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Tree lifespans in a warming world: unravelling the universal trade-off between growth and lifespan in temperate forests

Running Title: universal tree growth-lifespan trade-offs

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Abstract

Tree growth and lifespan are key determinants of forest dynamics, and ultimately control carbon stocks. Warming and increasing CO_2 have been observed to increase growth but such increases may not result in large net biomass gains due to trade-offs between growth and lifespan. A deeper understanding of the nature of the trade-off and its potential spatial variation is crucial to improve predictions of the future carbon sink. This study aims to identify key drivers of growth and lifespan, assess the universality of tree growth-lifespan trade-offs, explore the possible latitudinal patterns of trade-off strengths and their determinants, and project growth and lifespan under future climate scenarios. We analyzed 21,193 trees of 69 species (48 included in further analysis) at 445 sites (417 included in further analysis) in temperate forests in northeastern China to estimate early growth rate and tree lifespan. We find that temperature and human pressure enhance tree growth and reduce lifespan, while altitude increases lifespan. We further find evidence for growth-lifespan trade-offs at all studied levels, i.e. among trees, among species and communities, and within species and communities. Trade-offs are stronger at colder, higher latitudes compared to warmer sites, because of larger variation in tree growth and climate, larger range sizes for individual species and lower species' diversity for communities at high latitudes. We predict future increases in growth and reductions in tree lifespan in response to climate change for the 2050s. Taking growth lifespan trade-offs into account resulted in even larger predictions of decreases in tree lifespan of up to 8%. In conclusion, growth-lifespan trade-offs are universal, but the strengths may vary by environment and between different forests. Its effects are important to include in predictions of forest responses to global change and need to be considered more widely.

KEYWORDS: climate change, forest dynamics, tree growth, tree lifespan, trade-off, dendrochronology, carbon cycle

Introduction

Forests serve as a major sink for atmospheric CO_2, with the global forest sink estimated to offset nearly half of fossil fuel emissions in recent decades (Pan *et al.*, 2024). However, increasing levels of atmospheric CO_2 and climate change drive pervasive shifts in forest vegetation dynamics (e.g. increases in mortality), and the effect of these changes on forest carbon fluxes and carbon stocks remains unclear (McDowell *et al.*, 2020; Xu & Liu, 2022). Tree growth and lifespan are important determinants of forest dynamics, and have previously been shown to exhibit a trade-off (Locosselli *et al.*, 2020). Specifically, faster growth under global warming conditions may shorten tree lifespan (Brienen *et al.*, 2020), but the drivers and mechanisms behind such trade-offs remain unclear. Therefore, identifying factors influencing growth and lifespan, and an assessment of the universality of the growth–lifespan trade-off are crucial for understanding responses of forest dynamics to global warming, and for reducing uncertainties in the terrestrial carbon cycle models.

Climate change exerts a significant impact on both tree growth and lifespan, but these effects may vary between different environments and ecosystems. For example, increasing atmospheric CO_2 and warming stimulates tree growth in cold and temperate systems (Pan *et al.*, 2011), whereas high temperatures may detrimentally affect tropical trees (Vlam *et al.*, 2014; Schippers *et al.*, 2015). Climate dryness may expand the lifespan of evergreen needle-leaved trees and deciduous broad-leaved trees with high resistance to drought-induced embolisms (Xu & Liu, 2022), but leads to higher mortality risks for trees with low growth resilience to drought (DeSoto *et al.*, 2020), thus diminishing their lifespan. Furthermore, tree growth and lifespan are significantly influenced by human activities and altitude. Regions with limited human disturbance are more conducive to the persistence of old trees (Liu *et al.*, 2022), and species with broad biogeographic ranges tend to reach their oldest ages at higher elevations, where tree growth rates are lower (Di Filippo *et al.*, 2012; Piovesan & Biondi, 2021). Nevertheless, the effects of human pressure, altitude, and climate on tree lifespan and growth rate remain under-studied in temperate forests, despite the important role of these demographic rates in predicting the fate of forests and the future of the carbon sink (Anderegg *et al.*, 2020; Brienen *et al.*, 2020; Marqués *et al.*, 2023).

The trade-off between tree growth and lifespan has been observed among different species, ranging from "fast" species with rapid growth and shorter lifespans at one end of the spectrum of resource allocation strategies, to "slow" species exhibiting slower growth but higher survival rates at the other end (Stearns, 1989; Reich, 2014). This trade-off is supported by demographic studies showing a consistent interspecific trade-off between growth and mortality (Rees *et al.*, 2001; Russo *et al.*, 2008; Wright *et al.*, 2010; Stephenson *et al.*, 2011; Salguero-Gómez, 2017). In addition, tree ring studies show that trade-offs between growth and longevity, occur across species (Loehle, 1988; Brienen *et al.*, 2020; Locosselli *et al.*, 2020), as well as, within species (Black *et al.*, 2008; Bigler & Veblen, 2009; Bigler, 2016; Büntgen *et al.*, 2019; Brienen *et al.*, 2020). However, the universality of growth–lifespan trade-offs across different organizational levels (i.e., within and across species, and within and across communities) and comparison of the strengths of trade-offs across these levels, has not been explored in depth. Understanding these patterns is particularly important for temperate forests, as they constitute a significant global carbon sink (Keith *et al.*, 2009; Yang *et al.*, 2023; Pan *et al.*, 2024). Exploring the universality of the tree growth–lifespan trade-off and predicting the responses of tree growth and lifespan to future climate change is essential for anticipating the impacts of environmental shifts on temperate forests, especially considering that this carbon-rich ecosystem is currently confronted with rapid climate warming (Hartmann *et al.*, 2013; Fischer & Frazier, 2018).

While previous research has firmly proven the existence of a trade-off between lifespan and growth, several aspects remain unclear. For instance, the geographic variation in the strength of this trade-off remains largely unexplored. This is important as the strength of the trade-off indicates how quickly increases in growth rate might reduce lifespan, offering insight into the responsiveness of tree lifespan to growth increments. A global study on growth- lifespan trade-off within species has found slight variations in trade-off strength across climate zones and between gymnosperms and angiosperms (Brienen *et al.*, 2020). These findings prompt us to examine whether geographical variations exist in the responsiveness of lifespan to growth increments induced by climate warming or other stimulations. Such information is essential for understanding and anticipating changes in forest dynamics and informing forest management and conservation strategies in a warming climate.

