Major axes of variation in tree demography across global forests

Short running title: Global variation in tree demography

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Abstract

Aim: Global forests and their structural and functional features are shaped by many mechanisms that impact tree vital rates. Although many studies have tried to quantify how specific mechanisms influence vital rates, their relative importance among forests remains unclear. We aimed to assess the patterns of variation in vital rates among species and in space and time across forests to understand and provide a baseline for expectations of the relative importance of the different mechanisms in different contexts.

Location: 21 forest plots worldwide.

Time period: 1981-2021

Major taxa studied: Woody plants

Methods: We developed a conceptual and statistical framework (variance partitioning of multilevel models) that attributes the variability in growth, mortality, and recruitment to variation in species, space, and time, and their interactions, which we refer to as *organising principles* (OPs). We applied it to data from 21 forest plots covering more than 2.9 million trees of approximately 6,500 species.

Results: Differences among species, the *species* OP, were a major source of variability in tree vital rates, explaining 28-33% of demographic variance alone, and in interaction with *space* 14-17%, totalling 40-43%. Models with small spatial grain sizes (quadrats at 5 x 5 m) retained most of the spatial OP, but a large proportion of variance remained unexplained (31-55%). The average variability among species declined with species richness across forests, indicating that diverse forests featured smaller interspecific differences in vital rates.

Main conclusions: Decomposing variance in vital rates into the proposed OPs showed that taxonomy is crucial to predictions and understanding of tree demography. Our framework has a high potential for identifying the structuring mechanisms of global forest dynamics as it highlights the most promising avenues for future research both in terms of understanding the relative contributions of mechanisms to forest demography and diversity and for improving projections of forest ecosystems.

Keywords: tree demography, tropical forests, temperate forests, multilevel models, variance partitioning, vital rates, species differences, spatial and temporal variation

Introduction

Forests are an integral component of the global carbon cycle (Anderson-Teixeira *et al.*, 2021) and are home to a majority of the terrestrial biodiversity (Pillay *et al.*, 2022). Changes in climate and land use threaten forests but anticipating how these diverse systems might respond is challenging due to the array of mechanisms that determine forest structure and function. One approach to better understand how forests function is through the analysis of tree demography (Griffith *et al.*, 2016): the growth, survival, and reproduction of individuals. These vital (i.e. demographic) rates combine to determine key features of forests, such as biomass stocks and fluxes (Needham *et al.*, 2022), structural complexity (Kohyama, 1993), and diversity (Lasky *et al.*, 2014). Improving our understanding of demography may, for example, foster the development of ecological theories, such as, in community ecology, the coexistence and niche theory (Kohyama, 1993; Lasky *et al.*, 2014). Moreover, demography has been identified as critical for more accurately modelling the terrestrial component in earth system models (Fisher *et al.*, 2018) and projecting the future of the terrestrial carbon sink (Pan *et al.*, 2011). Even small changes, over space and time, in tree vital rates can affect carbon cycles (Needham *et al.*, 2022) and thus the extent to which climate change can be mitigated by forests (Canadell & Raupach, 2008).

Vital rates are influenced by interacting mechanisms across spatial and temporal scales creating a challenge to the inclusion of demography in forest models (Weng *et al.*, 2015). Many of these mechanisms are difficult or impossible to measure directly, leading to the use of imperfect proxies (Swenson *et al.*, 2020). There exists, however, a higher level of information that may guide studies in demographic analyses: the patterns of vital rates themselves. The most comprehensive source of forest demography are the growth, mortality, and recruitment data derived from inventories on permanent plots (Davies *et al.*, 2021). The three vital rates and the contextual variables ('dimensions') associated with them offer an opportunity to organise the elements of forest dynamics in ways that help to infer the potential mechanisms for structuring forests. For example, through natural selection species have developed different strategies to acquire and allocate resources. This has resulted in a species dimension that represents the range of phenotypes among species(Díaz *et al.*, 2016) and, thus, also the observed vital rates of individual species (Johnson *et al.*, 2018; Rüger *et al.*, 2018; Needham *et al.*, 2022). Moreover, as resource availability and stressors vary along spatial and temporal dimensions, the environmental conditions of a forest also structure the vital rates of the trees, e.g. soil and topography vary across space (Zuleta *et al.*, 2020) and drought conditions over time (Chen *et al.*, 2019). Finally, all these dimensions (species, space, and time) have interactive effects. Functional traits vary between species and cause differential responses along spatial and temporal dimensions, for example when drought tolerant and intolerant species respond differently to a climatic event (Kupers *et al.*, 2019). Gap dynamics change over both space and time, and tree responses change as forest gaps close (Wright *et al.*, 2003). Patterns of how variability in vital rates is partitioned along key dimensions can thus reveal how important various biotic and abiotic drivers are in influencing tree demography and by extension forest dynamics.

