Title: Can forests organize regular tree growth trends at the aggregate level?

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**Abstract:** Individual trees in natural forests often exhibit complex, inconsistent, and variable growth trajectories influenced by genetics, climate change, and uneven stand structure. These growth divergences pose a challenge in predicting the overall growth trend of trees. Here, we propose a radius-driven metabolic growth model (IGMR) to examine the radial growth of trees, thereby addressing this problem on a global scale. The IGMR suggests that tree ring growth pattern is determined by tree maximum radius and total growth time and can vary over some predictable range. Our results show that the best radial growth trajectory (BGT) at the aggregate level follows the IGMR, and its half also constrains the overall growth trend. Further analysis shows that climate change and uneven stand structure may cause the overall growth trajectory to undergo more growth drifts (changes in growth rate only) than adaptations (changes in maximum size). These results not only extend metabolic growth theory, but also imply that climate change is more likely to affect forest maximum carbon sequestration through community shifts than through changes in tree growth.

**Keywords**: Tree radial growth, Metabolic growth theory, Ontogenetic growth model, Overall growth trend, Global warming

*Glossary of main symbols*

|  |  |  |
| --- | --- | --- |
| Symbol | Meaning | Unit\* |
| *r* | *Tree current radius* | mm |
| R | *Tree maximum radius* | mm |
| Rm | *Tree maximum radius in the same forest* | mm |
| TGT | *Tree growth growth time* | y |
| TGTm | *Tree maximum growth growth time in the same forest* | y |
| *f*(*r*) | *Tree radial growth rate* | mm/y |
| *f*(*r*)a | *Tree radial mean growth rate in the same forest* | mm/y |
| *f*(*r*)m | *Tree radial maximum growth rate in the same forest* | mm/y |
| *m* | *Organism size or biomass* | g |
| *T* | *The formation time of unit tissue is primarily controlled genetically and by physiological activities, with the intrinsic or developmental growth rate independent of organism size* | y |
| *f*(*m*) | *Organism/tree mean growth increment during time T* | g |
| *gr* | *Cost of respiration needed to produce a unit of tissue* | mg g−1 |
| *mr* | *Rate of maintenance respiration per unit of tissue* | mg g−1 y−1 |
| *b* | *Metabolic exponent, taken here as 0.75* | 1 |

\* Units of time, respiration, and biomass are expressed as *y* (year), mg (carbon dioxide), and g (dry weight), respectively.

Worldwide, forest biomass gains more than 2 Pg C (carbon) annually (Pan *et al.* 2011). This increase is primarily attributable to forest growth. To understand forest growth, it is necessary to consider the drivers of tree growth over their lifespan. In this regard, tree ring analysis has significant advantages over monitoring studies, as it provides retrospective data on annual growth dating back to the establishment of individual trees (Bowman *et al.* 2013). More importantly, tree ring series contain valuable information regarding the responses of tree growth to various drivers operating on different time scales, ranging from years to centuries (Peters *et al.* 2015). Climate fluctuations (i.e., precipitation and temperature) (SCHÖNGART *et al.* 2006; Subedi & Sharma 2013; Wang *et al.* 2017), stand structure (influencing various forest processes such as water balance, nutrient cycling, carbon allocation, and light absorption) (Forrester 2019), and ontogenetic growth (partially related to genetics) (Peters *et al.* 2015) drive radial growth rates over different temporal scales at annual and decadal scales and spanning decades to centuries.

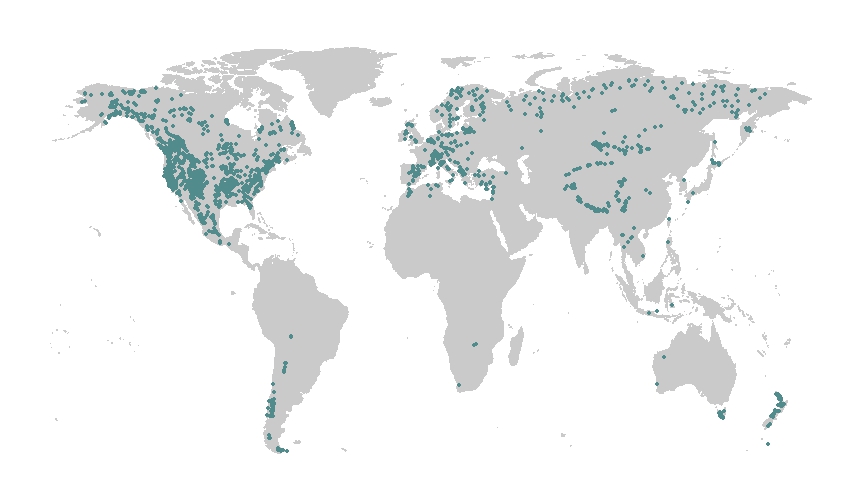
Numerous studies have reached a consensus regarding the relationship between drivers and tree radial growth. First, the specific drivers influencing tree radial growth vary widely among different biomes. For example, in subalpine regions, temperature has been identified as the primary driver (Shi *et al.* 2022), whereas in arid regions, precipitation takes precedence (Dannenberg *et al.* 2019). Second, trees can exhibit different growth responses to the same climatic driver, depending on factors such as temporal context and physiological state (Wang *et al.* 2017; Peltier & Ogle 2020). Furthermore, the effects of drivers operating on different time scales may interact. For example, changes in stand structure, such as leaf area and density, are associated with a continuous increase in the radial growth rate of old trees, instead of a decline along the ontogenetic growth trajectory (Stephenson *et al.* 2014). In addition to these factors, variation in resource availability and microenvironmental conditions can introduce uncertainty into tree growth trajectories. Given the inconsistencies, variability, and interrelationships among these driver effects, coupled with the uncertainties in tree growth, a fundamental question arises: Can forests organize regular tree growth trends at the aggregate level?