In this study, we investigate the effects of climate, human pressure and altitude on growth and lifespan in trees, elucidate the universality of growth-lifespan trade-offs, explore the possible latitudinal patterns and drivers of trade-off strength, and project the growth and lifespan under future climate scenarios. Our focus is on the temperate forests of northeastern China, as these forests have experienced a strong warming of 0.4°C to 0.6°C per decade (Ren et al., 2012) and play an important role in carbon sequestration. Yet, their possible responses in terms of forest dynamics to these changes remains unexplored. We analyze tree ring data from 21,193 individual trees, encompassing 69 species across 445 plots. These records provide estimates of tree longevity and early growth rate, and were used to test the following hypotheses: 1) Climate, human pressure, and altitude collectively influence early growth rate and lifespan; 2) The trade-off between early growth rate and lifespan exists across multiple organizational levels: among all trees, among species and communities, and within species and communities; 3) The trade-off is stronger at higher latitudes due to greater effects of environmental variation, particularly temperature, on growth; 4) Consideration of growth-lifespan trade-offs will result in additional reductions in lifespan due to warming, on top of the direct effect of temperature on lifespan.

Materials and methods

Site and tree-ring sampling

Encompassing diverse forest types and mostly natural forests, northeastern China holds significant value among global temperate regions. Our study area in northeastern China covers a diverse gradient of temperate forest natural distribution, spanning latitudes from 39°42′ to 53°19′ N and longitudes from 119°48′ to 134°01′ E, with elevations varying between 97 and 1,255 m. The investigated region spans approximately 700,000 km^2, with over one-third of its land area comprising temperate broadleaf and mixed coniferous forests. Annual rainfall in the region varies from 363.8 to 1073.7 mm, while mean annual temperatures range from -5.6 to 9.8°C (Fick & Hijmans, 2017). A total of 445 permanent forest plots were established in the summer of 2017 and 2018, each with a size of 0.1 ha and a radius of 17.85 m (Supplementary Figure S1). Plot selection criteria excluded areas with conspicuous disturbances, rivers, and rocky terrain. The longitude, latitude and elevation of each plot were recorded in real-time using GPS equipment. In each plot, all trees exceeding 10 cm in diameter at breast height (DBH) were tagged, identified and sampled. One core per tree was extracted at 1.3 m above the ground, with a total collection of 21,193 increment cores from 69 species. Increment cores were dried, sanded until the ring boundaries were clearly visible, and measured using the LINTAB 5 system at 0.01 mm precision to obtain annual tree ring widths and ring numbers (Stokes, 1996).

Climate data

Nine climate variables were utilized to comprehensively characterize climate conditions, including mean annual temperature (MAT), mean diurnal range (MDR), temperature seasonality (TS), mean temperature of the warmest (MTWQ) and coldest quarter (MTCQ), annual precipitation (AP), precipitation seasonality (PS), as well as the precipitation of the wettest (PWQ) and driest quarter (PDQ). Historical climatic data from 1970 to 2000 were extracted from the WorldClim database at a 1 × 1 km resolution to represent the current climatic situation (Fick & Hijmans, 2017). Future climatic data for the MAT, MDR, TS, MTWQ, MTCQ, AP, PS, PWQ and PDQ were extracted from the Coupled Model Intercomparison Project (CMIP6; https://esgfnode.llnl.gov/search/cmip6/). We chose the MRI-ESM2-0 model under four Shared Socioeconomic Pathways (SSPs): SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, spanning the period from 2041 to 2060, thus reflecting climatic conditions anticipated in the 2050s.

Human pressure data

To quantify human impacts, we used the recently proposed global human modification (HM) index (Kennedy *et al.*, 2019). This index provides a comprehensive assessment of 13 anthropogenic stressors across five primary categories: human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure. Ranging from 0 to 1, lower values denote generally remote areas with little human impact, and higher values signify highly anthropogenically modified environments.

Early growth rates, lifespan, and their trade-off estimation

For each tree, the early growth rate is calculated as the mean ring width over the first five years, and the tree age is determined by the total number of rings. Tree ring counts offer unique insights in tree ages, which cannot be inferred from tree size as this metric is often poorly related to tree age (Bigler, 2016; Brienen *et al.*, 2020; Begović *et al.*, 2023; Mu *et al.*, 2023). To assess the trade-off between early growth and lifespan among all trees, we performed 95th-quantile regressions between the early growth rate and the natural logarithm of tree age (Brienen et al., 2020). To assess the trade-off between early growth rate and lifespan across species and communities, we applied major axis regression between early growth rate and the natural logarithm of lifespan. Here, the early growth rate was calculated as the mean value at the species/community level, and lifespan was determined as the 95th percentile of its age structure distribution (Pérez-Harguindeguy et al., 2013; Xu & Liu, 2022). Before performing the calculation, we excluded species or communities with relatively even age structures. Such age structures are indicative of recent large-scale disturbances (natural or anthropogenic) and do not represent old-growth populations. As the maximum ages of such populations are simply determined by the time since disturbance they may not reflect species' or communities' potential maximum lifespan as well as populations with varied age structures (Brienen et al., 2020). Moreover, to establish trade-offs between growth and lifespan – the purpose of our study – even-aged data structures cannot be used, as a minimal range of ages is required to perform such analysis. We calculated the coefficient of variation in tree ages (CVAge = StandDevAge/MeanAge × 100) for each species or community, and omitted those with a CVAge of less than 10%. We considered only those with a minimum of 20 records (Di Filippo et al., 2015; Xu & Liu, 2022). This resulted in the selection of 48 species and 417 communities for inclusion in this study. To evaluate trade-off strengths within species and communities, we conducted 95th-quantile regressions between relative growth (early growth rate /maximum early growth rate) and the natural logarithm of relative age (age/maximum age) at the individual level, for each species and community. The use of relative growth and relative age ensures that comparisons of trade-off strengths are not confounded by variations in maximum growth rates and maximum lifespan among species or communities. For assessing within-species trade-offs, we selected only species with a minimum of 100 trees, resulting in the selection of 28 species. Additionally, we aggregated six nearest neighbor plots with similar climates to increase the sample size required for assessing within-community trade-offs. This ensured a minimum of 150 trees per community, resulting in a total of 74 metacommunities for evaluating within-community trade-offs.

Statistical analysis

To assess the effect of climate, altitude and human pressure on lifespan and early growth rates, we standardized all independent variables to ensure comparability and maintained variance inflation factors below five to mitigate multicollinearity issues (Coelho de Souza *et al.*, 2019), and then performed multiple linear regression analysis. Before modeling, we performed principal component analyses (PCA) on 9 climate variables to summarize their variation. The first principal axis, capturing the most variance in climate variables (0.66), was used to signify the predominant impact of climate. It was multiplied by -1 to positively correlate with temperature and precipitation (i.e., larger values indicate higher temperature and precipitation; see Supplementary Table S1). Besides, we performed correlation analysis between lifespan and climate variables to identify the climatic factor most related to lifespan. Similar analyses were also performed for early growth rates.

