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https://doi.org/10.1111/gcb.70310

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RESEARCH ARTICLE

Coexistence of Tropical Forest Tree Species Along the Demographic Buffering Spectrum

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Received: 13 February 2025 | **Revised:** 25 May 2025 | **Accepted:** 2 June 2025

Funding: This work was supported by the Innovation Program of Shanghai Municipal Education Commission (2023ZKZD36), National Natural Science Foundation of China (32030068), Stichting DOB Ecology (18626), and Bernina Initiative through the ETH Foundation (202-2F-S318).

Keywords: demographic buffering | environmental fluctuation | integral projection model | species coexistence | tree demography | tropical forest

ABSTRACT

Organisms have evolved diverse adaptive strategies to cope with environmental fluctuations. Slow-growing long-lived species tend to exhibit low temporal variability in population growth (strongly buffered demographically), whereas fast-growing short-lived species optimize growth in favorable years (weakly buffered). These patterns set up the expectation that differentiation in demographic buffering may reduce disparities in long-term fitness among species, enhancing the potential for coexistence in variable environments. Yet, this expectation has never been empirically tested for trees. Here, we quantified differences in long-term population growth among 204 co-occurring tropical trees spanning a life-history spectrum from strongly to weakly buffered. We found that interspecific differences in demographic buffering reduced disparities in long-term population fitness at low densities, highlighting demographic differentiation as a key mechanism promoting coexistence in fluctuating environments. However, simulated increases in temperature, precipitation, and drought variability produced divergent fitness responses among species and exacerbated interspecific fitness disparities. Together, these findings provide a novel perspective on the mechanisms that underpin the astounding tree diversity in tropical forests.

1 | Introduction

Tropical forests harbor the highest tree diversity on Earth, a phenomenon thought to be maintained by mechanisms that ensure all persistent species in a community have nearly identical per capita relative fitness (Hubbell 2001, 2006). These mechanisms shape diverse life-history strategies, ranging from conservative, slow-growing species to acquisitive, fast-growing ones (Salguero-Gomez et al. 2016; Rüger et al. 2020), forming an important paradigm for explaining tree species diversity in tropical forests (Rüger et al. 2018; Grady et al. 2024). Under this framework, fitness invariance persists despite species differences in vital rates, as interspecific trade-offs act to equalize fitness (Lin et al. 2009). Prominent examples include the well-recognized growth–survival trade-off and the more recently identified stature–recruitment trade-off, which together characterizes the spectrum of life-history variation among co-occurring tropical trees (Condit et al. 2006; Russo et al. 2021; Kambach et al. 2022). However, these studies focusing on static patterns of biodiversity overlook a critical aspect of natural systems: fluctuations in environmental conditions. This missing dimension is crucial for understanding the forces that drive species coexistence and for predicting community assembly under future climate scenarios, which project increasing climate variability and more frequent extreme events in regions hosting the highest biodiversity (Bathiany et al. 2018).

Emergent research highlights a critical link between life-history variation and environmental fluctuations (McDonald et al. 2017; Le Coeur et al. 2022; Jops et al. 2025; Gascoigne et al. 2025). At one end of the spectrum, slow-growing, conservative species may tend to buffer against environmental fluctuations by minimizing temporal variation in vital rates (i.e., strongly buffered), resulting in low temporal variability in vital rates and stable population fitness even under adverse conditions (Morris and Doak 2004; Hilde et al. 2020). Conversely, fast-growing, acquisitive species may exhibit weaker buffering, allowing them to track and benefit from environmental fluctuations (i.e., weakly buffered) (Koons et al. 2009; Jongejans et al. 2010). This weak buffering typically arises from nonlinear responses of vital rates to environmental variability, enabling species to substantially increase their vital rates during favorable conditions (Le Coeur et al. 2022; Gascoigne et al. 2025). This strategy enhances long-term fitness, despite it coming at the cost of reduced fitness during unfavorable periods (Le Coeur et al. 2022). Most studies of demographic buffering have focused on variations in key vital rates that most strongly influence population fitness (Koons et al. 2009; Jongejans et al. 2010). Recent findings, however, indicate that compensation among vital rates can also play a crucial role in buffering against environmental fluctuations (Villellas et al. 2015). Such compensation can occur within a single time step, allowing species with rapid growth and high reproductive output to recover quickly after environmental stress, thereby exhibiting weak buffering (Jongejans et al. 2010; Le Coeur et al. 2022). Differences in demographic buffering among species induce temporal variation in relative competition advantages, preventing prolonged dominance by any single species. Consequently, this variation may reduce disparities in long-term population fitness, thereby increasing the potential for coexistence (Figure 1).

The concept of demographic buffering has been explored across multiple organismal groups, including animals, insects, and herbaceous plants (McDonald et al. 2017; Hilde et al. 2020; Le Coeur et al. 2021). Despite these advances, whether tree species demonstrate predictable differences in temporal population dynamics along the demographic buffering spectrum remains largely unresolved. Life-history traits are hypothesized to provide critical insights into this spectrum, as species with long lifespans are generally expected to be positioned toward the strongly buffering end (Morris et al. 2008; Hilde et al. 2020). Nonetheless, empirical evidence does not consistently support these predictions, with some long-lived plant species shown to be demographically labile (Jongejans et al. 2010; McDonald et al. 2017). Furthermore, species' positions along the buffering spectrum may shift as climate variability intensifies. In particular, temporal fluctuations in temperature, precipitation, and drought have increasingly impacted demographic rates in tropical tree species in recent decades (Zuidema et al. 2022). In addition to the unknown role of demographic differentiation along the buffering spectrum in shaping fitness disparities among co-occurring species, an unresolved topic is how demographic differentiation responds to escalating climate fluctuations in tropical forests.

To address this knowledge gap, we investigated three pivotal questions: (1) Do tropical tree species exhibit predictable differences in their temporal population dynamics along the demographic buffering spectrum? (2) To what extent does demographic differentiation along the buffering spectrum reduce differences in long-term fitness among co-occurring species? (3) How do these long-term fitness disparities respond to increased climatic variability? To answer these questions, we developed species-specific integral projection models (IPMs) for 204 co-occurring tree species in a 50-ha tropical forest plot located in central Panama. These models utilized 25 years of vital-rate data from six censuses, allowing us to estimate the long-term fitness (λs) under observed climate conditions. This 25-year sequence included temporal fluctuations in temperature, precipitation, and drought (Figure S1).