Recent studies may support this imperceptible overall regularity underlying tree growth. On the one hand, a large-scale analysis suggests that metabolic scaling theory (MST) constrains tree growth such that forest net primary production (NPP) can be expressed as a general scaling function of stand age and forest biomass (Michaletz *et al.* 2014; Michaletz *et al.* 2018). On the other hand, classical life history theory suggests that at least four independent trait-defined axes (leaf-height-seed-stem) (Baraloto *et al.* 2010) can shape the core strategies plants use to acquire and invest resources (Falster *et al.* 2018), where 18 tree functional traits associated with leaf economics, wood structure, bark thickness, tree size and crown size, seed size, and root depth can be grouped into eight distinct trait clusters (Maynard *et al.* 2022). Under the role of the maximum entropy principle (i.e., the number of combinations in which all mutually independent functional traits favor or unfavor growth is relatively small), we can expect trait diversity to result in regular overall growth trajectories becoming more pronounced. Nevertheless, our theoretical understanding of overall growth trajectories remains inadequate. This key is not currently explicitly incorporated into any model projections of future forest growth or carbon sequestration.

To address this issue, we extend our earlier proposed iterative growth model (IGM) (Shu *et al.* 2021). The IGM is grounded in general principles related to biological transport systems and energy metabolism (see Box 1). Its extent at the radial scale shows that the tree radial growth rate (*f*(*r*)) is mediated by its current radius (*r*), total growth time (TGT), and potential maximum radius (R), which can be expressed as:

 (1)

where, *k* is a parameter that relates to both the "formation time" (*T*) of unit tissue and the metabolic exponent (*b*). We refer to this equation as the iterative growth model at the tree ring scale (IGMR). For trees with *b* = 0.75 (West *et al.* 1999; Mori *et al.* 2010), their *k* value gradually increases from 1/3 to 3/4 as the tree grows (see Box 1). Our core hypothesis is that the maximum radial growth rate *f*(*r*) (*f*(*r*)m) for any given *r* within the same forest should conform to Eq. 1. This is because changes in *f*(*r*)m along the *r* gradient reflect the best growth trajectory (BGT), which is less adversely affected by climate and stand structure and is mainly controlled by ontogenetic growth. This also suggests that the maximum radius (Rm) and total growth time (TGTm) may remain relatively stable for a given species. Below the BGT, however, tree radial growth trajectories, as well as R, TGT, and *f*(*r*) (at the same *r*) can vary widely among different trees depending on genetics and the microenvironment (related to uneven stand structure, e.g., size heterogeneity). Understanding the relationship between these variations and the BGT or the theoretical mean growth trajectory (i.e., half of the BGT, HBGT) is crucial for comprehending the overall growth pattern.

Here, we tested the IGMR and its related hypotheses and explored the overall growth of trees using the extensive tree ring dataset. This dataset contains over 2,000 chronologies representing more than 180 species across various biomes and regions, including the temperate and Arctic zones (see Fig. 1). Our objective was to unveil the metabolic kinetic mechanism of tree radial growth and provide new insights into the overall growth pattern of trees.

**Fig. 1 Global distribution of study sites.**

Green dots indicate sampling sites involved in this study

Box.1:

The IGM not only explains the energy processes involved in the growth of biological development but also expands the mathematical framework of classical metabolic growth theory by introducing the concept of "formation time" (*T*) for unit tissue. Assuming that the new biomass formed during time *T* is represented by *f*(*m*), the relationship between the growth rate (*f*(*m*)/*T*) and its current biomass (*m*), maximum biomass (*M*), and metabolic exponent (*b*) can be expressed as shown below (Shu *et al.* 2021):

 (1)

where *gr* and *mr* represent the stable respiration cost required to produce a unit of tissue and the variable maintenance respiration rate per unit of tissue, respectively. This equation encompasses two implicit constraints. The first constraint is the total growth time (TGT), which must conform to the equation TGT = *gr*/*mr* × (2*b* + 2)/(1 − *b*). This equation can be derived from the integral transform of *f*(*m*) to *M*. The second constraint is that *T* < *gr*/*mr*, dictated by the thermodynamic significance of respiration. Moreover, *T* → 0 and *gr*/*mr* can yield two smooth functions driven by time (*t*), known as the Richards and Gompertz equations (Shu *et al.* 2021). Mathematically, the actual growth dynamics do not have an explicit analytic solution in most cases and lie somewhere between these two equations.

Due to tree radius (*r*) ∝ *mb/2* (West *et al.* 1999), we can further derive tree radial growth. Assuming that *f*(*r*)*T* is the ring width formed during time *T*, the relationships between tree radial growth rate (*f*(*r*)), current radius (*r*), and potential maximum radius (*R*) can be expressed as follows:

 (2-a)

In theory, the range of occurrence of Eq. 2-a is determined by the interval of values of *T*. In the case of *b* = 0.75 (West *et al.* 1999; Mori *et al.* 2010), the following can be derived from *T* → 0 and *gr*/*mr*:

 (2-b)

 (2-c)

Theoretically, the faster a tissue unit grows (*T* → 0), the closer *f*(*r*) will be to Eq. 2-b. Conversely, when *T* → *gr*/*mr*, *f*(*r*) approaches Eq. 2-c (Shu *et al.* 2021). We thus refer to Eq. 2-b as the lower boundary (IGMR-L) and Eq. 2-c as the upper boundary (IGMR-U) of the IGMR. When considering Eq. 2-c, an integral transformation from *f*(*r*) to R shows that the total growth time (TGT) of an organism is 14 × *gr*/*mr*, which is consistent with the IGM calculation. However, the same integral transformation reveals that the TGT for Eq. 2-c is 32/3 × *gr*/*mr*. This difference suggests a shift in the pattern of tree radial growth from Eq. 2-b to Eq. 2-c over time, aligning the TGT of tree radial growth with that of biomass growth. Additionally, given the dependence of TGT on T, according to Eqs. 2-b and 2-c, we can further infer that the IGMR containing TGT can be expressed as

 (3)

## where k is a parameter related to both *T* and *b*, with a value range of 1/3 and 3/4, if *b* = 0.75. On average, *k* = 0.55.