We propose a conceptual framework that groups the mechanisms creating variation in vital rates as being related to species, space, and time. Together, these three dimensions and their interactions form seven organising principles (OPs, Table 1), which can be derived from forest inventory data. When the mechanisms that drive tree vital rates operate on unique combinations of these dimensions, quantifying the variability in vital rates that each OP describes may provide insights into the strength and importance of the associated mechanisms (Table 1). The statistical counterpart to this conceptual framework are multilevel models (McMahon & Diez, 2007; Visser *et al.*, 2016). These models allow decomposing forest demographic data across OPs and quantifying the relative importance of each OP by estimating and partitioning the variance in each vital rate (Browne *et al.*, 2005). In this framework, a broad assessment of the structure of variation in vital rates can be accomplished (Table 1).

We applied the framework decomposing variation in tree vital rates into the dimensions of species, space, and time as well as their interactions (OPs) for a set of 21 large (6 to 52 ha) and globally distributed forest dynamics plots (Davies *et al.*, 2021). We then compared the relative importance of the OPs for each vital rate at each forest with the goal of identifying consistent patterns in which OPs capture variation in vital rates: (1) among vital rates, i.e. investigating if some OPs are more important than others for specific vital rates; (2) across spatial scales (grain size), given the nature of scale dependency of ecological processes; and (3) among forests globally to understand how patterns may differ depending on forest diversity and structure. In achieving these goals, we provide macroecological patterns of the relative importance of OPs and, thus, the first approximate assessment of their associated mechanisms in generating variation in forest demography globally. Our framework, therefore, aims to facilitate hypothesis-driven research on mechanisms by first describing the higher-level patterns of vital rate variability.

Table 1. Seven organising principles (OPs) and the mechanisms that are associated with them, i.e., by creating variability of vital rates in the associated dimensions *species, space* and *time* and their interactions. References are example studies for the mechanisms.