To assess the universality of the growth–lifespan trade-off in temperate forests of northeastern China, we conducted our analysis at multiple levels: among all trees, among species and communities, and within species and communities. We also examined whether the trade-offs at these different levels varied between gymnosperms and angiosperms.

To examine potential latitudinal trends and drivers in trade-off strength, we quantified trade-offs and performed linear regression analysis between trade-off strength and latitude, growth variation, and environmental factors. We also performed linear regression analysis between species range size and trade-off strength within species, and between diversity and trade-off strength within communities. Furthermore, we utilized Structural Equation Modeling to explore the interrelationships among these variables, with $p > 0.05$ for the Fisher's C statistics indicating a satisfactory model fit. Trade-off strength was quantified by extracting exponents from significant trade-off relationships within species and communities, which were then multiplied by -1, with higher values indicating stronger trade-offs. The latitude value for each species and metacommunities was determined as the mean latitude of the constituent individuals within them. Growth variation was calculated as the coefficient of variation in early tree growth rates within both species and communities. For environmental factors, given the potential for species and metacommunities to span a wide range of environmental conditions, we accessed both the mean environmental conditions and environmental variations, with the latter quantified by assessing the range of altitude, human pressure, and climate variables for each species and metacommunity (Qiao *et* *al.*, 2022). We executed correlation analysis between these environmental factors and trade-off strength.

To check whether the observed trade-off between growth and lifespan are not a result of covariation of growth or lifespan with human pressure, we re-examined the trade-offs at multiple levels after excluding plots with a human pressure index ≥ 0.5. The significant trade-offs in the remaining data indicates that these trade-offs are not attributable to human pressure (Supplementary Figure S2). We also assessed the potential effect of recent growth stimulation on the observed trade-off. Due to climate warming and the CO_2 fertilization effect young trees may have a greater early growth rate (at the first 5 years of their life) compared to older trees affecting the trade-off strength. To check for this effect, we reanalyzed the data excluding trees younger than 40 years old the period with the greatest increase in temperature in temperate regions (Houghton *et al.*, 1996; Cao *et al.*, 2018). The consistency of our findings, both with and without the inclusion of younger trees, suggests that the observed trade-off existence or geographical variation in trade-off strength is not likely to be caused by a recent growth stimulation (see Supplementary Figure S3).

To forecast early growth rates and lifespans under projected future climate scenarios, we employed random forest machine learning models, which have been used in processing high-dimensional datasets in ecological and forestry studies (Steidinger *et al.*, 2019; Luo *et al.*, 2020). We developed three models: the first model assessed the influence of environmental conditions (climate, altitude, and human pressure) on early growth rates; the second model evaluated the impact of environmental conditions on lifespan; and the third model analyzed the effect of the growth and environmental conditions on lifespan, as detailed in Supplementary Table S2. For model verification, we employed a 90–10 cross-validation method and calculated the coefficient of determination (R^2) to assess the model performance (Luo *et al.*, 2020). This process was iterated 20 times to ensure model reliability, as detailed in Supplementary Table S3. To project climate-driven future early growth rates and lifespans, we implemented the first two models with future climate data (SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 for 2041 to 2060). To project future tree lifespans under the influence of climate change and trade-offs, we employed the third model incorporating both future climate data and anticipated climate-enhanced growth data.

All data processing and statistical analyses were performed in R software (R Core Team, 2022). Variables were transformed using log transformation, Gaussianization (Goerg, 2023), or Tukey's ladder of powers transformation (Mangiafico, 2024) when necessary to meet the normality requirement in the statistical analyses.

Results

Drivers of growth and lifespan

We observed that the community's mean early growth rate and lifespan covary, with the early growth rate decreasing from 5.4 to 0.7 mm/year (r = -0.44) and lifespan increasing from 21 to 170 years (r = 0.24) when moving toward higher latitudes (Supplementary Figure S4). This variation in lifespan and growth was strongly driven by climate, altitude and human pressure (Figure 1). Among the nine climate variables, mean temperature of warmest quarter (r = -0.38) exhibited the strongest correlation with lifespan, followed by annual mean temperature (r = -0.34), and mean diurnal temperature range (r = 0.32; Figure 1). We find opposite and somewhat stronger effects of climate on early growth rate. The strongest effects included mean temperature of warmest quarter (r = 0.50), annual mean temperature (r = 0.49), and mean temperature of coldest quarter (r = 0.44). Lifespan was negatively affected by human pressure (effect size = -0.27) and climate (effect size = -0.11), and positively affected by altitude (effect size = 0.15). Early growth rate was positively affected by climate (effect size = 0.30) and human pressure (effect size = 0.22), but was not significantly affected by altitude (Figure 1).

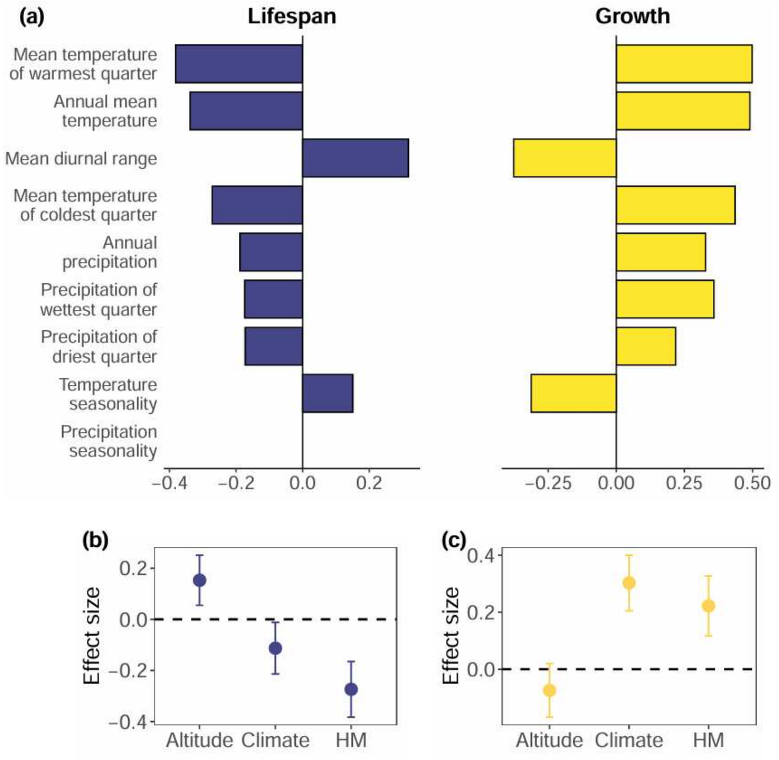

Figure 1. Effects of climate, altitude and human pressure on community lifespan and early growth rate. The upper panel (a) shows the correlations between each climate

variable and lifespan, and growth. The insignificant effect of precipitation seasonality is not shown. The below panels show the effect sizes of altitude, climate and human pressure (HM) on (b) lifespan and (c) early growth rate. Error bars represent 95% confidence intervals. The dashed line was drawn at a mean effect size of 0. This analysis includes data from across 417 communities (see Supplementary Figure S4).