**Materials and Methods**

**Tree ring data**

We first compiled over 7,000 tree ring chronologies from 188 species located worldwide, ranging from temperate to Arctic regions (Fig. 1). The data were sourced from ref. (Zhao *et al.* 2019) and the International Tree‐Ring Data Bank (ITRDB) (<https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>), where most of these tree cores were sampled from 1966 to 2004. To increase robustness, we selected only the chronologies with a sample size >20. Some analyses require a minimum sample size of more than 50 (Fig. 2D and Fig. 4). We then counted the diameter (*r*) of tree cores, their age, and the mean radial growth rate over the last 20 years (*f*(*r*)) according to these chronologies. Here, *r* represents the total width of tree rings and age refers to the number of tree rings. We further identified the 0.99 quantiles of tree radius and age for each chronology as proxies for maximum radius (Rm) and total growth time (TGTm), respectively. Other data with a radius or age exceeding Rm or TGTm were excluded. Since that many studies only sampled living trees, some trees may be hollow, or some tree core samples may lack pith, it is inevitable that TGTm will have some error from the true value. Nevertheless, the risk of underestimation of all TGTm is manageable as the sampling process did not vary much across sites and we only considered sample sites with a large span of tree rings. It has no directional effect on our core results, especially for large-scale assessments of growth rates and lifespan patterns. In addition, tree size heterogeneity was then quantified using the coefficient of variation for the radius. The final compliant dataset comprises approximately half of the original dataset, encompassing 183 species, over 2,000 chronologies, and more than 100,000 tree cores (Fig. 1).

**Statistical analysis**

We first tested whether Eq.1 can explain the best growth trajectory (BGT), where the BGT is defined as changes in the maximum radial growth rate with the radius. This test was performed on global and site scales. To eliminate species differences, we considered changes in normalized radial growth rates (*f*(*r*)/(Rm × TGTm)) relative to relative radius (*r*/Rm). Next, using normalized Eq. 1, we conducted quantile regressions on the distribution of normalized radial growth rates across the relative radius for different growth stages (stand age/TGTm ranging from 0 to 1, < 0.5 and > 0.5). Here, the regression was set at a percentile equal to 1 minus the ratio of the 0.01 quantile of *r* to Rm. These analyses were performed primarily using the *quantreg* package in R software version 4.1.2 (R Core Team, 2021).

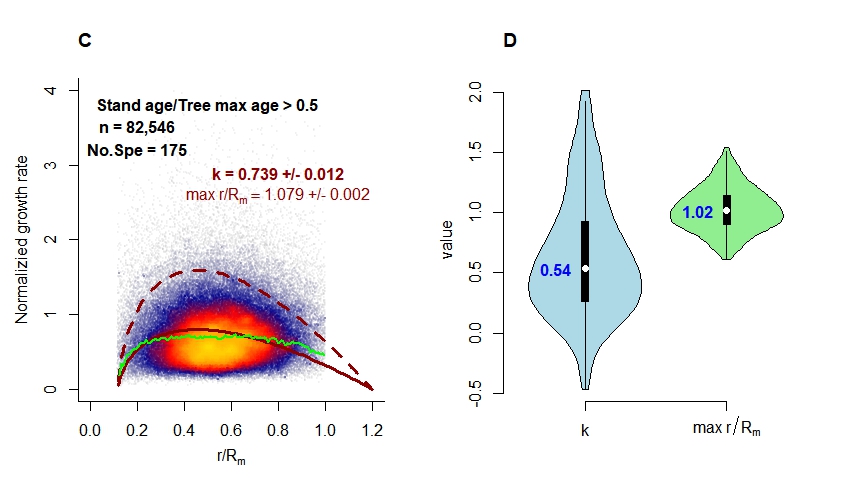
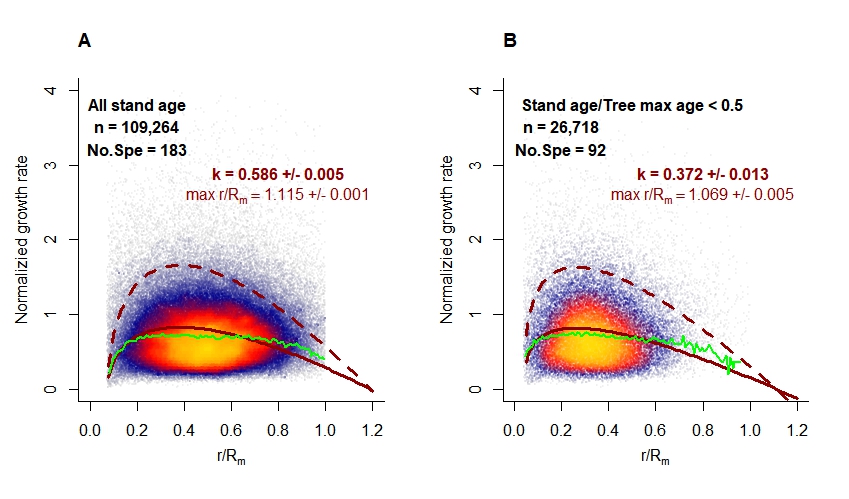
We then used Eq. 1 to predict the mean *f*(*r*) based on the current mean *r*, Rm, and TGTm for each forest, and compared these predictions to the actual results. To quantify the *f*(*r*) distribution, we focused on the relationship between the mean radial growth rates of tree cores over the last 20 years and their standard deviation. In addition, we calculated the total deviation of actual *f*(*r*) from the theoretical prediction in different forests based on Eq. 1 and explored the effect of tree size heterogeneity on this deviation. This total deviation can be expressed as ∑ (*f*(*r*)ob – *f*(*r*)pr)/*f*(*r*)ob, where *f*(*r*)pr and *f*(*r*)ob represent the predicted and observed *f*(*r*), respectively.