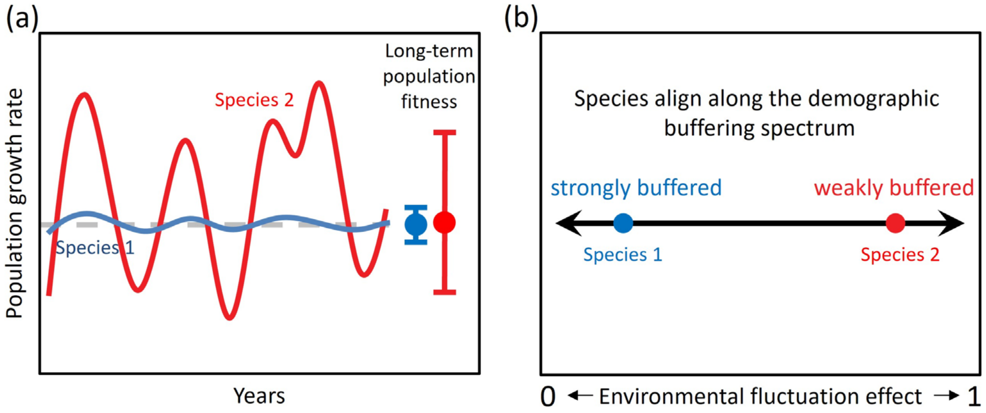

FIGURE 1 | Conceptual illustration of demographic buffering to environmental fluctuations, and how this may differ between species. (a) Variation in demographic buffering may induce temporal mismatches in population growth under variable environments, reducing fitness differences between strongly and weakly buffered species and increasing the potential for coexistence. (b) Species are ordered along the demographic buffering spectrum according to the environmental fluctuation effect, which is the overall effect of environmentally induced temporal variation in vital rates on long-term population fitness. The environmental fluctuation effect ranges between 0 and 1, where values close to zero means that temporal variation in vital rates has a negligible impact on long-term population fitness, indicating strong demographic buffering.

We then used IPMs to quantify the proportional contribution of environmentally induced temporal variation in vital rates to the long-term fitness for each species—termed the "environmental fluctuation effect"—to position species along the demographic buffering spectrum. Then, we evaluated how differences in long-term fitness among species responded to varying degrees of life-history differentiation by manipulating temporal variability in vital rates. Finally, we simulated increased temporal variability in climatic variables to explore the impact of environmental fluctuations on differences in the long-term fitness among species.

2 | Materials and Methods

2.1 | Demographic, Climate, and Competition Data

We utilized data collected from the 50-ha plot located on Barro Colorado Island (BCI) in Panama (Condit et al. 2019). The study site has a seasonally dry tropical climate, with a mean annual temperature of 27°C and an average annual precipitation of 2650 mm. The dry season, from January to April, receives only 10% of the total annual rainfall. The plot was first established and censused in 1981–1982, followed by subsequent surveys done every 5 years, from 1985 through 2015. In each census, the living stems ≥ 1 cm diameter at breast height (DBH) were identified, measured, and mapped (Condit et al. 2017). However, we excluded the data from the first two censuses due to small but significant differences in subsequent surveys (Condit et al. 2017). We also excluded species with less than 50 individuals in any census. The final demography dataset used in this study comprised a total of 408,946 individuals of 204 tree species from 1990 to 2015.

We selected three monthly climate variables, including temperature, precipitation, and relative humidity, all of which we obtained from the Physical Monitoring Program of the Smithsonian Tropical Research Institute. Given the well-documented influence of dry-season drought on tropical tree demographics (Zuidema et al. 2022), we derived vapor pressure deficit (VPD) from temperature and humidity data, as detailed in Supporting Information. For each census interval, we calculated monthly averages for temperature and precipitation, as well as seasonal averages for VPD. To address potential multicollinearity (Figure S1) and incorporate key climate conditions, we included monthly temperature (T_{monthly}), monthly precipitation (P_{monthly}), and dry-season drought (VPD_{dry}) as the primary climate variables in our subsequent vital-rate models.

To account for local competition, we calculated the neighborhood competition index (NCI) for each tree (Hegyi 1974; detailed in Supporting Information), which is a widely used metric in forest research (Weng et al. 2022). The index quantifies competition based on the size and distance of neighboring trees within a 20-m radius of each focal tree. We here calculated the index using only neighbors larger than a target individual to assess size asymmetry in competition for light and other resources. We calculated NCI using both conspecific and heterospecific neighbors, represented by $\text{NCI}_{\text{consp}}$ and $\text{NCI}_{\text{hersp}}$ respectively. The $\text{NCI}_{\text{hersp}}$ was then used to calculate the long-term population growth for species at low densities (invasion growth rate) while maintaining the effect of heterospecific competition.

2.2 | Integral Projection Models

IPMs describe the dynamics of continuously size-structured populations over discrete time intervals (Easterling et al. 2000; Ellner and Rees 2006). For each species, we constructed IPMs (details in Supporting Information) to estimate population growth rate (λ) at each census, with vital rates (survival, growth, and fecundity) modeled as continuous functions of individual size (DBH). Error distributions and link functions were specified to correspond to standard logistic regression for survival, ordinary least squares regression for growth, and Poisson or negative binomial regression for recruit number, depending on the data distributions. Data from all censuses were pooled for each species to construct separate global generalized linear mixed models for survival and growth. These models incorporated fixed effects for tree size, climatic variables (T_{monthly}, P_{monthly}, and VPD_{dry}), and local competition (NCI), with census treated as a random effect. For the number of recruits, we fitted a global generalized linear model that included the sum of reproductive tree sizes, climatic variables, and local competition as predictors. We employed an all-subsets regression approach to select environmental variables for each vital-rate model. This method involved fitting a series of candidate models that considered all possible combinations of environmental variables, with the optimal model selected based on the corrected Akaike information criterion (AICc). We excluded interaction terms and quadratic terms due to convergence issues.

Since data on individual reproductive states are not available, we set the reproduction probability to 100% for all individuals with a size exceeding half of the species' maximum diameter (D_{max}) (Visser et al. 2016). While this approach does not allow us to capture size-dependent variation in fecundity, it serves as a proxy for the mean number of recruits produced per tree within each census, which is useful for calculating species-level long-term fitness (λs) differences. To ensure the robustness of our demographic model outputs, we analyzed the effect of lowering and increasing the thresholds to 25% and 75% of D_{max}. We found that these changes had minimal impact on estimates of λs, with average differences of only 0.001 and −0.004, respectively (Figure S2). The size distribution of recruits was modeled with a normal distribution based on the empirical mean and standard deviation observed in each census.

2.3 | Population Growth Rate

We used the fitted vital-rate models to construct the IPM kernel (Supporting Information) for each census, which we then converted into a transition matrix with 50 categories using the midpoint rule (Easterling et al. 2000; Zuidema et al. 2010). We calculated the dominant eigenvalue of this matrix to represent the population growth rate over the census interval. Because censuses are conducted at 5-year intervals at the BCI plot, we obtained the annual population growth rate (λ) by adjusting the dominant eigenvalue by taking the 5th root.

This adjustment standardizes the population growth rate to a single-year timescale, enabling direct comparisons across species and censuses.

The stochastic population growth rate (λs) is widely used in demographic studies as an indicator of a species' long-term fitness (Morris and Doak 2002). It represents the expected population growth under environmental variability, accounting for fluctuations in vital rates across years. In a stochastic environment, λs is determined by the multiplicative effects of "bad" and "good" years on population growth and is mathematically defined as the long-run geometric mean of annual growth rates. We estimated λs using a well-established small noise approximation, implemented in the R package "*popbio*" (Tuljapurkar 1990; Stubben and Milligan 2007). A detailed description of the calculation method, including equations and model assumptions, is provided in the Supporting Information. The estimated λs values and their confidence intervals for all species studied are presented in Table S1.

To assess the contributions of different vital rates (survival probability, growth, number of recruits, and size distribution of recruits) to temporal differences in λ across censuses, we conducted a retrospective life table response experiment analysis (Supporting Information). We attributed the proportion of variance in λ to changes in each vital-rate parameter, calculating the contribution of each vital rate by summing all associated coefficients (e.g., the contribution from survival is the sum of the survival slope and intercept contributions). Finally, the contributions of all vital rates to temporal variability in λ were normalized to facilitate comparison (Figure S3).