The universal trade-off between growth and lifespan

We observed significant trade-offs between early growth rates and lifespan at various levels (Figure 2). Firstly, when combining all trees, species and sites (in total 21,193 trees), we find clear evidence for a growth-longevity trade-off (Figure 2a). We further observe a significant growth–lifespan trade-off among the 48 species (Figure 2b) and across the 417 communities (Figure 2c). Finally, a trade-off was observed within species and communities, with 20 out of 28 species (71.4%, Figure 2d), and 41 out of 74 metacommunities (55.4%, Figure 2e) exhibiting significant trade-offs. These findings collectively suggest that trade-offs between early growth rate and lifespan are a universal phenomenon in the temperate forests of northeastern China.

We do not find evidence for large differences in the trade-off strength between early growth rates and lifespan between angiosperms and gymnosperms (Supplementary Figure S5). At the individual tree level, trade-offs were evident across 17,866 angiosperm trees and 3,327 gymnosperm trees. At the species level, trade-offs were observed among 39 angiosperm species and 9 gymnosperm species. Significant within-species growth-lifespan trade-offs were observed for 17 out of 21 angiosperm species and for 3 out of 7 gymnosperm species. Among all individuals and species, gymnosperms have a slightly stronger trade-off than angiosperms.

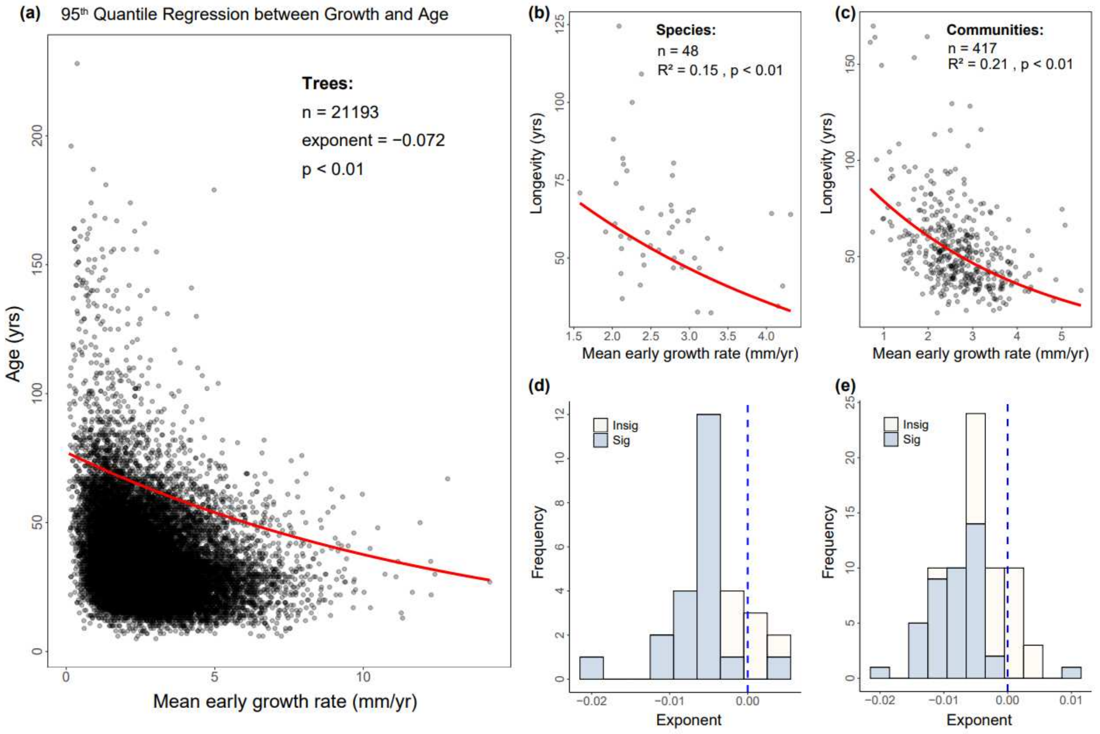

Figure 2. Relationship between early growth rate and lifespan. Panels (a), (b), and (c) show the relationship between tree early growth rate and lifespan across (a) 21,193 trees, (b) 48 species, and (c) 417 plots, with red lines indicating nonlinear regression trends. Panels (d) and (e) show the distribution of exponents from the relationship between early growth rate and lifespan (d) within each species and (e) within each metacommunity. The exponent reflects the exponential rate of decrease in tree lifespan with increasing early growth rate. The blue dashed line represents the exponent value of 0, and Sig and Insig indicate significant relationships ($p < 0.05$) and insignificant relationships ($p > 0.05$), respectively.

Latitudinal patterns and drivers of growth–lifespan trade-off

The trade-off strength within species (i.e., the exponent of the significant negative relationship between growth and lifespan within species, cf. Figure 2d) is weaker for lower latitude species, and increases towards higher latitudes (Figure 3a). In simple terms, this means that species at higher latitudes exhibit a stronger reduction in lifespan per unit of growth increase. The trade-off strength within species further exhibited a positive correlation with the growth variation within species (Figure 3b) and showed negative correlations with species' mean annual temperature (Figure 3c) and positive correlations with temperature seasonality (Supplementary Table S4). In general, the within species' tradeoff strength was positively related to the within species' variation in climate and altitude (Supplementary Table S4). We further find that species growing at higher latitudes exhibit larger range sizes (Figure 3d), and that species with larger range sizes have a higher growth variation and show stronger trade-offs (Figure 3e). These findings suggest that increases in trade-off strength for higher latitude species are at least partially (R^2= 54%) explained by their greater range sizes resulting in greater growth variation (Figure 3f).