To identify the effects of species, climate, and stand structure on the BGT, we conducted a linear mixed-effects model (LMM) analysis with species identity as a random effect. The climate drivers used, such as the annual mean temperature (ATM) and annual precipitation (AP), were extracted from WorldClim (2.5 min) (https://www.worldclim.org/data/worldclim21.html#). These climate drivers represent annual averages spanning the period from 1970 to 2000. They were largely matched to the sampling time of the tree cores. To ensure the robustness of the LMM, we only used data from species with a sample size greater than 50 and more than 5 sample plots for analysis. Before doing so, to avoid multicollinearity, variables with an absolute correlation value greater than 0.7 were initially excluded. Additionally, we employed a variance inflation factor (VIF) threshold of 5 to eliminate variables that still exhibited strong correlations in the results. When necessary, we standardized our data through Z-score transformation to improve normality and homogeneity. The mean and maximum radial growth rates were used as crucial indicators of the distribution of radial growth rates. Similarly, we also assessed the effects of climate on them using the LMM. These analyses were performed using the *lmerTest* package in R software version 4.1.2 (R Core Team, 2021).

**Results**

**IGMR constrains tree radial growth**

We first found that the IGMR constrains tree radial growth. This result can be obtained from the distributions of normalized mean radial growth rates (*f*(*r*)/Rm × TGTm) along the relative radius (*r*/Rm) for different forests over the last two decades (Fig. 2). The upper boundary of this distribution is close to the normalized IGMR with *k* = 0.586 and maximum *r*/Rm = 1.115 (Fig. 2A) (red dashed line in Fig. 2A). As predicted, 0.586 lies exactly in the middle of the theoretical range of values of *k* (1/3 to 3/4), and 1.115 is also close to the theoretical value of maximum *r*/Rm, i.e., 1. Not only that, but the results also confirm that the *k* values are variable, approaching 1/3 in the early stages of forest growth (Fig. 2B), and gradually changing to 3/4 over time (Fig. 2C). Overall, the *k* and maximum *r*/Rm values for different forests are normally distributed, with median values of 0.54 and 1.02, respectively (Fig. 2D). Furthermore, we observed that the mean growth trajectories (green lines in Figs. 2A, 2B, and 2C) are always around the HBGT (red solid lines in Figs. 2A, 2B, and 2C).

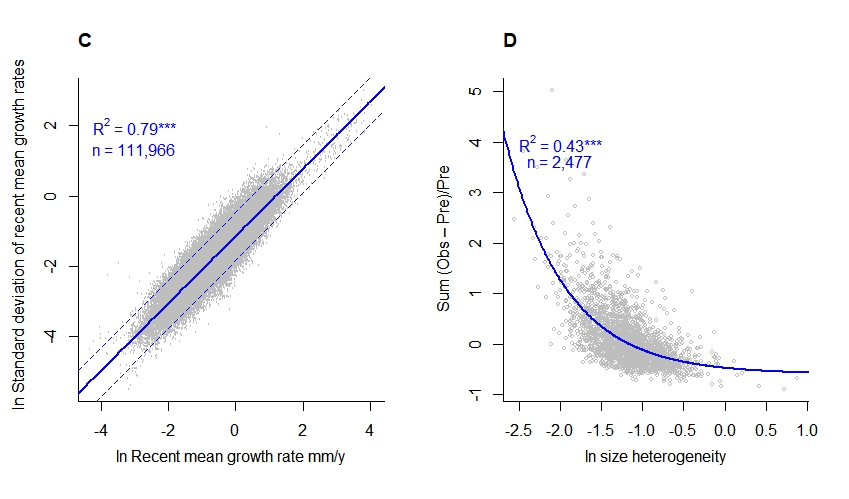
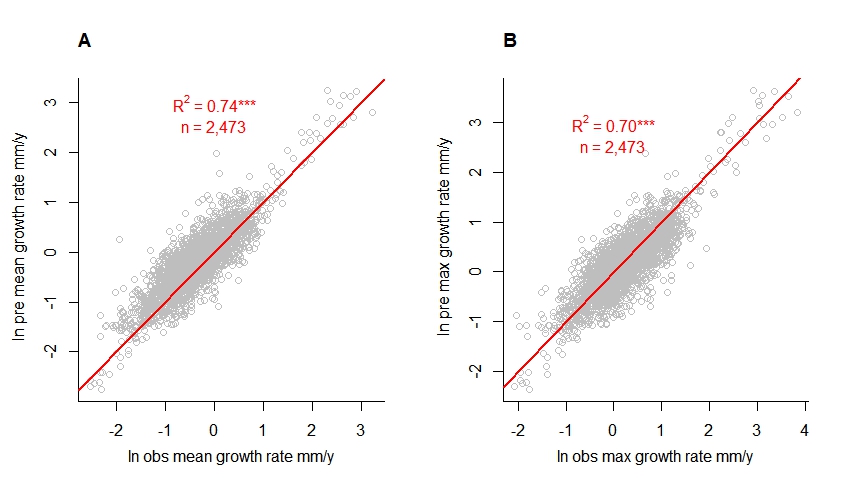


**Fig.2 Changes in normalized tree radial growth rate (*f*(*r*)/Rm × TGTm) with tree relative radius (*r*/Rm) (A, B, C and D).**

A, B and C: Dark red dotted and solid lines represent the fitted normalized best radial growth trajectory (BGT) and half of this trajectory. The green line shows the mean growth trajectory. The fitted parameters in the normalized BGT are shown in dark red. Each scatter in the plot represents a tree core. D: The medians of the parameters of the BGT between different sites are shown in blue.