Organising principles (OPs)	**Related mechanisms and examples**
Species	
Trees of different species have different vital rates.	**Natural selection** in response to biotic and abiotic stressors creates variation in evolutionary strategies that leads to **unique geno- and phenotypes** among individual trees manifested in different species. Species then display difference in their vital rates, as evidenced as follows: ● Species have different growth forms (e.g. shrubs and trees), dispersal abilities, and regeneration strategies (Martínez-Ramos *et al.*, 2021) that are related to different allocation strategies (Rüger *et al.*, 2020), also known as **life history strategies**, leading to different **demographic niches** (Condit *et al.*, 2006) and the emergence of interspecific **demographic trade-offs**, such as growth-mortality, recruitment-mortality (Russo *et al.*, 2008), and stature-recruitment (Rüger *et al.*, 2018). ● All these differences are potentially related to species functional traits (Poorter *et al.*, 2008; Adler *et al.*, 2014).
Space	
Trees in different locations (quadrats) have different vital rates.	Spatial heterogeneity created by variability in soil and topography as well as by differences in stand structure results in spatial differences of **resource availability** (nutrients, moisture, light) and **environmental stressors** (e.g. wind). In response, tree vital rates can be consistently higher in some areas than in others (Arellano, 2019): ● Tree mortality may be higher on hilltops given lower water availability in soil and higher wind disturbances (Zuleta *et al.*, 2020). ● Tree growth is faster and mortality higher in nutrient rich soils (Russo *et al.*, 2005; Lévesque *et al.*, 2016).
Time	
Trees during different time periods have different vital rates.	Environmental conditions are not stable in time but vary with **climate** and in response to **disturbances**, jointly affecting all species across a forest (synchronised effects): ● Cyclones and other drastic climatic disturbances can kill many trees at once in a forest (Uriarte *et al.*, 2019). ● Severe droughts can decrease growth and/or increase mortality directly (McDowell *et al.*, 2020) or indirectly by increasing the propensity of disease outbreaks (Negrón *et al.*, 2009). ● Irregular masting events and rainfall affect growth and survival of seedlings (Martini *et al.*, 2022).
Species x space	
Trees of different species in the same location (quadrat) have different vital rates.	Due to **spatial niche** effects, species have different environmental preferences that in combination with spatial variability create certain **habitats** where some species perform better than others. For example: ● Species adapted to low light availability have lower mortality in denser areas (Jurinitz *et al.*, 2013). ● Species with more dispersive seeds recruit more in open gaps (Clark *et al.*, 2018) ● Soil fertility affects species in different ways (Russo *et al.*, 2008). Conespecific and/or heterospecific negative density dependence may induce different vital rates in areas with different local population density (Hülsmann *et al.*, 2020).
Species x time	
Trees of different species during the same time period have different vital rates.	Species environmental preferences also create **temporal niche** effects that lead to asynchronous species responses to temporal variability (Fung *et al.*, 2020). For example: ● Species that are vulnerable to drought have higher mortality than those that are resistant or resilient (Chen *et al.*, 2019) ● Species with more dispersive seeds recruit more in a favourable year (Clark *et al.*, 2018) ● Species with high wood density suffer lower immediate mortality after hurricanes (Uriarte *et al.*, 2019).
Space x time	
Trees in the same location during different periods have different vital rates.	**Gap dynamics**: large tree falls open temporal gaps in the forest changing the environmental conditions of the surrounding area for a certain time (Kohyama, 1993): ● Fallen trees or trees killed by lightnings increase immediate local mortality in the area surrounding it (Gora *et al.*, 2021). ● Open gaps increase light availability, allowing faster growth (Brokaw, 1987) of understory trees and recruitment (Wright *et al.*, 2003) but just during specific time periods. **Climate effects** can manifest themselves differently **depending on the prevailing basic conditions in a given area**. For example: ● Drought events increase mortality disproportionally in valleys than on hilltops or ridges (Zuleta *et al.*, 2017). ● Soil nutrients can influence growth response to drought (Lévesque *et al.*, 2016).
Species x space x time + individual	
Trees of the same species in different locations and during different time periods have different vital rates.	**Individual variation** in vital rates given genetic and phenotypic variation, spatial variation at the microscale (Schwartz *et al.*, 2020), and ontogeny. ● Trees of different sizes and multi-stemmed trees have different mortality (Johnson *et al.*, 2018; Su *et al.*, 2020) and growth rates (Lu *et al.*, 2021), and their vital rates respond differently to climatic variation and disturbances. ● Functional traits influence growth depending on the size of the individuals (Gibert *et al.*, 2016)**.**

Individual trees have different vital rates.	• Local biotic interactions, as higher-order interactions, change individual vital rates (Li *et al.*, 2020). **Phenotypic plasticity** changes the observed vital rates of different species due to temporal and spatial environmental conditions. Plasticity may be seen in individual-level functional traits (Burns & Strauss, 2012).

Methods

Tree census data

We used data from 21 forest dynamics plots (Fig 1A) from the Forest Global Earth Observatory network (ForestGEO, Davies *et al.*, 2021). In each plot, all stems with dbh ≥1 cm were mapped, identified, and repeatedly measured using a standardised protocol. Plots used in this study range in size between 6 and 52 ha, with an inter-census measurement interval of approximately 5 years (range 3 to 10 years). The area within each forest plot was subdivided into quadrats of equal sizes (see *Organizing principles across spatial scales*). All forest plots had at least 2 censuses. The forest plots cover a wide range of environmental, climatic, and edaphic conditions, with the number of species per plot varying two orders of magnitude from 12 to 1402 (including morphospecies). In total, approximately 2.9 million trees from more than 6,500 species were repeatedly censused over periods of 3 to 40 years in more than 575 ha. For summary information on the plots and further details on how tree census data were processed see Appendix S1 in Supporting Information.

Vital rate definition and modelling

We analysed growth, mortality, and recruitment as annual rates by using vital rate information at the level of individual trees and fitting suitable multilevel models per forest plot and vital rate. Annual individual growth was calculated as dbh increment in millimetres of alive trees, divided by the individual's census interval length in years, and modelled using multilevel models with a normal distribution.