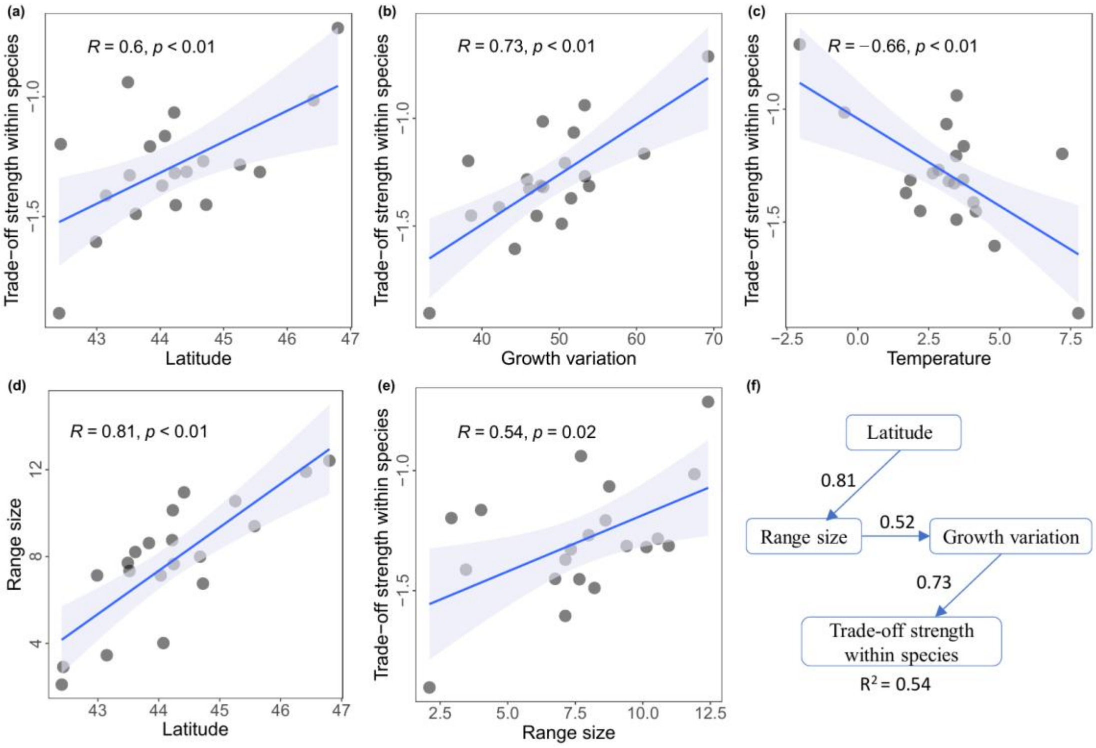

Figure 3. Latitudinal patterns and possible drives of trade-off strength within species. (a) the latitudinal patterns of trade-off strength within species; (b) the correlation between growth variation and trade-off strength within species. Growth variation is calculated as the coefficient of variation in the early growth rate for each species; (c) the correlation between mean annual temperature and trade-off strength within species; (d) the correlation between latitude and species range size. Species range size is defined as the latitudinal range of each species; (e) the correlation between species range size and trade-off strength within species; (f) structural equation model for the relationships between trade-off strength within species, latitude, species range size and growth variation. Fisher's C = 7.62, and p = 0.27. The solid lines represent the significant influence paths ($p < 0.05$). Trade-off strengths and latitude were transformed to meet the normality requirements of data analysis.

The strength of trade-offs within communities increases similarly towards higher latitudes (Figure 4a), towards communities with greater growth variation (Figure 4b), and towards colder climates (Figure 4c). In addition, communities at higher latitudes display lower diversity (Figure 4d), and those with lower diversity display a stronger trade-off (Figure 4e). SEM indicates that 19% of the increases in trade-off strength with latitude is explained by the lower species diversity at higher latitudes (Figure 4f).

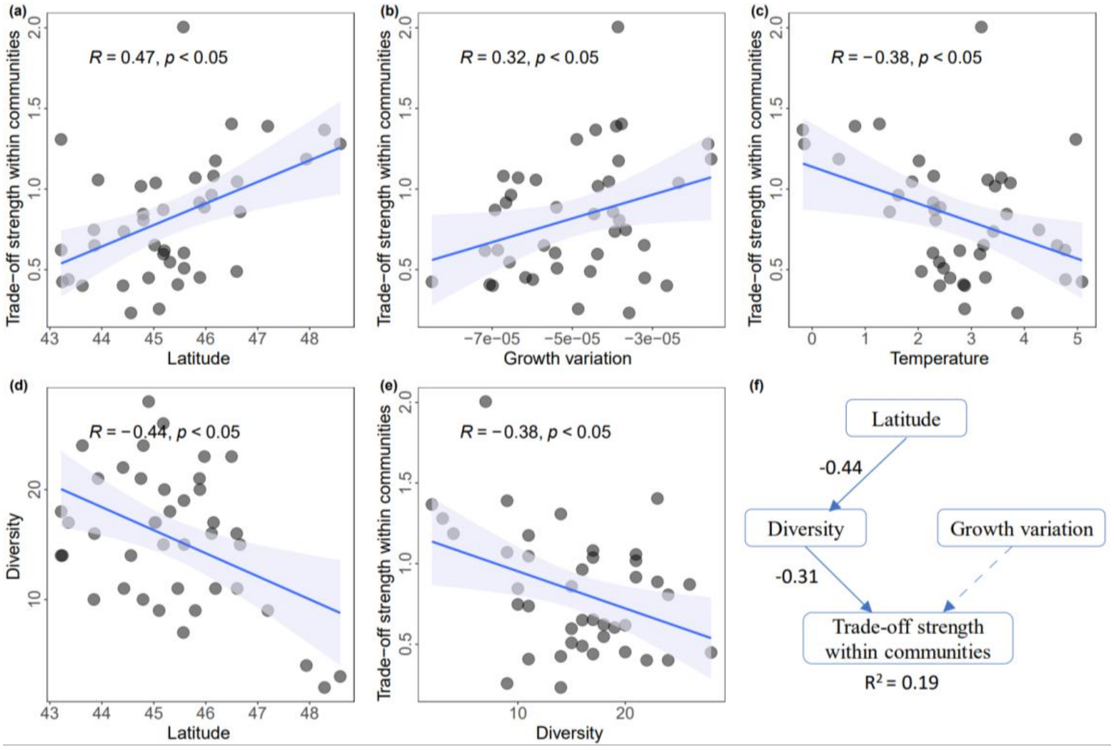

Figure 4. Latitudinal patterns and possible drives of trade-off strength within communities. (a) the latitudinal patterns of trade-off strength within communities; (b) the correlation between growth variation and trade-off strength within communities. Growth variation is calculated as the coefficient of variation in the early growth rate for each community; (c) the correlation between mean annual temperature and trade-

off strength within communities; (d) the correlation between latitude and community diversity. Diversity is calculated as the species richness within each community; (e) the correlation between community diversity and trade-off strength within communities; (f) the relationships between trade-off strength within communities, latitude, community diversity and growth variation. Fisher's C = 8.48, and $p = 0.08$. The solid lines represent the significant influence paths ($p < 0.05$), dotted lines represent the non-significant paths. Trade-off strengths, latitude, growth variation and temperature were transformed to meet the normality requirements of data analysis.