2.4 | Test for Demographic Buffering

To assess how tree species align along the demographic buffering spectrum (Q1), we used stochastic elasticities with the R package "*Rage*" to quantify the effects of temporal variation in vital rates on the λs (Tuljapurkar et al. 2003; Haridas and Tuljapurkar 2005; Haridas et al. 2009). Stochastic elasticities ($E^s_{a_{ij}}$) estimate the sensitivity of λs to small changes in the mean and variance of a given matrix element, a_{ij} (or vital rate v). The sum of stochastic elasticities across all matrix elements ($\sum E^s_{a_{ij}}$) equals to 1. This can be partitioned into elasticities to the mean ($\sum E^\mu_{a_{ij}}$) and to the temporal variance ($\sum E^{\sigma^2}_{a_{ij}}$) components. Under the small-variance approximation, the stochastic growth rate is reduced relative to the deterministic rate due to environmental variation (Haridas and Tuljapurkar 2005). This can be expressed as:

$$\log\left(\lambda_s\right) \approx \log\left(\lambda_0\right) + \frac{1}{2}\left[\sum E^s_{a_{ij}}\right]$$

This equation shows that $\sum E^s_{a_{ij}}$ is a summary measure of how temporal variability in vital rates affects long-run fitness: more negative values reflect greater reductions in population fitness. In our study, we used the absolute value of this term ($\sum E^{\sigma^2}_{a_{ij}}$), termed the "environmental fluctuation effect," to index each species' position along the demographic buffering spectrum. A value near zero indicates that temporal variation in vital rates has minimal impact on λs, placing the species at the strongly buffered end of the spectrum. This approach provides a process-based, comparative measure of buffering strength across species. Unlike correlation-based methods, which may yield spurious results due to mathematical interdependencies and overlook lagged or nonlinear demographic effects (McDonald et al. 2017), our elasticity-based framework explicitly incorporates temporal lags and nonlinear demographic feedback, offering a more robust evaluation of stochastic buffering (Supporting Information and Figure S4).

To assess whether the observed interspecific variation in demographic buffering could arise purely from demographic stochasticity, we conducted a randomization test (Supporting Information and Figure S5). In this test, individual-level demographic data was shuffled across censuses while preserving total population size, generating null expectations for interspecific variation in environmental fluctuation effects. To test whether demographic buffering represents an independent life-history axis, we performed a phylogenetically informed principal component analysis (pPCA) using demographic traits (Supporting Information and Figure S6).

To further explore the demographic basis of interspecific buffering variation, we decomposed the stochastic elasticity of variance in λs into survival/growth and recruitment sub-kernels (Gascoigne et al. 2025). For each species, we calculated the proportion of total variance elasticity attributable to recruitment-related terms and tested its correlation with the environmental fluctuation effect (Figure S7).

We then explored how life-history traits influence species' positions along the demographic buffering spectrum by using phylogenetically corrected regression models. Specifically, we implemented phylogenetic generalized least squares (PGLS) to account for shared ancestry among species. We examined the relationships between environmental fluctuation effects and traits: maximal lifespan, damping ratio, population size, and temporal variation of population size. The species-level phylogeny was generated using *V.PhyloMaker2*, and PGLS models were fitted with the maximum-likelihood estimation of Pagel's λ using the *caper* package in R (Orme et al. 2013). Pagel's λ quantifies the strength of the phylogenetic signal in the trait-buffering relationship, with values near 0 indicating trait independence from phylogeny and values near 1 suggesting strong phylogenetic conservatism. Maximal lifespan was calculated from the transition matrix—considering transitions dependent solely on survival and growth—as the age at which cumulative mortality reached 95% in a cohort of individuals with an initial DBH of 1 cm (Horvitz and Tuljapurkar 2008; Supporting Information). Damping ratio, calculated as the ratio of the subdominant to dominant eigenvalues of each transition matrix (Capdevila et al. 2020), reflects the intrinsic speed at which a population returns to its stable structure after perturbation. While it does not capture all aspects of transient dynamics (e.g., amplification or sensitivity to initial conditions; Stott et al. 2011), the damping ratio is widely used as a standardized proxy for population resilience. It is also strongly correlated with measures of maximum amplification and attenuation (Capdevila et al. 2020), reinforcing its relevance in comparative demographic analyses. We used the R package "*popbio*" for all calculations. Population size was defined as the total number of individuals recorded across all census periods, and its temporal variability was quantified as the coefficient of variation (CV) in species-level abundance across censuses.

2.5 | The Role of Demographic Differentiation in Reducing Fitness Disparities Among Species

To investigate the impact of demographic differentiation on reducing differences in long-term fitness among co-occurring species (Q2), we conducted a perturbation analysis (Caswell 2001). Specifically, we adjusted the interspecific variance of temporal variability in vital rates ($\text{Var}_{\text{intersp}}(\sigma^2)$) by ±20% to simulate broader or narrower differences in species' responses to environmental fluctuations (Figure 4). Species were classified as strongly or weakly buffered based on whether their environmental fluctuation effect was below or above the median of all species. To simulate broader demographic differentiation, we increased the temporal variance (by 1%) of the intercepts and slopes in the vital-rate models (survival, growth, and reproduction) for weakly buffered species and decreased it by 1% for strongly buffered species, while holding their mean values constant. The reverse adjustment was applied to simulate narrower differentiation. These modifications altered the standard deviation of the intercepts and slopes without changing their mean values, thereby increasing or decreasing interspecific differences in environmental fluctuation effects ($\text{Var}_{\text{intersp}}\left(\left|\sum E^{\sigma^2}_{a_{ij}}\right|\right)$), without modifying the climate time series.

Species coexistence can be assessed by their capacity to grow from low density in the presence of interspecific interactions (i.e., invasion growth rate) (Chesson 2000; Hallett et al. 2019; Ellner et al. 2022). Therefore, to characterize species' ability to coexist with other species, we calculated the species-specific invasion growth rate ($\lambda s_{\_\text{inv}}$) by re-running the IPMs with conspecific competitive interactions set to zero while keeping interspecific competition intact ($\text{NCI}_{\text{consp}} = 0$). We calculated disparities in invasion growth rates for all species pairs, specifically the mean pairwise differences in $\lambda s_{\_\text{inv}}$ ($\Delta_{\text{pair}}(\lambda s_{\_\text{inv}})$). This metric is defined as the average of the absolute differences in $\lambda s_{\_\text{inv}}$ across all pairs of species:

$$\Delta_{\text{pair}}\left(\lambda_{s\_\text{inv}}\right) = \frac{N(N-1)}{2} \sum_{i<j} \mid \lambda s_{\_\text{inv},i} - \lambda s_{\_\text{inv},j} \mid$$

where N is the number of species, and $\lambda s_{\_\text{inv},i}$ and $\lambda s_{\_\text{inv},j}$ are the invasion growth rates of species i and j, respectively. A lower value of this metric indicates reduced disparities in invasion growth rates among species. Under the scenario of 20% wider interspecific differences, we further evaluated changes in $\Delta_{\text{pair}}(\lambda s_{\_\text{inv}})$ to assess the contribution of each vital rate to $\Delta_{\text{pair}}(\lambda s_{\_\text{inv}})$.