Variance partitioning of mortality and recruitment is less intuitive than growth, because although every individual has a unique, observable growth rate, individual trees only provide an observable status (i.e., individuals are either alive or dead). However, we can estimate latent mortality and recruitment rates for individuals belonging to the same population, space, and time by calculating per-capita vital rates (sensu Kohyama *et al.*, 2018). Further, although the variance of individual binary observations is fixed at 1.68 (the standard deviation of a logistic distribution [see below]), this term has meaning when compared to other sources of measurable variance, such as across populations, years, or spatial aggregations. Therefore, mortality was estimated from the status of trees - alive or dead - in each consecutive census assuming a binomial distribution (Kohyama *et al.*, 2018). Mortality rates were annualised by using a complementary log log link function (cloglog), where the log-transformed time between individual measurements is included as an offset term (Fortin *et al.*, 2008; Johnson *et al.*, 2018).

Recruitment was defined as the final per-capita recruitment rate (Kohyama *et al.*, 2018), which denotes the proportion of trees that are new recruits (i.e. not present in the previous census) and can be interpreted as the probability of an individual tree being new. Recruitment rates were estimated using the same modelling approach as for mortality, i.e., a binomial model with a cloglog link function and time interval length as an offset term. Because there is no time interval associated with individual recruits as they have not been monitored in the previous census, the time interval for recruits was calculated as the mean time interval of the survivors in the same quadrat. If there were no survivors in a specific quadrat, we used the mean time interval between the respective censuses from the entire plot.

Multilevel models

In order to quantify the variation in vital rates associated with each OP, we applied variance decomposition to multilevel models (MLMs) fitted separately for each vital rate and forest plot. MLMs are particularly useful for variance decomposition as they are able to reflect that ecological datasets contain identifiable hierarchical units, groups, or clusters (Browne *et al.*, 2005; McMahon & Diez, 2007). MLMs can account for such interdependence by partitioning the total variance into different components of variation due to each cluster (see example in Table 1). We included *species*, quadrat (*space*) and census interval (*time*) and their two-way interactions as variance components (also known as random effects) in each MLM. With that, we estimated the variance associated with each OP while respecting the hierarchical structure of the data. Following the convention of MLMs, the general structure of our models is:

$$Y_{ijkl} = \beta_0 + s_i + q_j + t_k + sq_{ij} + st_{ik} + qt_{jk} + e_{ijkl} \qquad \text{(eq. 1)}$$

where Y_{ijkl} is the vital rate for individual observation *l*, from species *i*, in quadrat *j* and time interval *k*. β_0 is the intercept. s_i, q_j, t_k are random effects for the OP *species*, *space* (quadrat) and *time* interval, respectively. $sq_{ij}, st_{ik}, qt_{jk}$ are random intercepts for the interactions *species x space*, *species x time*, and *space x time*. All random effects are taken to be independent, each represented by a normal distribution with mean zero and their respective variances $\sigma_s^2, \sigma_q^2, \sigma_t^2, \sigma_{sq}^2, \sigma_{st}^2, \sigma_{qt}^2$. The residual variance (e_{ijkl}) represents the variance explained by the three-way interaction *species x space x time*, and any unexplained variation among observations including non-separable measurement error and individual variation (Table 1). Residual variance is equivalent to σ_e^2 in growth models that assume a normally distributed error. For mortality and recruitment, modelled with binomial distributions, the residual variance at the link scale (i.e. linear predictor scale) is the expected variance for the binomial distribution ($\pi^2/6$ ~1.68) (Nakagawa *et al.*, 2017). We decided not to include the three-way interaction *species x space x time*, nor the individual variance, because of computational time limitation as these random effects would exponentially increase the number of parameters to estimate. Thus, repeated measures of the same individual are not accounted for in the model, but we expect that, like Rüger et al (2018), the potential bias caused by repetitive tree observations is negligible.

To partition the total variance of the vital rates among the individual OPs, we calculated **variance partition coefficients (VPCs)** (Browne *et al.*, 2005). The VPC of each OP was calculated as the proportion of its variance to the total variance of the model.

It is worth noting that we intentionally included no fixed effects in the models, in contrast to the usual statistical approach when searching for specific mechanisms, e.g., including dbh as a predictor to estimate ontogenetic effects in vital rates (Needham *et al.*, 2022). In our framework, all mechanisms are considered through OPs, which represent the dimensions at which they generate variability. By applying the framework using a global dataset, we provide a baseline approximation of the relative importance of the OPs. These models could be extended by adding variables related to the mechanisms of interest as fixed effects (e.g., Camac *et al.*, 2018).

