

Research Article

Individual Asynchrony Encourages Stable Tree Growth At The Population Level.

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Abstract

It is commonly believed that species richness and asynchrony improve community-level stability. The degree to which population size and individual within-population asynchrony may influence population-level stability is unclear, though. 2. We measured the impact of population size and within-population tree growth asynchrony on the temporal stability of population-level tree growth rate using a sizable collection of global tree-ring data. Additionally, we looked at the connection between population-level tree growth stability and the global distributions of within-population tree growth asynchrony. According to our findings, population size is the second most important factor instabilizing population-level tree growth rate, after individual asynchrony. This result emphasizes how crucial individual-level variations are in reducing environmental stressors on forest growth.

Keywords : *Scimate Zones, Ecological Stability, Forest Resilience, Global Distribution Of Forest Stability, Individual Asynchrony, International Tree-Ring Data Bank, Population Size, Tree Growthstability, Within-Population Variability.*

INTRODUCTION

Understanding how a biological system's complexity could maintain its performance, such as the yearly production of grasslands or forest communities, is a major ecological concern (Jucker et al., 2014; Schindler et al., 2010; Yachi & Loreau, 1999). While a lot of research has been done on this topic over the past few decades, most of it has concentrated on how biodiversity affects community stability (Hector et al., 2010; Tilman, 1996; Walter et al., 2021). The mechanisms by which individual-level differences impact population-level stability have received less attention (Waddle et al., 2019). It is crucial to close this gap since individual-level variation defines population-level variation and, in turn, higher ecological levels respectively. Two primary mechanisms are thought to be responsible for the stability of ecological communities: the portfolio effect (also known as statistical averaging) (Doak et al., 1998; Tilman, 1996), which shows that stability rises with the number of species, and the insurance effect (Blüthgen et al., 2016; Yachi & Loreau, 1999), which shows that stability rises with the temporal asynchrony among species (species

asynchrony). Community stability and population stability can be compared, with population size being equivalent to species richness and individual within-population asynchrony to species asynchrony. For instance, it is well known that climate, particularly the water-energy balance, has a significant influence on tree development (Peltier & Ogle, 2020).

Therefore, changes in the climate would unavoidably result in changes in the pace of growth. In addition to climate, growth asynchrony of conspecifics can result from a variety of other factors, including tree age, genetic and trait variations, and micro-habitat conditions (Cater & Chapin III, 2000; Peltier & Ogle, 2020; Takenaka, 2000; Tejedor et al., 2020). The population-level mean tree growth rate is kept stable by these individual disparities, which enable the growth rates of the faster-growing individuals to offset those of the slower-growing individuals when averaged over the population. The ecological implications of this stabilization process could be significant in reducing the adverse effects of climate change on the forest ecosystem. The degree to which population size and within-population asynchrony can control the stability of population-level tree growth rate, however, is not well understood.

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Tree growth asynchrony is not uniformly distributed across various biomes and can be influenced by a variety of circumstances (Defriez & Reuman, 2017; Shestakova et al., 2016; Tejedor et al., 2020; Walter et al., 2017). For instance, Tejedor et al. (2020) demonstrate that, on a worldwide scale, the mean annual temperature and precipitation have a positive correlation with the within-population asynchrony in tree growth rate, with the tropics having the highest growth asynchrony and arid regions the lowest. Such regional heterogeneity in asynchrony may have an impact on the stability of tree growth variation worldwide. Gaining an understanding of this mechanism would enable us to better understand how tree growth asynchrony contributes to reducing the adverse effects of climate change on the stability of forest ecosystems across various climate zones.

We looked at how individual tree growth variations affected the stability of tree growth at the population level. In particular, we (1) measured the relationship between population-level tree growth stability (STBP) and population size (N) in order to test the population-level portfolio effect; (2) measured the relationship between population-level tree growth stability and within-population tree growth asynchrony (WPA) in order to test the insurance effect; (3) measured the contributions of these two effects to population-level tree growth stability in comparison to individual-level tree growth stability (STBI); and (4) measured the global variation of within-population tree growth asynchrony and investigated its impact on the variation of population-level tree growth stability across various climatic zones.