2.6 | Effects of Climatic Variability on Fitness Disparities Among Species

To assess how the long-term fitness disparities among species respond to increased climatic variability over time (Q3), we first identified the predominant climatic factor limiting the λs of each species. Using a perturbation analysis, we examined the effect of environmental variables on λs by varying each factor individually while holding all other variables constant at observed values. We calculated proportional changes in λs by increasing the temporal variance of each environmental variable by 1%. The variable with the highest elasticity value was considered the most influential for each species. If a factor's second-highest elasticity was more than half that of the largest, it was also included as predominant. We summed the number of species with positive and negative elasticities across the studied species to identify trends. By determining these key variables on a per-species basis, we gain insight into the collective impact of increasing climatic variability on species' long-term fitness. Additionally, we analyzed how $\Delta_{\text{pair}}(\lambda s_{\_\text{inv}})$ responded to changes in climatic variability. If λs exhibited a predominantly positive response and $\Delta_{\text{pair}}(\lambda s_{\_\text{inv}})$ decreased, this would suggest that greater climatic variability enhances species' long-term fitness while reducing inequalities in invasion growth rates among species, which may potentially increase the chance of stable coexistence.

3 | Results

3.1 | Variation Along the Demographic Buffering Spectrum

Substantial interspecific variations in environmental fluctuation effects were detected across 204 tropical tree species, spanning four orders of magnitude (Figure 2a; Table S1). The lowest value (0.07×10^{-3}) occurred in *Sloanea terniflora* and the highest (0.53) in *Piper cordulatum*. These variations significantly exceeded that obtained using randomized demographic data ($p < 0.001$; Figure S5), indicating that observed differences in buffering are not solely due to demographic stochasticity. And phylogenetically corrected PCA revealed that the environmental fluctuation effect loaded most strongly on PC4 (−0.59), orthogonal to the first three components (Figure S6; Table S2), suggesting that buffering represents a complementary, partially independent axis of life-history variation. Species with larger environmental fluctuation effects exhibited greater temporal variability in annual population growth rates (λ) (Figure 2b). Life table response experiment analysis showed that temporal variation in λ was driven primarily by variation in the number of recruits (50%), followed by growth (23%), the size distribution of recruits (14%), and survival (13%) (Figure S3). To evaluate whether species-level buffering is specifically linked to reproductive variation, we decomposed the stochastic elasticity of variance in λ into survival/growth and recruitment components. On average, 54% of the total variance elasticity was attributable to recruitment. However, the relative contribution of recruitment showed no significant correlation with the environmental fluctuation effect ($r = 0.07$, $p = 0.32$; Figure S7), suggesting that interspecific buffering variation is not solely driven by reproductive dynamics.

Species' environmental fluctuation effects were significantly associated with life-history traits after phylogenetic correction (Figure 3). Species with stronger demographic buffering (i.e., lower environmental fluctuation effects) had longer lifespans (PGLS slope = −0.98, $p < 0.001$), larger population sizes (−0.17, $p < 0.05$), and lower temporal variability in abundance (0.77, $p < 0.001$). Damping ratio was positively associated with environmental fluctuation effects (2.57, $p < 0.001$). Corresponding Pagel's λ values (0.29–0.54) indicated a low to moderate phylogenetic signal. Additionally, λs was positively associated with lifespan and damping ratio but negatively with population variability (Figure S8). Most species (93%) showed an inverse relationship between the temporal variance and the importance of

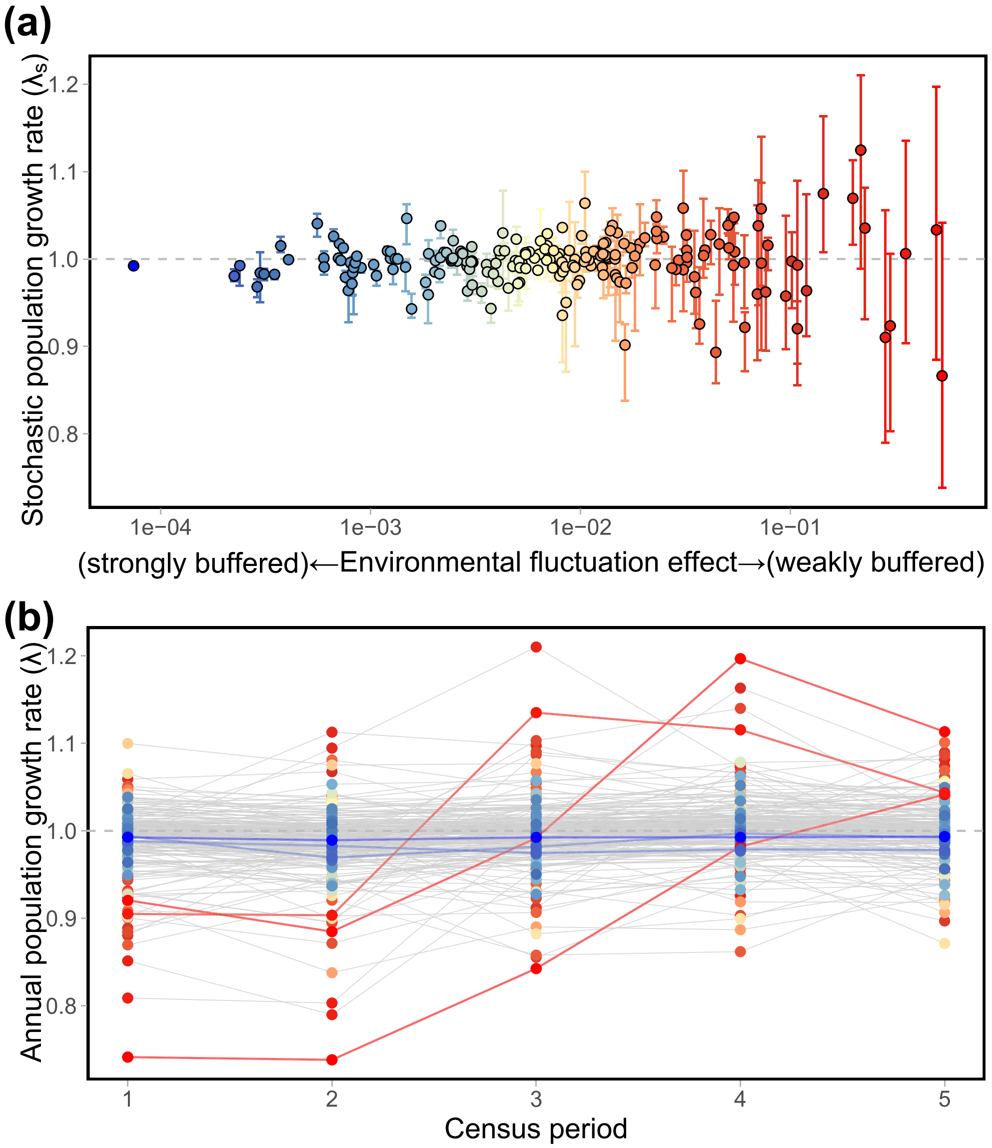

FIGURE 2 | Demographic differentiation along the buffering spectrum within a species-rich tropical forest community. (a) Stochastic population growth rate (λs) of 204 studied tree species spanning a demographic spectrum from strongly to weakly buffered. Each point denotes a tree species, with error bars indicating the range of observed annual population growth rate (λ) across censuses. The *x*-axis is log-transformed to aid visualization. (b) Temporal performance of λ for all 204 studied tree species. The color of each point matches that in panel (a), with gray lines connecting consecutive observations for each species. Lines for the three species with the lowest and highest environmental fluctuation effects are highlighted in blue and red, respectively, in panel (b).

vital rates (Figure S4), consistent with the demographic buffering hypothesis.