All data analyses were performed using R (R Core Team, 2022), using the R package `brms` (Bürkner, 2017) to build Bayesian MLMs. For all estimated parameters, we used brms default prior distributions. For each model, we ran three Monte Carlo Markov chains with 3,000 iterations, discarding the first 1,000 iterations and thinning with an interval of 5, resulting in 1200 posterior samples. We checked convergence of the chains using the Gelman–Rubin criterion and by visually inspecting trace plots of estimated coefficients.

Analysis framework

Organising principles among vital rates

To assess the relative importance of the OPs among vital rates, we compared the VPC results for each vital rate among the 21 forest plots. However, because 16 forests had too few census intervals to fit the full model (see below), i.e., less than three (Table S1.2), we fit a reduced version of the model (eq. 1) without the temporal OPs (dropping the variances σ_t^2, σ_{st}^2, σ_{qt}^2). The reduced models were run separately for each time interval of a forest plot, and variances were averaged across time intervals for forests with more than one census interval.

Temporal organising principles

Currently, a bottleneck of our analysis is the scarcity of data for the temporal dimension of vital rates variability. For MLMs, the estimation of the variance of a grouping variable (i.e., *time* OP) with less than four to five levels may be biased towards zero (Oberpriller *et al.*, 2022). In our data, only five forest plots in the (sub)tropics (Table S1.2) presented a reasonable number of census intervals (i.e., at least three spanning between 15 and 40 years) to be considered suitable for the full VPC analysis including temporal OPs (eq.1). We fit these MLMs to ten random subsets of 5 ha each sampled from the full forest plots, where each subset was composed of five non-overlapping quadrats of 1 ha. This procedure was necessary to restrict computational time resulting from the large number of observations, especially on the large plots that are species-rich and of high tree density (i.e., Barro Colorado Island 50 ha, Lambir 50 ha, Pasoh 50 ha, Fig 1a and Table S1.2). Variance estimates of the OPs for each forest plot were averaged across estimates of the ten subsets.

Organising principles across spatial scales

To assess how the relative importance of OP varies with spatial scale, i.e., how the choice of a specific grain size impacts VPCs, we divided each forest plot into non-overlapping quadrats with increasing size: 5x5 m (0.0025 ha), 10x10 m (0.01 ha), 20x20 m (0.04 ha), 50x50 m (0.25 ha) and 100x100 m (1 ha). Depending on the size of the plot, we trimmed the data to fit within a rectangular region with edges that were even multiples of 100 m, discarding the data outside this area. This guaranteed that each plot could be evenly divided into quadrats of 1 ha and that the same area was analysed at all spatial scales. We fitted MLMs for the models without (reduced) and with temporal OPs averaged VPCs over all forest plots for each grain size and vital rate. We did not consider any spatial autocorrelation among adjacent quadrats to keep VPCs readily interpretable.

Organising principles across a global species richness gradient

Globally, species richness is one of the most distinguishing characteristics of forests and strongly correlates, for instance, with latitude (Keil & Chase, 2019), precipitation (Adler & Levine, 2007), and biome history (Wiens & Donoghue, 2004). The plots used in this analysis span two orders of magnitude in the number of species (12 to 1402, including morphospecies) offering a unique opportunity to explore if and how sources of variability in vital rates are associated with species diversity. We therefore assessed the effect of log-transformed rarefied species richness (cf. Appendix S5) on the VPCs of *species*, *space*, *species x space* and *residual* OP using dirichlet regression from the R package `DirichletReg` (Maier, 2021), appropriate for response variables that are multiple categories of proportional data (Douma & Weedon, 2019).

Robustness analyses

We performed four main robustness analyses to make sure our VPCs estimates from the forest plots are robust (1) to different forest plot sizes (6 to 50 ha) for the models without temporal OPs, by subsampling and comparing VPCs of the same forest (Lambir) with both procedures (Appendix S2); (2) to the approach of computing average VPCs for the model with temporal OPs from subsampled plots (10 samples of 5 ha) (Appendix S2); (3) to changes in the modelling procedure, by including or excluding temporal OPs from the VPC analysis (Appendix S3); and (4) the presence of rare species, by excluding or including rare species, to test the influence of rarity on VPCs (Appendix S4).

VPCs estimates from all forest plots were robust to changes in plot size, and VPC estimates remained reliable after removing temporal OPs. Specifically, our main results are also robust to the presence of rare species, though excluding or regrouping rare species does result in small decreases in the *species* VPC, balanced by an increase in the *residual* and *species x space* VPC (Appendix S4).