MATERIALS AND METHOD

Tree-ring data

The International Tree-ring Data Bank now the largest public tree-ring repository in the world, provided us with global tree growth data. The annual resolved tree-ring width series in ITRDB are categorized into individual datasets, each of which represents a single population by including records from a single species in a single site. We downloaded all population-level dataset that was accessible on ITRDB by May 2022. The datasets were cleaned using a popular technique that Zhao et al. (2019) presented. This procedure mostly involved eliminating duplicate records and fixing data formatting mistakes. After that, we kept population-level datasets with at least five tree-ring series that covered the years 1971–2000. The study's focus is on this time frame.

It is usual procedure in dendrochronological analysis to detrend (standardize) raw ring-width measurements in order to reduce the impact of non-climatic tree growth trends, which are primarily long-term growth fluctuations brought on by elements such shifting competitive environments and growing tree ages and stem diameters (Cook et al., 1990). We

employed a flexible spline to detrend our tree-ring data in accordance with the methodology of an earlier study on tree growth asynchrony (Tejedor et al., 2020). To do this, we first fitted the raw ring-width series to a 30-year spline function with a 50% frequency cut-off, which caught the long-term growth variations. In order to eliminate the long-term signals while maintaining the short-term growth variations, we next divided the raw ring-width series by the fitted spline (Cook et al., 1990).

keeping aside the fluctuations in short-term growth (Cook et al., 1990). In our investigation, the annual tree growth rate was determined by using the resulting non-dimensional ring-width index (RWI). In this case, we decided to calculate RWI using the division approach as opposed to the subtracting method. In addition to the fact that the ratio approach is most frequently employed in tree-ring detrending, the latter also skews the results by artificially introducing a declining trend in the variation in the RWI series as trees get bigger and the annual rings get thinner. The R software package *dplR* (Bunn, 2008) (<https://r-project.org>) was used to carry out the aforementioned procedures. Additionally, we employed raw data and RWI generated by alternative detrending techniques, such as a more aggressive 10-year spline detrending and a more conservative negative exponential detrending, neither of which significantly altered the outcomes.

Classification of climate zones

We collected monthly temperature and precipitation data for each population from 1971 to 2000 from the CRU-TS4.04 database (<http://climexp.knmi.nl>) in order to categorize climate zones. The climate zones were categorized using the “Köppen's climate classification” methodology, which was outlined by Kottek et al. (2006). The five main climate zones—Tropical, Dry, Temperate, Continental, and Polar—are categorized based on the average annual temperature and precipitation for a specific time period, in our case, 1971–2000.

Quantifying tree growth asynchrony and stability

The temporal growth asynchrony between individual trees is measured by the within-population tree growth asynchrony (WPA). It was defined using the approach Tejedor et al. (2020) outlined. We first determined the average pairwise Pearson's correlation coefficients (r), sometimes referred to as r_{bar} in dendrochronology, between the RWI (detrended tree growth rate, see above) series of each constituent tree for each.

population-level dataset

Thibaut and Connolly (2013) state that r_{bar} can range from $-1/(N-1)$ to 1, and as the minimum N was limited to 5, the minimum r_{bar} was -0.25 . Consequently, WPA is between 0 to 1.25, where 0 denotes fully synchronized growth and 1 denotes

random correlation. Only a small number of populations that were eliminated as outliers due to their falling inside the ± 0.01 quantiles (see below) showed negatively linked growth, as indicated by a WPA greater than 1. It should be noted that the observed WPA is unaffected by the variation in N between populations (Methods S1; Figure S2). The inversed coefficient of variation, or $1/CV$, of a tree's RWI series was used to quantify the temporal stability of individual-level tree growth rate (Egli et al., 2020; Jucker et al., 2014).

Calculating the portfolio effect at the population level

We looked at how population-level tree growth stability (STB P) varies with population size N, in accordance with the portfolio effect in community ecology, which suggests that community stability rises with species diversity. In doing so, we identified that within-population tree growth asynchrony (WPA) may have an impact on STB P. Therefore, we randomly selected a varying number of trees (N's) from each population, ranging from 5, 10, 20, and 100, in order to control the confounding influence of WPA on the STB P–N relationship. The anSTB P was computed for every N. We conducted this sampling 100 times for every population, resulting in 100 STB P for every N. Ultimately, we calculated a mean STB P for each N by averaging these 100 STB P.

For every population, the Pearson's correlation coefficient between STB P and N was also computed. The aforementioned research was limited to populations with more than 100 trees (there were 53 such populations), while the majority of populations had fewer than 100 trees. We plotted the STB P/STB Pmax ratio against N in order to determine the number of trees needed to fully stabilize a population's mean growth rate (i.e., when STB P levels off as it approaches the maximum population-level tree growth stability, or STB Pmax). The N at which the ratio reached 0.95 was identified as the population size needed to fully stabilize the population, or Nmax.