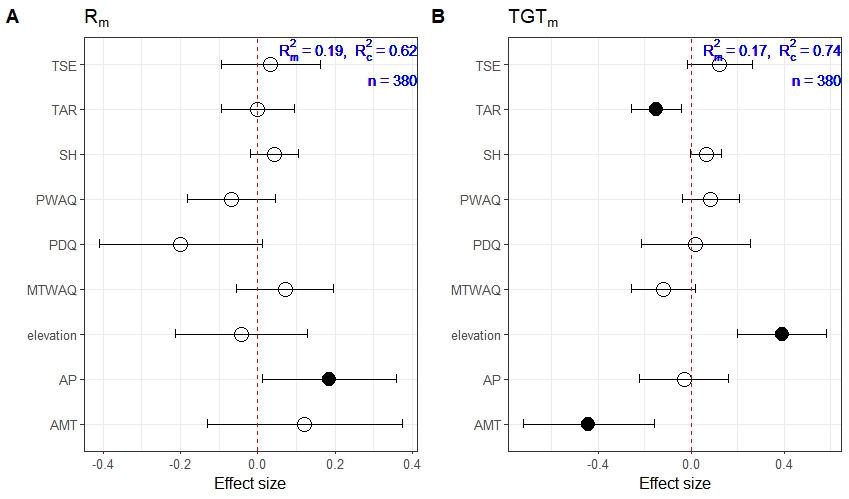
**Overall radial growth trends of trees and their influencing factors**

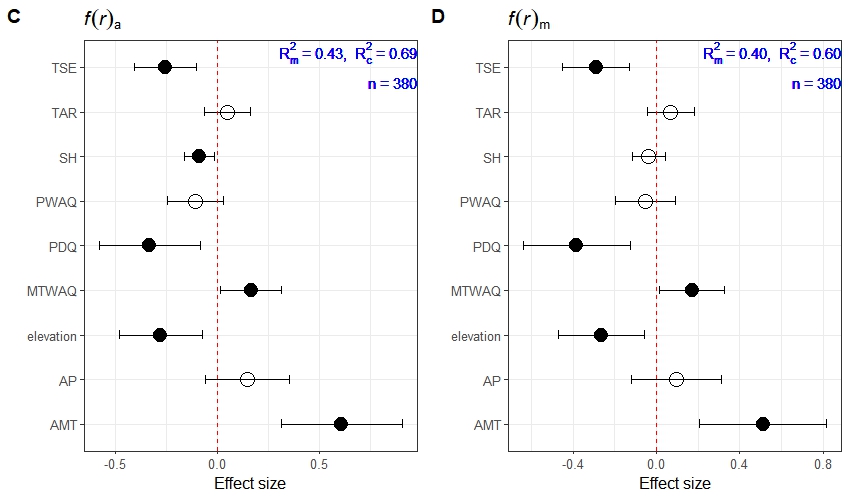
The IGMR reveals the control of radius on radial growth, which makes us realize that the overall growth trend of trees may follow certain patterns. This regularity is first reflected in the relationship between individual tree growth and overall growth. For example, Eq.1 shows that the mean and maximum radial growth rates occur at *r*/Rm values of 0.052 (or 0.63) and 0.264, respectively. That is, we can calculate the the mean and maximum radial growth rate for tree population based on the individual-scale Rm and TGTm (Figs. 3A and 3B). Second, the regularity also includes the stable distribution of *f*(*r*). Specifically, the mean (*x*) of *f*(*r*) and its corresponding standard deviation (*y*) for different forests over the last two decades or earlier can be described by the equation *y* = 0.34*x*0.94 (R2=0.79, *p* < 0.01) (Figs. 3C and S2). Not only that, the fit coefficient (0.34) and the exponent (0.94) indicate that *f*(*r*) follows a normal distribution with a mean of the HBGT (Fig. S3). While tree size heterogeneity can cause overall radial growth rates to deviate from the HBGT, this effect remains predictable and relatively limited. We found that as tree size heterogeneity increased or stand age decreased, there was a gradual shift in the overall radial growth rate from above to below the HBGT (Figs. 3D and S4). It is global in scale and can be observed in Fig. 2. The parameters Rm and TGTm determine the length and/or height of the IGMR. Their responses to climate and tree size heterogeneity greatly impacts the overall growth trajectory of trees. We used a linear mixed effects model (LMM) with species identity as a random effect to assess the impact of these drivers on forest Rm, TGTm, mean radial growth rate (*f*(*r*)a), and maximum radial growth rate (*f*(*r*)m). Our results indicate that these factors together explained 19% of the total variance in Rm (Fig. 4A). Notably, LMM accounted for approximately one third of the variance, with precipitation emerging as the only significant driver. Similarly, the influence of climate on TGTm was relatively limited, explaining only 16% of its total variance (Fig. 4B), with temperature showing the most significant effects. Furthermore, we found that species identity was the most important factor influencing the variation in forest Rm and TGTm. Several consistent temperature-related climate drivers can significantly explain a substantial part of the observed variance in *f*(*r*)a and *f*(*r*)m (Fig. 4C and 4D). This also supports the idea that the distribution of radial growth rates within the same forest remains stable and independent of both species composition and stand age. Although gradual warming will increase radial growth rates (Fig. 4C and 4D), it will also decrease tree TGT (Fig. 4B and S5). Mathematically, this trade-off is due to *f*(*r*)a and TGT containing *mr* and 1/*mr*, respectively, regardless of how the temperature affects *mr* (Thornley & Cannell 2000; Shu *et al.* 2019; Shu *et al.* 2021). Therefore, temperature changes affect the height rather than the length of the unimodal growth curve, implying that gradual warming may not directly impact the size of adult trees. In contrast, annual precipitation (AP) has a more direct and pronounced impact on Rm.



**Fig.3 Prediction of mean (A) and maximum (B) radial growth rates of tree populations predicted by the IGMR, relationship between the recent mean radial growth rates of tree cores and their standard deviation (C), and the relationship between tree size heterogeneity and the total deviation of radial growth rates relative to theoretical predictions (D).**

A and B: The red line represents *y* = *x*, with the explained variance (R2) of the model shown in red. C: The blue line represents *y* = 0.94*x* - 1.17, with the explained variance (R2) of the model shown in blue. The blue dashed lines represent the 0.05 and 0.95 quantile fits, which are *y* = 0.94*x* - 1.84 and *y* = 0.95*x* - 0.49, respectively. D: The blue curve represents *y* = exp(-1.35*x*-2.07) - 0.61, with the explained variance (R2) of the model shown in blue. Each scatter in A, B and D comes from a forest, while in C, it comes from a tree core.