Results

Organising principles among vital rates

When comparing the relative importance of the OPs for all 21 forests distributed globally, we found that, despite large differences among the plots with respect to climate, environment, species richness etc., the relative importance of the OPs was relatively similar (Fig. 1). Generally, *species* was the most important OP for explaining variance in all three vital rates, after the *residual* OP. At the smallest spatial grain (quadrats at 5x5 m), average *species* and *species x space* VPCs varied little among vital rates, ranging from 28 to 33%, and 14 to 17%, respectively. Average *space* VPC was smaller for growth (4%), intermediate for mortality (10%) and larger for recruitment (19%). *Residual* VPCs were on average about half of the total variance for growth and mortality (55 and 47%, respectively) but smaller for recruitment (31%).

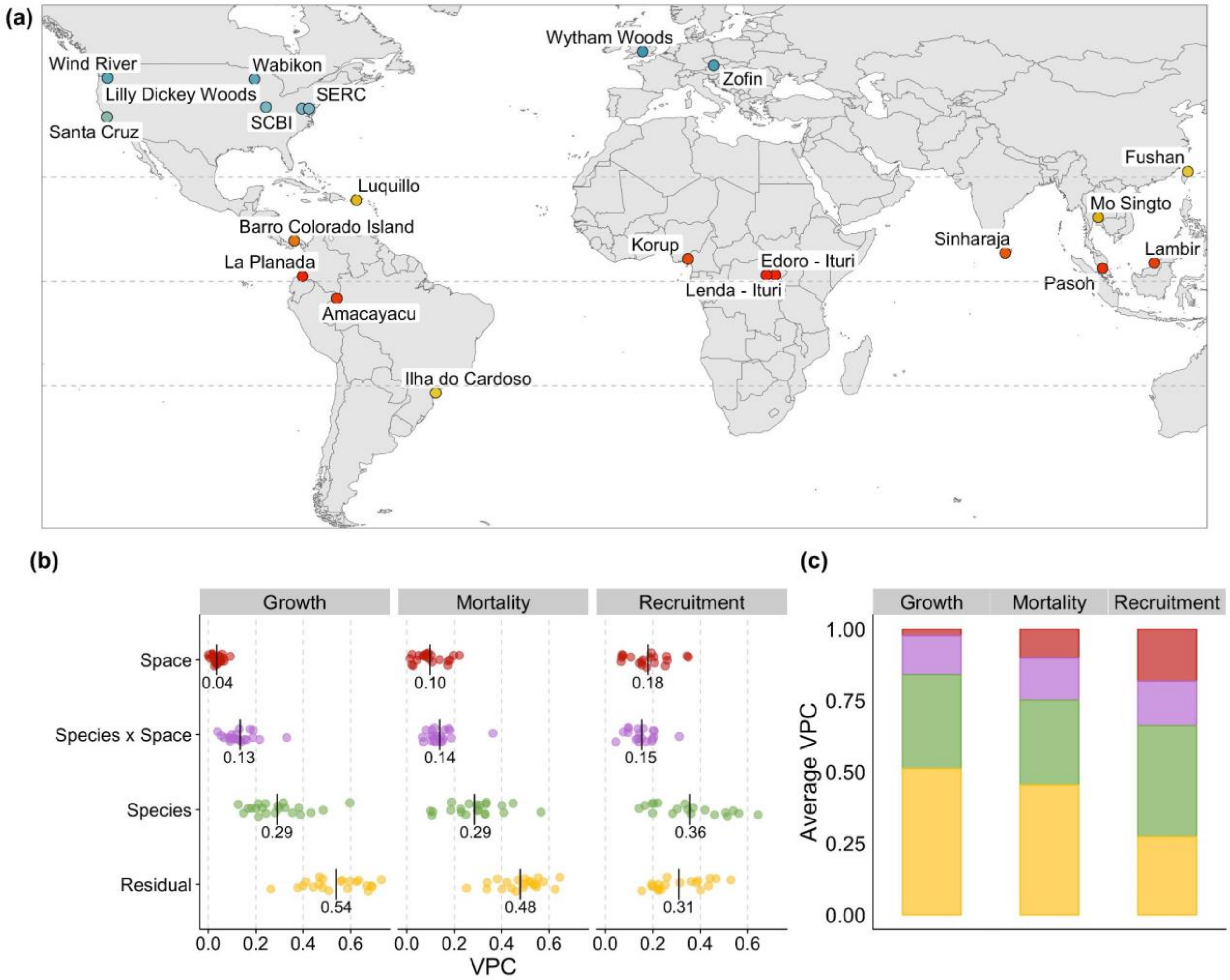

Figure 1. (a) Global distribution of the 21 forest plots. (b) Variance partition coefficients (VPC) of the organising principles (OPs) per vital rate - growth, mortality, and recruitment - with mean values indicated as black vertical lines and numbers. (c) Average VPCs across all plots, where colours correspond to the same OPs as in (b). Models were fitted at the 5x5 m grain size. Each forest plot in (a) is coloured by latitude.

Temporal organising principles