Quantifying the insurance effect

We can measure the insurance effect by examining the connection between STBP and within-population tree growth asynchrony (WPA). However, since our population-level datasets vary in N and STBP also increases with N (i.e., the portfolio effect defined above), utilizing STBP directly estimated from the original population-level datasets may skew the STBP–WPA relationship. To be sure that N wouldn't skew this relationship, we evaluated how population growth stability altered with within-population tree growth asynchrony using the STBPmax–WPA relationship rather than modeling the STBP–WPA relationship. As previously mentioned, STBPmax eliminates the confusing effect of varying N by representing the greatest value of STBP when $N \rightarrow \infty$ (see Equation 5 and Methods S2).

Quantifying the overall stabilizing effect

We obtain $\text{STBP} = \text{STBI}$ for the extreme situation of $\text{WPA} = 0$ in Equation, when there is no variation in the tree growth rate among individuals. In practice, when $N > 1$, such perfectly synchronized growth is unlikely to occur. Rather, STBP will consistently surpass STBI in size. For the same rationale as previously stated, we therefore computed the overall stabilizing effect (STBeff) in a population as follows: where STBPmax is used in place of STBP. This STBeff calculates the difference between the stability of individual tree growth and the stability of population-level tree growth. The climatic-zone level and worldwide mean values were then calculated by averaging the STBeff over the populations in each climate zone and globally, respectively. To control outliers, STBeff's top and lower 0.01 quantiles were also eliminated.

WPA's effects on the stability of tree growth dispersion worldwide

Our goal was to investigate the effects of WPA variation on the global distribution of population-level tree growth stability across various temperate zones. We determined the average WPA, STBI, STBPmax, and STBeff for each of Köppen's five main climate zones—Tropical, Dry, Temperate, Continental, and Polar—in order to respond to these queries. For each of the four variables across climate zones, multiple comparisons with Tukey's p-value adjustment were carried out using the R package emmeans (Lenth et al., 2018). It was also determined how WPA and STBeff correlated among climate zones.

RESULTS

Stabilization of population-level tree growth rate

For all 53 investigated populations, we found a widespread and positive correlation ($r > 0.6$, $p < 0.001$) between population-level tree growth stability (STBP) and population size (N), suggesting a large within-population portfolio effect. However, as N increased, the portfolio effect rapidly saturated. At approximately $N_{\text{max}} = 26$, STBP averaged 95% of maximum population-level tree growth stability (STBPmax); individual populations' N_{max} es ranged from 10 to 80. Additionally, we discovered that within-population tree growth asynchrony (WPA) and N_{max} had a positive correlation across populations. Across all 2133 populations worldwide, a substantial positive correlation between WPA and STBPmax was found ($R^2 = 0.54$, $p < 2.2 \times 10^{-16}$), indicating a robust within-population insurance effect.

Global variation in population-level tree growth stability

Global variation in population-level tree growth stability illustrates how the mean STBI differed considerably among the five main climate zones of the world, with the tropical zone having the lowest STBI and the polar zone having the

highest. In contrast to STBI, the tropical zone's STBPmax was considerably greater than the dry zone's ($p < 0.05$) and did not deviate significantly from the world mean. Furthermore, we found a strong and favorable connection between WPA and STBeff throughout the five climate zones. With an STBeff of 84% and the greatest WPA in the world, the tropical zone outperformed all other climate zones ($p < 0.05$).

DISCUSSION

Through the portfolio effect (stability increases with population size) and insurance effect (stability increases with within-population tree growth asynchrony), we demonstrated in this study that the differences in growth rates among individual trees were crucial in preserving population-level tree growth stability. According to this finding, population-level stability is maintained by the same set of mechanisms that govern stability at the community level. The population-level tree growth stability also asymptotically rose with population size, reaching 95% of its maximum value at an average population size of 26, as illustrated.

Globally, within-population tree growth asynchrony differed significantly between climate zones, with the Tropical zone showing the most asynchrony and the Dry zone showing the lowest. This could be because the dry zone presents the most challenging conditions for tree growth. In the dry zone, drought primarily controls tree development and synchronizes annual growth rates, resulting in less growth asynchrony (Tejedor et al., 2020). Tree development is more heavily influenced by a variety of stochastic elements, including microhabitat characteristics like soil, terrain, and competition, which results in a larger asynchrony. In contrast, the water and energy circumstances are significantly better in the tropical zone.