**Fig.4 Effects of climatic variables and size heterogeneity on maximum radius (A), maximum growth time (B), mean radial growth rate (C) and maximum radial growth rate (D) globally.**

The solid circles represent significant effects (*p* < .05), and the open circles represent nonsignificant effects (*p* > .05). The explained variance (R2) of the model is shown in blue. R2m and R2c are the mean marginal R 2 and conditional R 2, respectively.

TSE, temperature seasonality (standard deviation ×100); TAR, annual temperature range; SH, size heterogeneity; PWAQ, precipitation of wettest quarter; PDQ, precipitation of driest quarter; MTWAQ, mean temperature of warmest quarter; AP, annual precipitation; AMT, annual mean temperature.

**Discussion**

The best radial growth trend of trees agrees with the theoretical derivation based on the assumption of the IGM (Fig. 2). This not only supports the statement that ontogenetic growth trends dominate or constrain other growth changes but also validates the existence of the "formation time" (*T*) of unit tissues. Similar to the classic metabolic growth model (i.e., ontogenetic growth model, OGM), the IGM or IGMR is also based on metabolic scaling theory (MST) and the growth-maintenance respiration paradigm (GMRP). MST provides a power relationship between body size and metabolic rate, while GMRP distinguishes between growth and maintenance metabolism (Clarke 2019). On the one hand, these laws or concepts are established independently of species and climate and have been shown to be effective in predicting and explaining the growth of endotherms and ectotherms (Hou *et al.* 2008; Zuo *et al.* 2012), as well as forest carbon sinks (Michaletz *et al.* 2014; Shu *et al.* 2019). On the other hand, the derivation of the IGMR is not affected by the debate regarding the specific metabolic exponent in MST (Thornley & Cannell 2000; Moses *et al.* 2008; Cheng *et al.* 2010; Mori *et al.* 2010) and takes into account genetic and physiological activity controls on growth rates. The IGMR suggests that even under ideal conditions, the tree radial growth trajectory can spontaneously change as trees age (Figs. 2A, 2B and 2C). This finding strengthens the ability of metabolic growth theory to explain plant growth, which implies that the plant growth trajectory varies within a predictable range. For example, some studies found that crop growth dynamics follow the logistic curve more than the OGM (Shi *et al.* 2013). This mismatch can be reconciled if a growth range perspective is introduced.

The overall radial growth trend of trees can be regularly organized by forests. Our results confirm that both the mean and maximum radial growth rates of trees in a forest follow consistent growth kinetics mechanism, and can be predicted by the radius and longevity of the largest trees of the same species (Figs. 3A and 3B). Moreover, we revealed that the overall radial growth trajectories of trees converge to the HBGT (Fig. 2) and are unaffected, or less affected, by species, individual variation, climatic variability, and uneven stand structure (Figs. 3C, 3D, and S2). In addition to the constraint of the IGMR on the BGT, we speculated that this self-organizing stability may be largely attributable to the relative independence of functional traits involved. We found that the relative deviation of tree ring growth rates from the HBGT began to decrease with greater tree size heterogeneity (Fig. 2D). Although disturbances may further increase tree size heterogeneity and adversely affect tree growth, this relative deviation remains limited as tree size heterogeneity increases (Fig. 2D). Since tree size is often associated with functional traits—tree size that is itself important functional trait—this result indirectly confirms our assertion that functional trait diversity plays a role in shaping the stable overall growth trajectory of trees.

The specific overall growth trajectory of trees is determined by the size and total growth time of the largest tree. While temperature-related climatic variables have an impact on the mean and maximum growth rates of the overall trajectory (Fig. 4C and 4D), the maximum radius that the trajectory can reach exhibits more species dependence (Figs. 4A and 4B) due to inherent trade-offs between growth and longevity (Fig. S5) (Brienen *et al.* 2020; Locosselli *et al.* 2020). This finding suggests that climate change, particularly global warming, is more likely to result in drift (apparent plasticity, i.e., changes in growth rate only) than adaptation (true plasticity, i.e., changes in adult size) in overall tree growth trends.

Our findings can be further extended to the forest scale. Since tree size has a strong effect on tree abundance (i.e., Yoda's law), the best and overall growth trajectories driven by size necessarily control forest net primary productivity (NPP). This control is first reflected in the fact that NPP can be explained by the largest tree biomass (Michaletz et al. 2014) and forest biomass (Kohyama *et al.* 2023). Second, in the long run, the average carbon sequestration of individual trees in the same species is stable. This is because we found that, globally, Rm exhibits more species dependence due to growth-longevity trade-offs (Fig. 4A). Consequently, climate change is more likely to affect forest maximum biomass (FMB) by altering the composition and structure of forest communities (Allen *et al.* 2010; Piao *et al.* 2014; Stephenson *et al.* 2014; Millar & Stephenson 2015; McDowell *et al.* 2016). Third, the gap between the best and overall growth trajectories controls the relationship between community shifts and NPP or FMB. When this trajectory gap is small, trees tend to have lower growth rates, longer lifespans, and less variation in functional traits. Such conditions are often found in less productive environments (high latitude regions), where tree abundance is directly related to NPP or FMB. In contrast, the gap between these two trajectories is relatively large in more productive environments (lower latitudes), which also implies a greater variation in growth rates and functional traits. In this case, the effect of species diversity on NPP or FMB is more pronounced. These speculations are supported by recent studies (Locosselli *et al.* 2020; Madrigal-González *et al.* 2020).

Finally, the IGMR reveals that the climate sensitivity of tree radial growth depends on both the *r* and the BGT. Rapid responses (i.e., high-frequency signals) of radial growth trajectories to climate variability are often assumed to be stable, known as the stationary assumption or uniformity principle (Wilmking *et al.* 2017; Peltier & Ogle 2020). Based on this principle, we can obtain high-resolution global information on tree species' responses to global change, forest carbon and water dynamics, and past climate variability and extremes from tree ring dynamics (Wilmking *et al.* 2020). The IGMR challenges this principle because as *r* or HBGT varies, *f*(*r*)m is different and the standard deviation of *f*(*r*) varies with *f*(*r*)m.