3.2 | Demographic Differentiation Reduces Differences in Population Growth Among Species

When we simulated increased interspecific variance of temporal variability in vital rates ($\mathrm{Var}_{\mathrm{intersp}}\left(\sigma^2\right)$), we found a marked rise in the interspecific variance of environmental fluctuation effects ($\mathrm{Var}_{\mathrm{intersp}}\left(\left|\sum E_{a_{ij}}^{\sigma^2}\right|\right)$), indicating greater differences in species' responses to environmental fluctuations (Figure 4a). Concurrently, a decline in mean pairwise differences in invasion population growth rates ($\Delta_{\mathrm{pair}}\left(\lambda s\_{\mathrm{inv}}\right)$) suggests a reduction among species in differences in population growth. For example, a 20% simulated increase in $\mathrm{Var}_{\mathrm{intersp}}\left(\sigma^2\right)$ led to a 30% increase in $\mathrm{Var}_{\mathrm{intersp}}\left(\left|\sum E_{a_{ij}}^{\sigma^2}\right|\right)$ and a 0.3% decrease in $\Delta_{\mathrm{pair}}\left(\lambda s\_{\mathrm{inv}}\right)$, suggesting that greater differentiation in species' responses to environmental fluctuations is linked to broader interspecific differentiation in demographic buffering and reduced fitness disparities. Under the scenario of a 20% increase in $\mathrm{Var}_{\mathrm{intersp}}\left(\sigma^2\right)$, the reduction in $\Delta_{\mathrm{pair}}\left(\lambda s\_{\mathrm{inv}}\right)$ is primarily contributed by changes in the temporal variability of survival probability (Figure 4b).

3.3 | Responses of Fitness Disparities to Climatic Variability

A simulated 1% increase in the temporal variability of temperature, precipitation, and dry-season VPD led to more species experiencing a decline in their λs compared with those showing

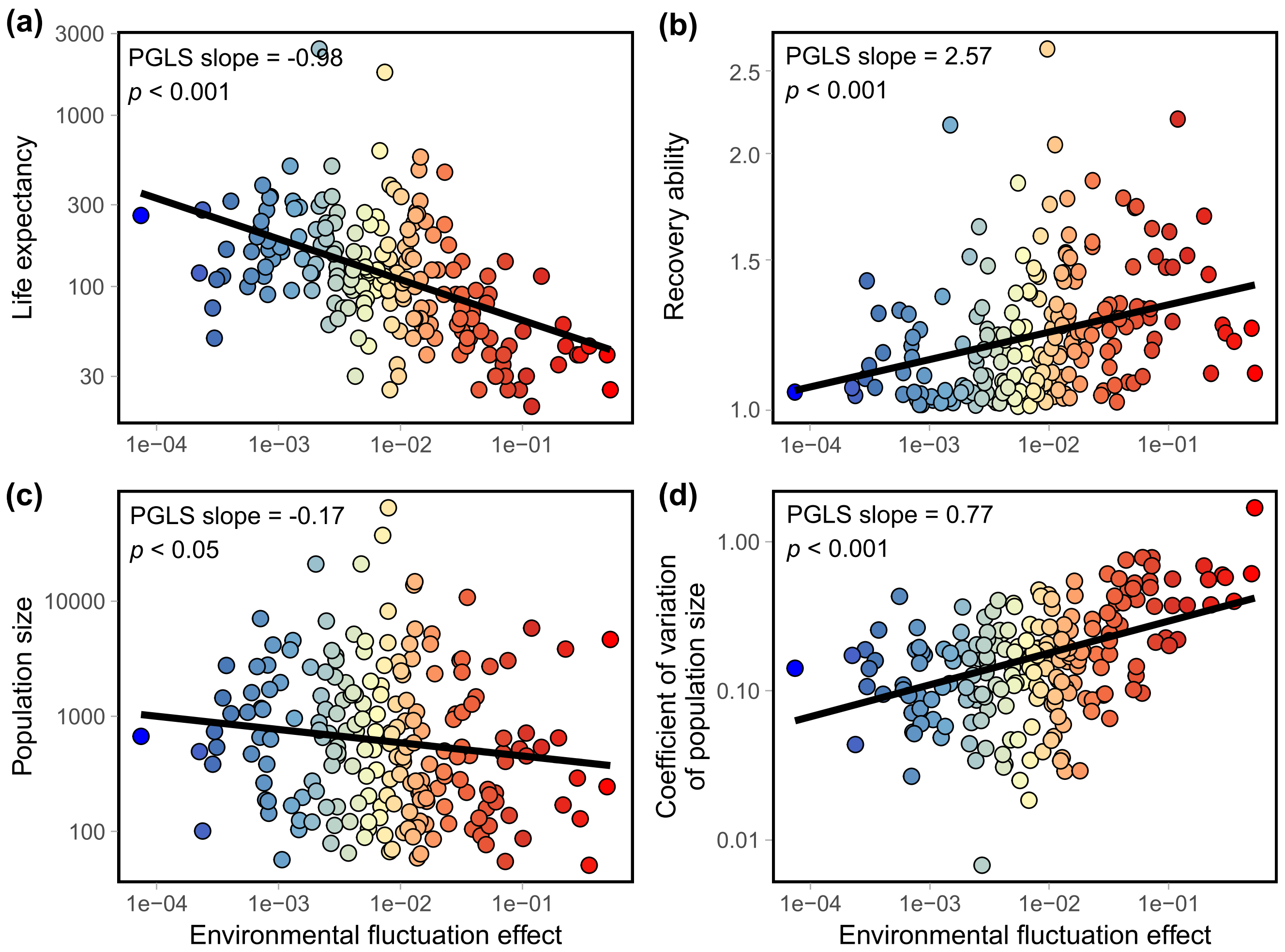

FIGURE 3 | Correlations between the environmental fluctuation effect and life-history traits across 204 tropical tree species: (a) maximal lifespan, (b) damping ratio, (c) population size, and (d) temporal changes in population size. Each point represents one tree species. Colors represent the environmental fluctuation effect, consistent with Figure 1. The x- and y-axes are log-transformed for visualization. Regression lines are derived from phylogenetic generalized least squares (PGLS) models. Corresponding slopes and p-values are shown. Estimated Pagel's λ values were 0.29 for lifespan, 0.35 for damping ratio, 0.54 for population size, and 0.36 for its coefficient of variation, indicating a low to moderate phylogenetic signal.

an increase (Figure 5a). For example, increased temperature variability resulted in 82 species (40%) experiencing a decrease in λs, while 64 species (31%) showed an increase. Similar patterns were observed for increased variability in precipitation and dry-season VPD. These findings indicate that increased climatic variability has divergent effects on species' long-term fitness. Furthermore, the increased variance in all climate variables consistently led to a rise in $\Delta_{\text{pair}}(\lambda s_{\text{\_inv}})$ (Figure 5b), indicating that greater climatic variability amplifies fitness disparities among species.