The exponential increase in stability with asynchrony and the finding that the population size needed to achieve maximum population-level growth stability increases with tree growth asynchrony demonstrate that within-population tree growth asynchrony significantly impacted population-level tree growth stability. According to this conclusion, populations with higher tree growth asynchrony are able to stabilize their growth by using a larger population size, and they often achieve greater stability than populations with lower asynchrony. This population-level result is consistent with the hypothesis of the link between stability and biodiversity at the community level.

Globally, within-population tree growth asynchrony differed significantly between climate zones, with the Tropical zone showing the most asynchrony and the Dry zone showing the lowest (Figure 3b). This could be because the dry zone presents the most challenging conditions for tree growth. In the dry zone, drought primarily controls tree development

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Furthermore, there were notable global variations in the stability of tree growth at the individual level, with Tropical having the lowest value and Dry coming in second. We propose that there are two different mechanisms responsible for the low individual-level tree growth stability in these two zones. Low individual-level tree growth stability in the Dry zone is probably caused by the regularly fluctuating drought conditions (Loik et al., 2004). The growth of individual trees is highly susceptible to the ever-changing biotic environment in the tropics because of the high species diversity and turnover rate. This includes herbivory and neighborhood competition brought on by the growth and mortality (gap formation) of nearby trees (Hubbell et al., 1999; Kong et al., 2024).

Although interspecific interactions like competition, herbivory, and parasitism cannot be evaluated using the ITRBD data, they may nevertheless have an impact on population size, asynchrony in within-population tree growth, and ultimately forest stability (Alexander et al., 2021; Ford et al., 2017; Zhao et al., 2023). Increased precipitation and fewer fires over the past century, for instance, are thought to have contributed to the decline of oak populations in the eastern United States by favoring fast-growing and shade-tolerant oak species over slow-growing and shade-intolerant ones (Alexander et al., 2021). By modifying the health and microenvironments of individual trees, these species interactions can also impact the stability and asynchrony of tree growth.

Although the growth of a tree's stem (or trunk) is the main focus of our research, we see no reason why our framework for analysis cannot be used to examine the stability of population expansion for other species, such as insects and small mammals. It could be necessary to consider the ontogenetic distinctions between animals and trees when applying the approach to them. For instance, as an insect reaches adulthood, its body size development may rapidly slow down or cease. Therefore, rather than individual growth rate or biomass, population size primarily determines their ecological functions and temporal stability. The within-population tree growth asynchrony in our study may be comparable to reproductive asynchrony among individuals in such communities. The effects of the insurance and portfolio should continue to be significant.

The so-called climate sensitivity bias is caused by the possible overrepresentation of climatically sensitive trees in the database (Babst et al., 2018). This issue stems from the fact that a large number of the datasets in ITRDB were initially

gathered in order to rebuild the climate. Therefore, in order to optimize the climatic signals embedded in the ring-width series, the tree-ring series in ITRDB were usually sampled from larger, older trees growing in rather harsher conditions. It is unknown how the climate sensitivity bias affects growth asynchrony and stability, even though it did not seem to be a major worry in many earlier studies (Babst et al., 2019; Klesse et al., 2018).

For instance, only the climate reconstruction group shows a significant difference, even though the maximum population-level growth stability is higher in Tropical than in Dry in both groups (Figure S8a,c). This implies that while the observed regional variations in tree growth stability may be somewhat explained by the climate sensitivity bias of the ITRDB data, the bias is insufficient to alter the qualitative findings. We should also point out that there is a significant variation in the number of tree-ring series and species among the five climate zones, with the Tropical zone having the smallest sample size (63 populations, 21 species). Although it is challenging to determine whether those 21 species are typical of tropical woods, we do know that 19 of them do not historically had a wide range outside of tropical regions.

CONCLUSION

According to our research, population-level tree growth stability is significantly influenced by the portfolio and insurance effects that underpin community stability. While the importance of the insurance effect in promoting population-level tree growth stability remains strong even at large population sizes, the capacity of the portfolio effect in promoting population stability is saturated at about 26 trees, which is equivalent to the number of species required to reach the maximum stability for a community. This result suggests that the intensity of the population-level stability process for tree radial growth is primarily determined by the insurance effect, with the portfolio effect coming in second. Our research advances our knowledge of the mechanisms that support forest resilience to environmental changes and uncertainty by integrating the stabilization mechanisms of populations and communities.

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