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Supervision: XW, WZ

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Writing – review & editing: TX, KG, XW, WZ, WW, XZ

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**Data and materials availability:** Tree radial growth data are available at <https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring>

Climate data are available at

https://www.worldclim.org/data/worldclim21.html

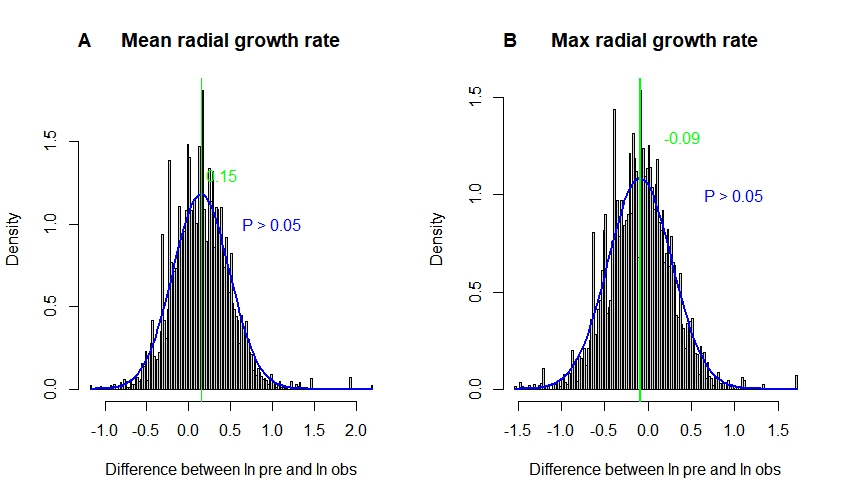
Code will be made available on request.

Supplementary Materials

Materials and Methods

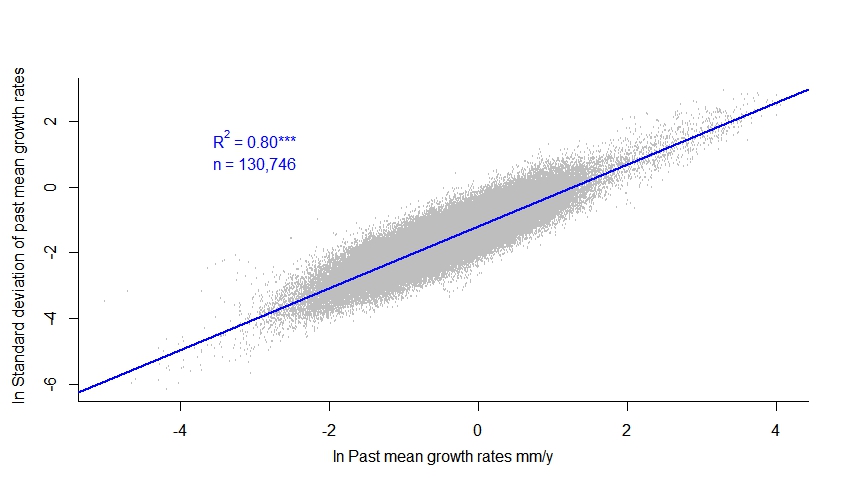
Figs. S1 to S5

**Supplementary Materials**

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**Fig. S1 Distribution of the difference between the predicted and actual values for ln mean (A) and ln maximum (B) radial growth rates.**

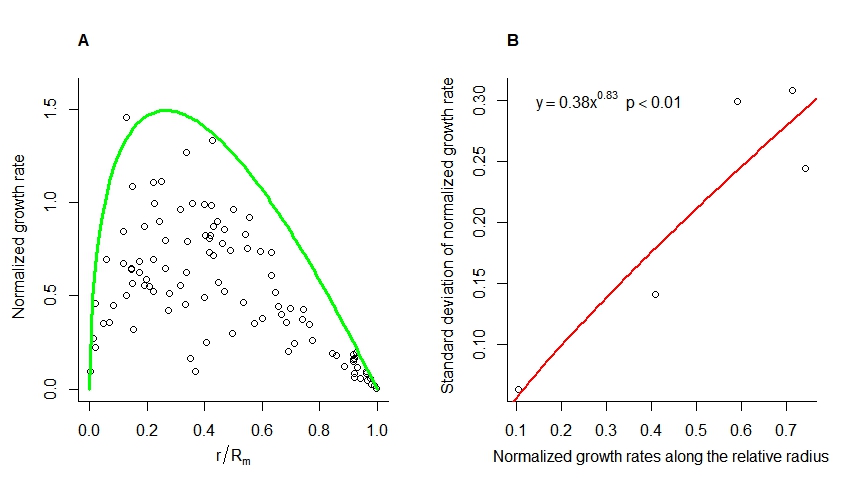
The blue curve represents the normal distribution. The *p*-value, which indicates the significance of the difference between the actual distribution and the normal distribution, is shown in blue. The green vertical line represents the mean fit residual, whose value is shown in green.