4 | Discussion

Compelling intuitive arguments suggest that demographic differentiation may provide an unrecognized pathway for species coexistence (Adler et al. 2007; Ellner et al. 2022). However, these hypotheses have rarely undergone rigorous quantitative evaluation. To our knowledge, this study is the first empirical assessment of the expectation that tropical trees systematically vary in life-history strategies along a buffering spectrum, potentially reducing long-term differences in population growth and enhancing coexistence likelihood. This perspective complements the well-established fast–slow and stature-recruitment continua within tropical tree communities, providing a broader framework for understanding life-history strategies. A randomization test showed that the observed life-history differentiation among species does not solely arise from demographic stochasticity (Figure S5), supporting recent findings that life-history variation helps explain abundance fluctuations in the BCI forest (Jops et al. 2025). However, increasing climate variability imposes species-specific fitness impacts, amplifying disparities in long-term fitness and potentially disrupting coexistence by exacerbating competitive asymmetries. Together, these results highlight the importance of demographic differentiation in maintaining tropical tree diversity and offer a foundation for modeling shifts in forest community assembly under climate change.

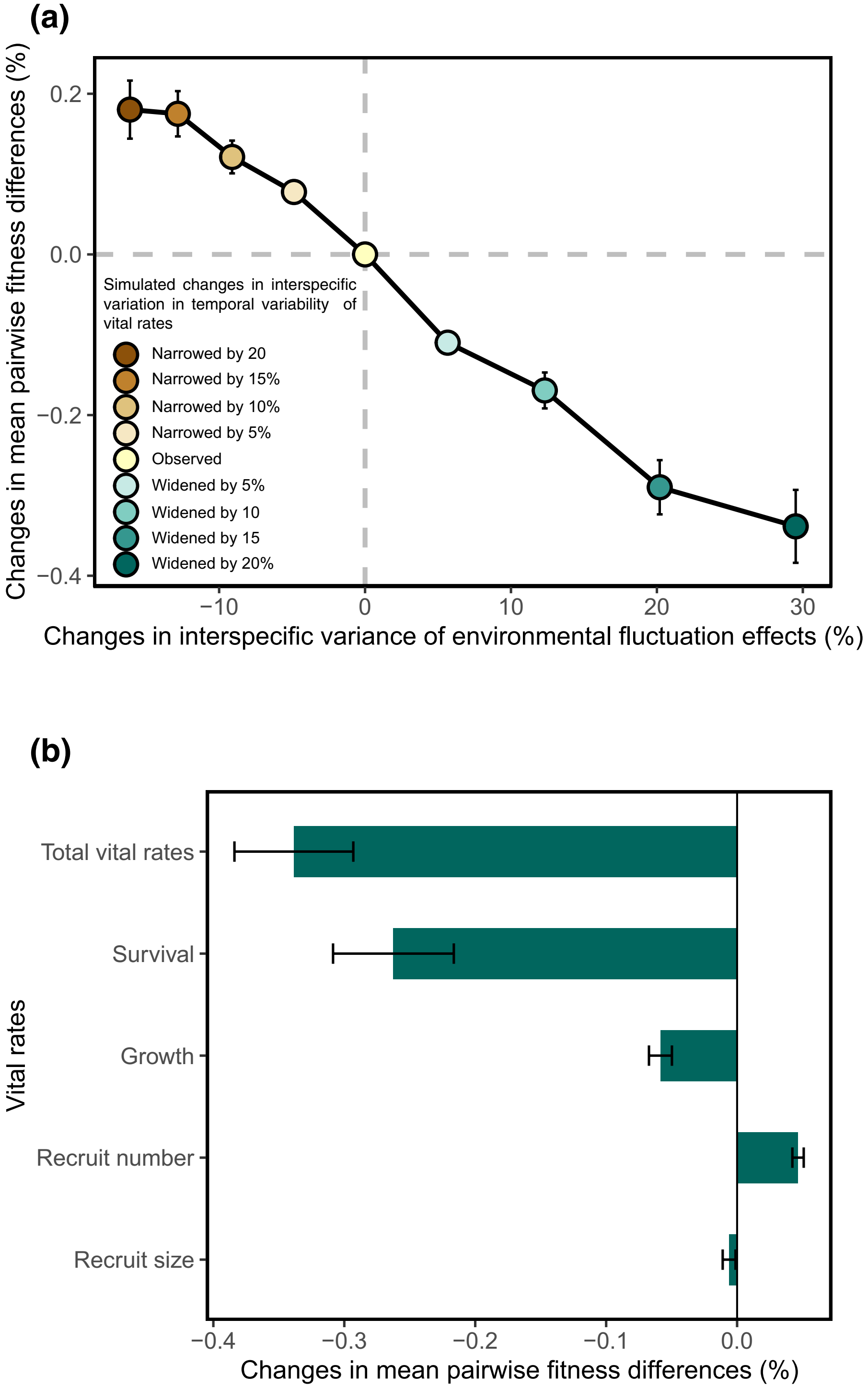

FIGURE 4 | The role of demographic differentiation in reducing differences in long-term fitness among species. (a) The mean pairwise fitness differences ($\Delta_{\text{pair}}(\lambda s_{\text{\_inv}})$) and the interspecific variance in environmental fluctuation effects ($\text{Var}_{\text{intersp}}\left(\left|\sum E^{\sigma^2}_{a_{ij}}\right|\right)$) in response to ±20% simulated alterations in the interspecific variance of temporal variability in vital rates ($\text{Var}_{\text{intersp}}(\sigma^2)$). A greater $\text{Var}_{\text{intersp}}\left(\left|\sum E^{\sigma^2}_{a_{ij}}\right|\right)$ indicates a higher degree of demographic differentiation among species, while a reduced $\Delta_{\text{pair}}(\lambda s_{\text{\_inv}})$ suggests decreased fitness inequalities among species. Panel (b) illustrates the contribution of each vital rate to changes in $\Delta_{\text{pair}}(\lambda s_{\text{\_inv}})$ under the scenario of 20% wider interspecific differences. Error bars represent standard errors.