Future growth and lifespan

Under current climatic conditions, the observed early growth rate of the tree community averaged 2.66±0.04 mm/year, with a lifespan of 54.6±1.1 years. Using the predicted mean temperature increase for the 2050s (i.e., 2.4°C based on SSP5-8.5), we estimate, using random forest models, that early growth rates could increase to 3.07±0.02 mm/year, and that lifespans may decrease to 51.6±0.4 years. These predictions are based on direct climate-growth and climate-lifespan relationships. However, when incorporating both climate and growth, projected lifespans decreased more strongly to 50.1±0.3 years. Our results indicate a projected increase of approximately 15.4% in early growth rate under future climatic conditions, a projected decrease of nearly 5.4% in lifespan, and a larger decrease of nearly 8.2% in lifespan when additionally considering the negative effect of growth (Figure 5).

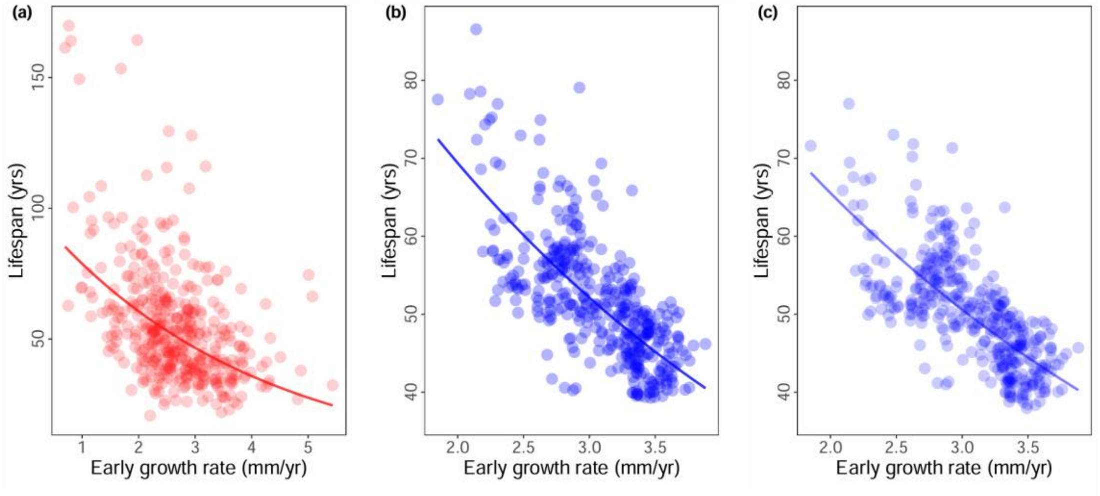

Figure 5. Early growth rate, lifespan, and their trade-off under the (a) current and (b, c) future climate scenarios. In panel (b), lifespan is predicted based on the environmental conditions only, while in panel (c), lifespan is predicted by both environment and growth-lifespan trade-offs. The results under the future climate scenario are derived from the SSP 5-8.5, employing the MRI-ESM2-0 model for the 2050s. The results of all other SSPs are presented in Supplementary Figure S6.

Discussion

Covariation of growth and lifespan with environment

We observed a decrease in early growth rates and an increase in lifespans with increasing latitudes, consistent with previously observed global patterns (Locosselli *et al.*, 2020). Our results indicate that tree lifespan is affected by human pressure, climate, and altitude, and that tree growth is affected significantly by human pressure and climate. A negative effect of human pressure on tree lifespan has been observed globally (Sandel & Svenning, 2013; Liu *et al.*, 2022), and has been attributed to the past logging of old trees. Similarly, human pressure could increase growth rates as past logging may have released trees from competition (Gerhardt, 1996; Bigler, 2016). In addition, atmospheric nitrogen deposition might be higher in sites closer to human activities (Liu et al., 2013), potentially stimulating tree growth (Schulte-Uebbing & de Vries, 2018).

Among all selected climate variables, temperature, particularly during the warmest quarter, exerts the strongest influence on lifespan and growth. Increasing temperatures increase growth and reduce tree lifespan. As a result, we find that lifespan increases at higher altitudes, consistent with other studies (Brienen *et al.*, 2020; Locosselli *et al.*, 2020; Liu *et al.*, 2022). Positive effects of elevated temperatures on growth rates have been observed widely (Pretzsch *et al.*, 2014; Locosselli *et al.*, 2020; Begović *et al.*, 2023), and can be explained by higher photosynthesis (Dusenge *et al.*, 2019), longer periods of cell division and expansion (Körner, 2003; Ryan, 2010) and longer growing seasons (Barichivich *et al.*, 2013). The negative effect of elevated temperatures on tree lifespan aligns with previous research conducted in temperate regions, indicating that trees inhabiting harsh environments tend to exhibit longer lifespans (Di Filippo et al., 2015; Liu et al., 2022). There are various possible explanations for the prolonged lifespan for slower growing trees at lower temperatures. Firstly, lower temperature directly reduces growth which could result in an extension of trees' lifespan at lower temperature via trade-offs between growth and longevity (see next section). Secondly, increases in tree lifespan in colder climates could be due to lower metabolic rates. This "Rate Of Living" (ROL) theory of aging proposes that senescence is related to rates of metabolism (photosynthesis, respiration), and that lower metabolism in colder climates could increase tree longevity through slowing senescence (Issartel & Coiffard, 2011). Thirdly, the colder temperatures at higher altitudes restrict the presence of herbivores and pathogens. This not only directly reduces tree mortality rates from diseases and pests (Stephenson *et al.*, 2011) but also enables trees to allocate resources away from defense (Raffa *et al.*, 2013) towards investment in functional traits helping to cope with abiotic stress (Callis-Duehl *et al.*, 2017; Midolo *et al.*, 2019), thereby enhancing survival and longevity. For example, it has been observed that trees in colder regions invest more in non-structural carbohydrate reserves to cope with those harsher conditions (Hoch & Körner, 2012). Further studies in this area are needed to disentangle the contributions of these various effects to variation in tree longevity.

