between demographic trait diversity and remotely sensed estimates of potential aboveground net primary productivity (NPP) (Fig. 1C, H3, and SM, materials and methods) (*48*). The expectation is that the diversity of life history trait strategies that are expressed by trees should vary predictably across biogeographic gradients, with higher demographic diversity being positively associated with aboveground productivity.

Our results illustrate that the demographic trait diversity of forests follows well-established patterns in species richness [Fig. 4A, adjusted coefficient of determination (adj R^2) = 0.65, P < 0.001]. We also found that the demographic diversity of forests varied predictably across biogeographic gradients, with high demographic trait diversity across warm tropical forests and low diversity of predominantly slow-growing, long-lived species in the cold temperate and boreal forests (adj R^2 = 0.40, P < 0.001; Fig. 4B and table S7). Lastly, we found a positive correlation between the demographic diversity of forests and remotely sensed estimates of ecosystem productivity (Pearson's r = 0.71).

The emergence of a positive association between the demographic trait diversity and ecosystem productivity is in line with two nonmutually exclusive hypotheses. From an evolutionary perspective, ecosystem productivity is thought to drive species diversification and niche differentiation (*49*). Conversely, following widely established relationships between biodiversity and ecosystem function, more demographically diverse forests are commonly assumed to have access to a larger resource pool and should thus be more productive (*50*, *51*). In this study, we found moderate support for both hypotheses. Specifically, we found that ecosystem productivity was predictive of demographic trait diversity across broadscale biogeographic gradients (adj R^2 = 0.49, P < 0.001; Fig. 4C and table S7). At the same time, ecosystem productivity was jointly influenced by temperature (average marginal effect = 0.83, P = 0.04; Fig. 4D) and demographic trait diversity (average marginal effect = 1.43, P < 0.001; Fig. 4D). This positive association was consistent across the tropics (adj R^2 =0.26, P < 0.01; table S7) and extra-tropics (adj R^2 = 0.84, P < 0.01; Fig. 4D and table S7). It should be noted that NPP was strongly correlated with mean annual temperature (Pearson's r = 0.94), which did not allow us to explicitly test for the individual and combined effect of these variables on demographic trait diversity. Although our broadscale analysis does not establish causality in the direction of these relationships, it does highlight the inextricable link between demographic trait diversity and ecosystem productivity across forest biomes.

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 aboveground 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 multiyear averages in remotely sensed NPP from 1997 to 2013 and from mean estimates of tree growth–longevity–stature relationships that were based on the current distribution of species (i.e., derived from dynamical data collected from the 1900s to 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 broadscale 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.

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

Conclusions

Our broadscale analysis reveals the remarkable diversity of life history strategies that exist for tree species across the Americas. Weak tradeoffs between tree growth, longevity, and stature across biogeographic gradients demonstrate the modular and flexible nature of trees, highlighting the diversity of evolutionary trajectories that have arisen to address the ecological puzzle of survival. In addition, from a functional perspective, we found that although acquisitive trees sequester carbon at faster rates, they also generally appear constrained to smaller maximum sizes and shorter life spans that translate to lower carbon storage and faster carbon turnover. More importantly, we found that more demographically diverse forests tend to be more productive at the ecosystem scale across the tropics and extratropics. These findings have important implications for informing global restoration and conservation efforts and for understanding the fundamental feedback between biodiversity and climate change mitigation.

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However, this file does not include data from networks with sensitive species or a need for indigenous data sovereignty. These data are available upon request for research purposes by emailing the following networks: Alberta Agriculture and Forestry Division https://www.alberta.ca/permanent-sample-plots-program, email: af.fm-biometrics@gov.ab.ca, Saskatchewan Minister of Environment Forest Service Branch https://www.saskatchewan.ca/contact-us, ForestGeo https://forestgeo.si.edu/explore-data (*20–22*), and ForestPlots.net https://forestplots.net/en/using-forestplots/in-the-field, email: admin@forestplots.net (*18, 19*).

SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S15
Tables S1 to S7
References (*57–68*)

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