4.1 | Demographic Buffering Is Correlated With Life-History Traits

Our results demonstrate that species with longer lifespans, lower damping ratios, and larger population sizes tend to exhibit stronger demographic buffering. Conversely, species with acquisitive life histories are more responsive to environmental fluctuations. These patterns highlight the close relationship between demographic strategies and life-history traits (Jiang et al. 2022; Hilde et al. 2020). Specifically, species

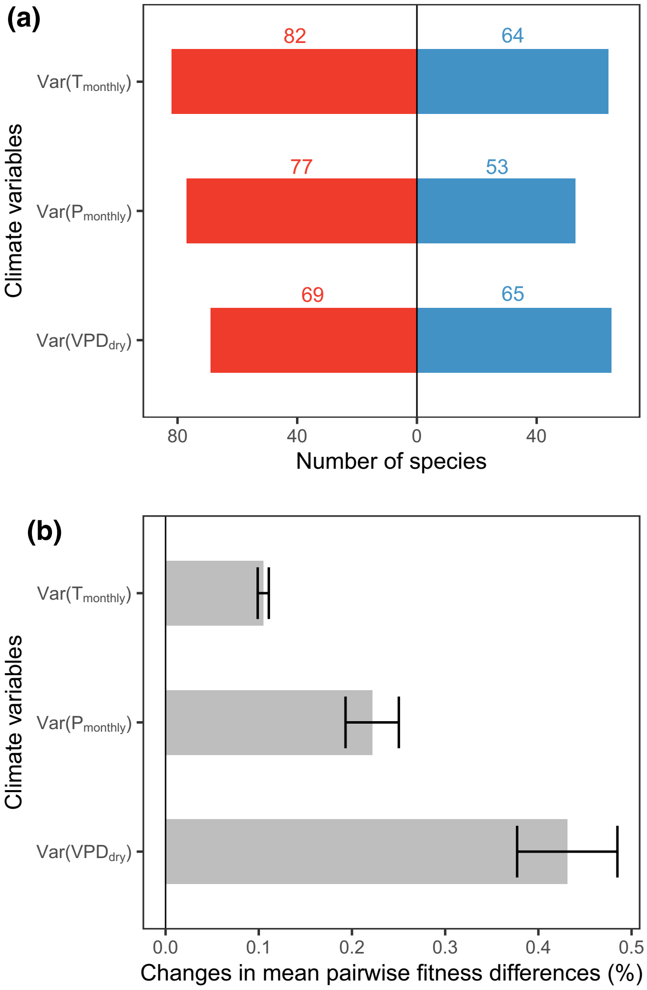

FIGURE 5 | The effects of simulated alterations in climate variability on long-term fitness and interspecific fitness inequalities. (a) The number of species showing positive (blue) and negative (red) responses for λs, and (b) the response of mean pairwise fitness differences $\Delta_{pair}(\lambda s_{\_inv})$, both resulting from a 1% increase in the temporal variability of each climatic variable compared with the actual. In panel (b), positive values indicate an increase in interspecific fitness inequalities. Error bars represent standard errors. Abbreviations: Var($T_{monthly}$)—temporal variance of monthly temperature; Var($P_{monthly}$)—temporal variance of monthly precipitation; Var(VPD$_{dry}$)—temporal variance of monthly dry-season vapor pressure deficit.

with longer lifespans tend to adopt demographic strategies that minimize temporal variation in vital rates, particularly mature-stage survival, thereby enhancing population stability under environmental fluctuations (Morris et al. 2008; Jongejans et al. 2010). Conversely, shorter-lived species often capitalize on fluctuations in their reproduction and growth during early life stages to exploit favorable conditions (Hilde et al. 2020; Le Coeur et al. 2022). Additionally, weakly buffered species, which are also characterized by demographic liability, may enhance their potential for recovery through demographic stochasticity and nonlinear responses, particularly in conditions of environmental variability and smaller population sizes (Le Coeur et al. 2022). Thus, while the present results regarding the importance–variability correlation of vital rates support the idea that demographic buffering is generally favored in tree species (Figure S4), our analysis reveals that species with larger population sizes tend to exhibit stronger demographic buffering. This pattern is consistent with theoretical expectations that environmental stochasticity, which buffering mitigates, plays a greater role in fitness variation for large populations—while in small populations, demographic stochasticity dominates and may obscure the effects of environmental variability (Engen et al. 1998). A randomization test showed that the observed interspecific variation in buffering strength is unlikely to result solely from demographic stochasticity, supporting the interpretation that demographic buffering represents an ecologically structured and meaningful axis of life-history variation. Together, these results reveal a more intricate and species-specific response to environmental fluctuations among tropical woody plants than previously recognized (McDonald et al. 2017).

Previous studies have suggested that tree demographics do not adhere strictly to a single axis of life-history variation (Bialic-Murphy et al. 2024; Stott et al. 2024). Recent theoretical work has proposed the demographic buffering spectrum as a third axis of life-history strategies, alongside the fast-slow and stature-recruitment continuums (Rüger et al. 2020; Salguero-Gómez 2021; Jaggi et al. 2024). Unlike the other two axes, which promote diversity through trade-offs among vital rates (Detto et al. 2022), demographic buffering reflects a trade-off within each vital rate, between its contribution to long-term fitness (importance) and its temporal variability. In species with strong buffering, vital rates that are critical for fitness tend to exhibit lower year-to-year variability, stabilizing population growth (Hilde et al. 2020). Our findings support this framework, demonstrating the presence of a demographic buffering spectrum among tropical tree species and providing a complementary perspective for understanding life-history variation and species coexistence under fluctuating conditions.

4.2 | Species Coexistence Along the Demographic Buffering Spectrum

Life-history studies suggest that demographic trade-offs among tropical tree species contribute to diversity maintenance by influencing species' long-term dynamics (Russo et al. 2021). However, in the context of quantitative coexistence theory, fitness equalization typically refers to the equalization of species' competitive abilities, which do not directly correspond to stochastic fitness measures. Here, we examine a different perspective: how demographic buffering influences species' responses to environmental fluctuations and may contribute to long-term species persistence. Our findings indicate that variation in demographic buffering affects disparities in stochastic population growth rates (λs) under fluctuating conditions, potentially influencing coexistence through two complementary processes. First, demographic differentiation among species may reduce their disparities in intrinsic growth rate, which depend primarily on abiotic conditions. For example, during early census periods influenced by extreme drought events between 1982 and 1992 (Condit et al. 2017), strongly buffered species (e.g., *Sloanea terniflora*, *Trophis racemosa*, and *Posoqueria latifolia*) maintained annual population growth rates (λ) close to 1. Their stability, driven by small survival rate fluctuations (Figure S4), may enhance persistence under deteriorating conditions (Hilde et al. 2020). In contrast, weakly buffered species (e.g., *Piper cordulatum*, *Palicourea deflexa*, and *Psychotria chagrensis*) exhibited significant declines in λ during severe drought periods but later rebounded, reflecting post-drought recovery (Condit et al. 2017). Since intrinsic growth rate is an important component of competitive ability (Godoy and Levine 2014; Hart et al. 2018), reducing disparities in intrinsic growth rates can diminish differences in competitive ability among species, promoting coexistence through equalizing mechanisms (Chesson 2000). Second, temporal mismatches in population dynamics between strongly and weakly buffered species reduce long-term interspecific competition, influencing species' persistence. Weakly buffered species tend to fluctuate more, taking advantage of favorable conditions, whereas strongly buffered species maintain stability under unfavorable conditions. This asynchrony may lead to reduced competitive overlap over time, potentially increasing niche differentiation (Chesson 2000; Godoy and Levine 2014; Chu and Adler 2015).