Besides temperature effects, our findings reveal a negative correlation between precipitation and lifespan and a positive correlation between precipitation and growth. This is consistent with the effect of precipitation on lifespan observed by Xu & Liu (2022), but it contradicts with global and tropical studies that show increases in longevity with precipitation (Locosselli et al., 2020; Liu et al., 2022). We believe that the apparent precipitation effect arises from a strong covariation between rainfall and temperature in our dataset (Supplementary Figure S7a). This is supported by the low variance explained by precipitation compared to temperature (Supplementary Figure

S7b).

The universal trade-off between growth and lifespan

Previous studies observed trade-offs between growth and lifespan among (Bugmann & Bigler, 2011; Locosselli *et al.*, 2020) and within species (Di Filippo *et al.*, 2012; Bigler, 2016; Büntgen *et al.*, 2019; Brienen *et al.*, 2020). We here have extended these observations and show that trade-offs are present at all studied levels: among individual trees, within and across species, and within and across communities. The existence of trade-offs across multiple levels and scales indicates that growth-lifespan trade-offs are truly universal attributes of trees and forests and are not confined to specific levels or contexts. The average trade-off strength within species from our study is of very similar magnitude to that observed in temperate forests globally (0.0074 in our study vs. 0.008 in the study of Brienen *et al.*, 2020; Supplementary Figure S8). We further find that both gymnosperms and angiosperms show trade-offs although the strength of the trade-offs are slightly greater in gymnosperms than in angiosperms, consistent with global tree ring analysis (Brienen *et al.*, 2020). All together our findings suggest that trees exhibit a consistent reduction in tree lifespan in response to increases in growth regardless of the type of species or forest, climate, or geographical location. These findings are consistent with demographic studies showing growth-survival trade-offs across species in tropical forests (Wright et al., 2010; Russo et al., 2020), temperate forests (Kunstler et al., 2009; Zhu et al., 2017; Fan et al., 2022), and within continents (Bialic-Murphy et al., 2024).

Several hypotheses have been proposed to explain the trade-off between growth and lifespan, including the size limitation hypothesis and the resource allocation strategy hypothesis (Herms & Mattson, 1992; Reich, 2014). The size limitation hypothesis posits that increases in tree mortality risks as trees grow bigger constrain tree longevity (Ryan & Yoder, 1997; Mencuccini *et al.*, 2005; Bigler, 2016; Büntgen *et al.*, 2019; Brienen *et al.*, 2020). Potential mechanisms for such increases in mortality risks include increased vulnerability to water stress (Rowland et al., 2015; Liu et al., 2019), lightning and wind disturbances (Gardiner et al., 2016; Yanoviak et al., 2020), pathogen and insect outbreaks (Pfeifer et al., 2011; Pennisi, 2019), increased respiratory load that relative to their photosynthetic tissue (Yoda *et al.*, 1965), reduced soil nutrient availability (Mencuccini et al., 2005), and reduced maintenance due to the reallocation of resources toward reproductive organs (Thomas, 2013; McMahon, 2024) for large trees. While our findings could be explained by this theory, we also do observe that faster growing trees reach greater sizes compared to slower-growing individuals (Supplementary Figure S9; S10). This is consistent with the widely observed phenomenon that tree size is poorly relater to tree age, and that the oldest individuals are often not the largest (Bigler, 2016; Brienen *et al.*, 2020; Begović *et al.*, 2023; Mu *et al.*, 2023). These results indicate that there is no absolute threshold on the maximum tree size or height that trees may reach, but it also does not necessarily discredit the size limitation hypothesis, and various studies show that mortality rates strongly to increase with an increase in tree size, especially once trees have passed the critical juvenile phases (Hurst *et al.*, 2011; Bennett *et al.*, 2015; Johnson *et al.*, 2018). Faster growing trees may reach greater maximum tree size by outcompeting other trees or by growing in sites with greater resource availability (Di Filippo *et al.*, 2015; Bigler, 2016).

Various aspects of the size limitation hypothesis are related to resource allocation strategies, which involve balancing growth with other essential functions such as mechanical stability (Bazzaz, 1979; Rötheli *et al.*, 2012), hydraulic safety (Torres-Ruiz *et al.*, 2016; Roskilly *et al.*, 2019), and defense (Fine *et al.*, 2006; de la Mata *et al.*, 2017; Kichas *et al.*, 2020). For instance, the resource allocation hypothesis suggests that trees in resource-rich, and thus more competitive, environments prioritize allocating resources to growth at the expense of defense and stress tolerance, resulting in higher mortality from herbivores, pathogens, or environmental stress. Conversely, trees in resource-poor, and less competitive, environments invest less resources towards growth and instead allocate more towards enhancing resistance to herbivores and pathogens, as well as increasing stress tolerance (Herms & Mattson, 1992; Stamp, 2003; Bigler, 2016). Moreover, resource allocation strategies are often reflected in the contrasting effects of functional traits on growth versus their influence on lifespan. For instance, faster-growing species often show lower wood density (Chave *et al.*, 2009), meaning fast-growing trees are more susceptible to breakage or uprooting by wind due to weaker mechanical stability (Canham et al., 2001; Rich et al., 2007; McDowell et al., 2020), attacks by pests and pathogens due to lower plant defenses (Bentz et al., 2017), and hydraulic failure due to lower hydraulic safety margins (Xu & Liu, 2022), ultimately resulting in higher mortality and shorter lifespans (King et al., 2006; Wright et al., 2010; Reich, 2014). Similar patterns were observed within *Larix gmelini*, where fast-growing populations exhibit lower wood density and shorter lifespans (Supplementary Figure S11), supporting resource allocation strategies at intraspecific levels. A comprehensive analysis encompassing various functional traits (e.g. leaf traits and hydraulic traits) is required to further elucidate the mechanisms underlying the universal trade-off between growth and lifespan.

One important consequence of growth-longevity trade-offs is that growth stimulation due to e.g. CO_2 fertilization (Walker *et al.*, 2021), increases in temperature (Dusenge *et al.*, 2019) or nitrogen deposition (Liu et al., 2013), might lead to decreases in tree longevity and increases in mortality. Indeed, increases in tree mortality have been observed globally, including in the western boreal forests of Canada (Searle & Chen, 2018), the Amazon (Brienen et al., 2015), the western Americas (van Mantgem *et al.*, 2009), and European forests (Pretzsch *et al.*, 2014; Pretzsch & Grote, 2024). In at least three of these studies (Pretzsch *et al.*, 2014; Brienen *et al.*, 2015; Searle & Chen, 2018), these mortality increases were associated with accelerated tree growth. While there may be various factors explain these patterns, one of the most parsimonious explanations is that faster growth increases tree turnover due to the growth-lifespan trade-offs. Modelling studies indicate that these internal demographic feedbacks may eventually reduce or even fully neutralize the forest carbon sink (Bugmann & Bigler, 2011; Brienen *et al.*, 2020; Marqués *et al.*, 2023).