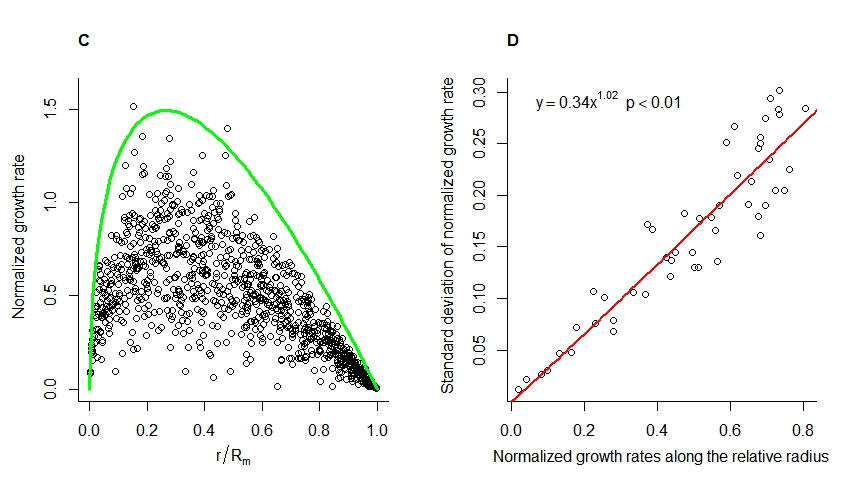


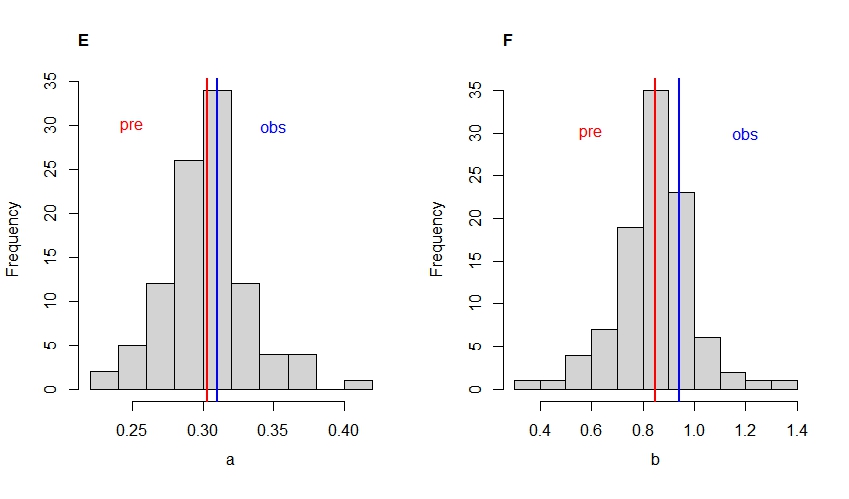
**Fig. S2 Relationship between the mean radial growth rate of tree cores in the past (from the last 60 years to the last 40 years) and their standard deviation.**

The blue fitting curve is *y* = 0.94*x* - 1.20.

The fitted slope and intercept here are not significantly different from those in Fig. 3C.

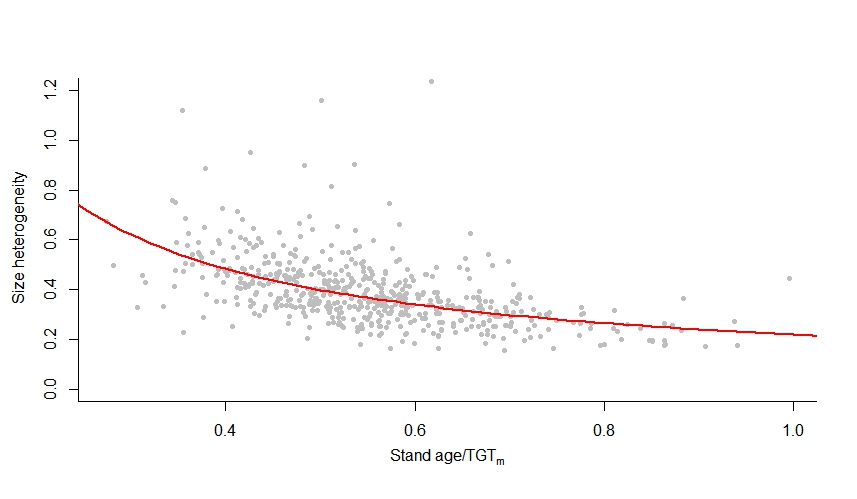






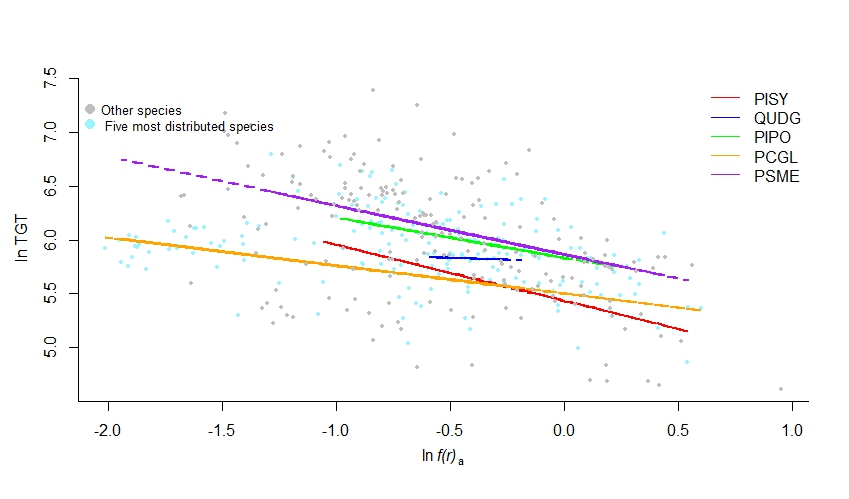
**Fig. S3 Distribution of normalized radial growth rates over relative radius based on the assumption of normal distribution and distribution of parameter values obtained from 100 data simulations.**

The sample sizes for the simulations were 100 (A) and 1000 (C). We divided the relative radius into 5 equal parts for A and 50 equal parts for C according to the sample size. For each equal part, we calculated the mean normalized radial growth rate and its standard deviation. These calculated results are plotted in B and D, respectively. The fitted trajectories of their relationship are shown as red solid lines (B and D). We then performed 100 random simulations (with sample sizes between 100 and 1,000) and fitted an exponential relationship between their normalized radial growth rate and relative radius. The resulting values of the constant term (*a*) and the exponential term (*b*) are shown in E and F. The red and blue lines indicate the simulated mean and the actual observations, respectively.



**Fig. S4 Changes in tree size heterogeneity with forest growth.**

The red curve is *y* = 0.22 *x* -0.86 (R2 = 0.28, *p* < 0.01)



**Fig. S5 Trade-offs between mean radial growth rate (*f*(*r*)a) and total growth time (TGT).**

PISY, *Pinus sylvestris L*; QUDG, *Quercus douglasii Hook*. *and Arn*; PIPO, P*inus ponderosa Douglas ex C. Lawson*; PCGL, *Picea glauca (Moench) Voss*; PSME, *Pseudotsuga menziesi (Mirb.) Franco*.