However, whether this contributes to stabilizing coexistence mechanisms requires further investigation. Demographic buffering is related to, yet distinct from, other fluctuation-dependent mechanisms like storage effects and relative nonlinearity of competition (Chesson 2000; Stump and Vasseur 2023). Storage effects enable species to persist under fluctuating conditions by accumulating resources or individuals during favorable periods, thereby smoothing over the impacts of environmental variability (Usinowicz et al. 2017; Ellner et al. 2019). Similar to strong demographic buffering, storage effects promote species persistence by ensuring consistent long-term fitness despite temporal fluctuations. However, the storage effect primarily relies on asynchronous reproductive output across species and does not explicitly account for species-specific sensitivities to environmental change (Usinowicz et al. 2012). Recent critiques have also highlighted limitations in its general applicability and potential for overstating coexistence potential under temporally autocorrelated environments (Stump and Vasseur 2023). In contrast, demographic buffering incorporates temporal variation in all vital rates (e.g., survival, growth, reproduction), which means it directly influences a species' sensitivity to environmental fluctuations and reduces long-term disparities in population growth rates, thereby serving as both a stabilizing and equalizing mechanism. On the other hand, the relative nonlinearity of competition promotes coexistence by enhancing intraspecific competition relative to interspecific competition under fluctuating resource conditions (Letten et al. 2018; Zepeda and Martorell 2019). While weak demographic buffering shares similarities with relative nonlinearity, the latter enhances intraspecific competition via environmental fluctuations, whereas weak demographic buffering relies on nonlinear responses of vital rates to environmental variability, inducing temporal shifts in species' comparative advantages (Le Coeur et al. 2022; Gascoigne et al. 2025). In summary, while demographic buffering shares similarities with storage effects and relative nonlinearity, it uniquely fosters temporal mismatches in population dynamics and reduces disparities in long-term population growth rates. This dual role underscores the distinct contribution of demographic buffering to species coexistence, setting it apart from other fluctuation-dependent mechanisms.

4.3 | The Impact of Environmental Variability on Tree Diversity

Increasing climatic variability in tropical regions due to climate change heightens the urgency to understand its impacts on tropical tree diversity and coexistence (Zuidema et al. 2022). Tropical forests are particularly sensitive to changes in temperature variability, as many species are already near their thermal tolerance limits (Sullivan et al. 2020). In our study, more species experienced a decline in long-term fitness compared with those that showed an increase in response to increasing temperature variability (Figure 5a), suggesting that temperature variability may reduce the likelihood of population persistence. As these forests approach critical physiological thresholds (Doughty et al. 2023), even long-lived species, which typically buffer against short-term climatic variability, could face elevated extinction risks from intensified climatic extremes. This could exacerbate biodiversity loss and lead to the thermophilization of tropical forests, where heat-tolerant species dominate.

Conversely, forests accustomed to hotter and drier baseline conditions might be partially protected due to their prior adaptation to extreme circumstances (Bennett et al. 2023). However, the observed increases in fitness inequalities among species (Figure 5b) indicate that rising variability of VPD can amplify species' differences in long-term fitness, probably undermining coexistence. This is consistent with previous findings from the BCI forest, where droughts during and after El Niño events significantly increased mortality among moisture-demanding species (Condit et al. 2017). Such selective pressures could ultimately erode tropical forest biodiversity by favoring drought-tolerant species over others (Lebrija-Trejos et al. 2023), potentially reshaping community composition and ecosystem functions.

4.4 | Caveats and Limitations

The study of demographic buffering and its potential role in coexistence comes with inherent limitations. First, while our results suggest that demographic buffering may influence species coexistence, we do not directly test a coexistence mechanism. Specifically, we did not quantify density-dependent competition or niche differentiation, which are key equalizing and stabilizing processes in coexistence theory (Wright 2002; Levine and HilleRisLambers 2009; Adler et al. 2010). Moreover, although we interpret reduced interspecific variation in stochastic growth rates λs as being consistent with fitness equalization, we acknowledge that λs is not equivalent to invasion fitness as formally defined in modern coexistence theory. Our simulations do not incorporate species interactions or invasion analyses and therefore cannot directly assess competitive asymmetry. The term "equalization" in our study refers to the potential for demographic buffering to reduce performance disparities among species under environmental variability and at low densities, rather than to formal mechanisms of coexistence. We also note that our analysis did not explicitly partition the relative contributions of demographic and environmental stochasticity nor assess how their importance varies with population size. Therefore, our findings should be interpreted as theoretical rather than empirical in this context. Future research should explicitly link demographic buffering to competition intensity, resource acquisition, immigration, and environmental stochasticity to assess its role in promoting long-term persistence (Hart et al. 2016; Van Dyke et al. 2022; Jops et al. 2025).

Second, our estimates lacked direct quantitative data on individual seed production, potentially underestimating the extent of demographic buffering differentiation among species. This limitation is particularly relevant because seed reproduction often exhibits asynchronous and delayed responses to environmental fluctuations, which may contribute to the storage effect (Usinowicz et al. 2017; Evers et al. 2023). Moreover, reproductive output varies significantly with individual size, and for many species, there are substantial time lags (often > 10 years) between seed production and seedling emergence (Visser et al. 2016). Incorporating size-specific reproductive output and seedling establishment data (Comita et al. 2023) in future studies will help refine our understanding of reproduction's role in demographic buffering.

Lastly, our framework for evaluating the environmental fluctuation effect primarily focuses on species-level life-history strategies, making it challenging to disentangle the relative contributions of specific demographic rates. Recent advances in fitness decomposition methods (e.g., nonlinear responses and variance-covariance structures; Condit et al. 2017; Le Coeur et al. 2022; Tuljapurkar et al. 2023) and stochastic life table response experiments (Tuljapurkar 1990; Jacquemyn et al. 2012; Davison et al. 2013) offer promising approaches for future refinement. Moreover, temporal autocorrelation, the tendency for consecutive years to experience similar environmental conditions, can substantially influence recovery times and amplify nonlinear demographic responses, potentially favoring particular life-history strategies under recurrent stress (Gascoigne et al. 2025). Incorporating structured temporal dynamics into future modeling could deliver further insights into how environmental stochasticity may alter demographic buffering and species coexistence.

Author Contributions

Xianyu Yang: conceptualization, data curation, formal analysis, methodology, software, validation, visualization, writing – original draft, writing – review and editing. **Amy L. Angert:** conceptualization, methodology, supervision, writing – original draft, writing – review and editing. **Pieter A. Zuidema:** conceptualization, methodology, writing – review and editing. **Gabriel S. Santos:** conceptualization, formal analysis, methodology, software, writing – original draft, writing – review and editing. **Shengman Lyu:** conceptualization, methodology, writing – original draft, writing – review and editing. **Lalasia Bialic-Murphy:** conceptualization, methodology, supervision, writing – review and editing. **Jian Zhang:** conceptualization, methodology, resources, supervision, writing – original draft, writing – review and editing.

Acknowledgments

The BCI Forest Dynamics research project was founded by R. B. Foster and S. P. Hubbell, and it is now managed by R. Condit, S. Lao, and R. Pérez under the Center for Tropical Forest Science and the Smithsonian Tropical Research Institute in Panama. Numerous organizations have provided funding, and hundreds of field workers have contributed. The authors express deep gratitude to Prof. Fangliang He, Prof. Rachel Germain, and members of the Angert and Zhang labs for excellent comments that improved earlier versions of this manuscript. This research was financially supported by the Innovation Program of Shanghai Municipal Education Commission (2023ZKZD36 to J.Z.), the National Natural Science Foundation of China (32030068 to J.Z.), Stichting DOB Ecology (18626), and the Bernina Initiative through the ETH Foundation (202-2F-S318).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R scripts that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.26298793. BCI data was obtained from Dryad at https://doi.org/10.15146/5xcp-0d46.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.