Spatial variation in growth–lifespan trade-off

While our results indicate that trade-offs are universal, we do observe spatial variation in the trade-off strength. Specifically, we find that trade-offs within species and within communities are stronger at higher latitudes (Figure 3a, 4a). This is consistent with findings at the global scale that boreal forest species exhibit a slightly stronger trade-off within species compared to temperate species (Brienen et al., 2020). The latitudinal change of trade-off strength within species is likely connected to the observed increase in growth variation with latitude. We find that species growing at higher latitudes show greater growth variation (Supplementary Figure S12), which in turn could be due to greater range sizes and greater climate variability for higher latitude species (Figure 3d; Supplementary Table S4). The enhanced growth and age variation for high-latitude, low-temperature species is most likely the key reason for the stronger trade-offs (Figure 3c, e), as trade-offs arise from differences among trees in the first place.

We also studied the variation in the trade-off strengths within communities. These patterns are consistent with those observed for within-species and show increasing trade-off strength towards higher latitudes (Figure 3). This is not surprising given that community level trade-offs strengths are determined at least partially by intra-specific trade-offs, which as we have seen increases towards higher latitudes. To assess to what degree these community level trade-offs are driven by intraspecific (i.e., within species) versus interspecific (i.e., between species) trade-offs, we removed interspecific variation in age and growth (i.e. that part of the variation that is due to differences in mean growth and age between species, see Supplementary Figure S13). This shows that intraspecific variation in growth and longevity indeed plays a dominant role in controlling the strength of trade-offs at higher-latitude communities. In contrast, intra-specific trade-offs are less important at lower latitudes, where species diversity is higher and where species relative abundance is lower. One could expect that higher species diversity at lower latitudes could increase growth variation and lead to stronger within-community trade-offs, but our results did not support this as we find that lower latitudes show much weaker trade-offs. This indicates that increases in variation in life history strategies for more the species-rich, low-latitude communities, do not necessarily correspond to increases in variation along the "fast-slow" plant economics spectrum (Reich, 2014). A major independent plant strategy axis that does not align along this fast-slow axis is that of plant size (Díaz *et al.*, 2016; Joswig *et al.*, 2022). Introduction of greater diversity of species may thus contribute to weakening trade-offs within communities. Consistent with this several studies show that growth-mortality trade-offs are not necessarily universally applicable (Russo *et al.*, 2020; Bialic-Murphy *et al.*, 2024). To further understand these patterns future investigations should focus on species functional trait diversity.

Future growth and lifespan

Our analysis predicts an increase in growth rates and a reduction in lifespan due to climate change by the 2050s, with a larger reduction in lifespan when additionally considering the adverse impacts of increasing early growth rates. This suggests that although a warmer climate may initially enhance tree growth, the negative impacts on tree longevity must be considered, not only due to climate-induced factors such as elevated cell metabolism rates, reduced reserves of non-structural carbohydrates, and the proliferation of diseases and pests potentially shortening lifespans, but also due to trade-offs where accelerated growth leads to reduced lifespan. Elevated temperatures, atmospheric CO_2 concentrations, water use efficiency, and extended growing seasons are anticipated to increase tree growth rates (Luo *et al.*, 2020) and decrease tree lifespans (Locosselli *et al.*, 2020), thereby reducing carbon sequestration and accelerating carbon turnover (Bigler & Veblen, 2009; Körner, 2017; Au *et al.*, 2023). The universal existence of the growth-lifespan trade-off, observed here and elsewhere, is poised to expedite this process by reducing the global carbon sink (Brienen *et al.*, 2020).

Various measures have been proposed to mitigate climate warming, including natural climate solutions to increase the land carbon sink, such as forest conservation, afforestation, and restoration efforts (Mo *et al.*, 2023). While such efforts are indeed needed to combat the continuing rise of atmospheric CO_2 while transition to net zero, it needs to be realized that the tradeoffs presents a true conundrum: fast-growing young trees may quickly soak up carbon from the atmosphere, but they might contribute less significantly to mitigating warming compared to slow growing, but long-lived trees, owing to their propensity to reach their maximum lifespan earlier, resulting in a shorter carbon residence time and reduced carbon storage (Körner, 2017; Piovesan & Biondi, 2021). Moreover, old trees play a critical role in buffering and stabilizing microclimates in the understory, while also serving as irreplaceable genetic resources (Au *et al.*, 2022; Cannon *et al.*, 2022; Begović *et al.*, 2023), a role that younger trees cannot fulfill. Therefore, the protection of old-growth forests is important and urgent, particularly given the prevailing global trend toward younger forest stands (McDowell et al., 2020). Our analysis highlights the negative impact of the growth-lifespan trade-off on tree turnover in a warming climate. Further research however is necessary to gain a deeper understanding of these demographic feedbacks by explicitly incorporating these trade-offs into process-based models, which can simultaneously account for not only the effects of climate change, elevated atmospheric CO_2 concentrations, and nutrient availability on tree growth, but can also account for the identified demographics feedbacks as well as effects of competition. Efforts to incorporate the growth-lifespan trade-off into global dynamic vegetation models, such as through an explicit accounting for size-dependent mortality, should receive greater attention (Brienen et al., 2020; Needham et al., 2020; Marqués et al., 2023).

Conclusions

Utilizing tree ring data from temperate forests in northeastern China, we assessed the influence of climate, altitude, and human pressure on tree growth and lifespan, with a specific emphasis on the impact of temperature. We confirm the universality of the growth–lifespan trade-off. Higher latitudes have stronger trade-off because of greater growth variation, related to greater species range sizes. These species level trade-offs filter also through to community level trade-offs, but these trade-offs are slightly weaker possibly because greater species richness introduces additional variation in life history strategies, which are not necessarily aligned along the "fast-slow" plant economics spectrum. Furthermore, our study anticipates an increase in growth rates and a decrease in lifespan due to the direct effect of global warming on these vital rates. Taking growth lifespan trade-offs into account resulted in even larger predictions of decreases in tree lifespan of up to 8%. The results of this study may contribute to more reliable predictions of forest responses to global warming.

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