When analysing demographic data from the five forest plots with more than four consecutive censuses (grain size 5x5 m), we found that *species* remained the most important OP to explain variance in tree vital rates, except for growth, where the *species x space* VPC was larger for four of the five plots (Fig. 2). Temporal OPs (*time*, *species x time* and *space x time*) were especially important for mortality and recruitment, where VPCs of *space x time* (on average 10 and 15%, respectively) were larger than VPCs of *species x space* (on average 6 and 10%, respectively).

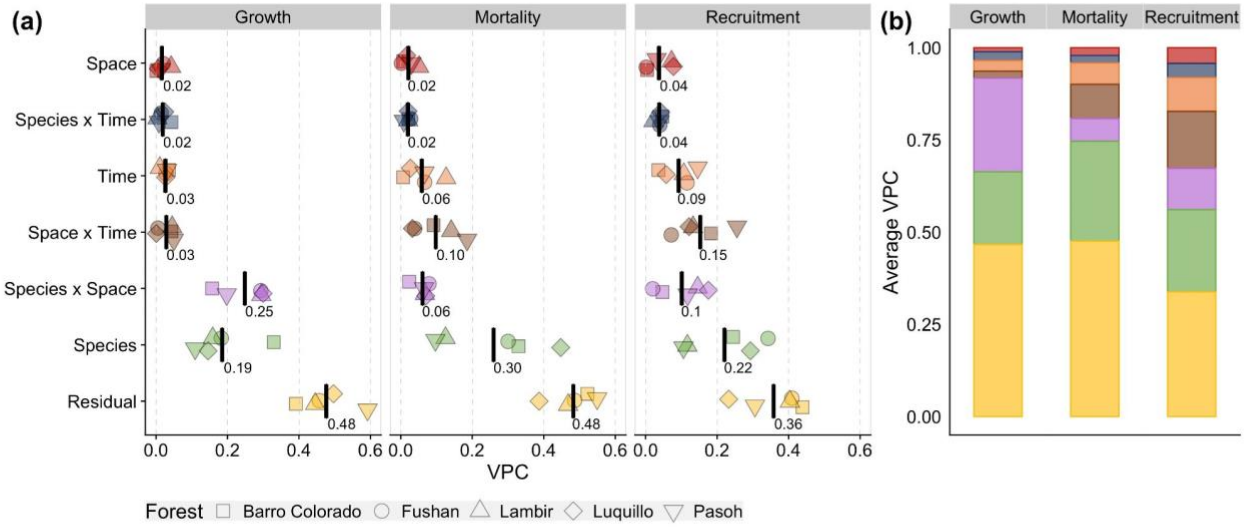

Figure 2. (a) Variance partition coefficient (VPC) of the organising principles (OPs) per vital rate - growth, mortality, and recruitment - for the five forest plots with at least four censuses. Mean VPCs across plots are presented as black lines and numbers. (b) Average VPCs across the five plots, where colours correspond to the same OPs as in (a). Models were fitted at the 5x5 m grain size. See Fig. 1a for forest plot locations.

Organising principles across spatial scales

When comparing average VPCs across five spatial grain sizes, we found that the relative importance of residual variation increased with grain size for all vital rates and more accentuated for growth (Fig. 3). For instance, for the models including temporal OPs (Fig. 3b), residual variation increased from 46% at the smallest grain (quadrats at 5x5 m) to 71% at the largest grain (100x100 m). In turn, the spatial OPs - *space*, *species x space* and *space x time* - consistently decreased in relative importance with increasing spatial grain for all vital rates. The OPs *species* and *species x time* remained almost equally important across spatial grains.

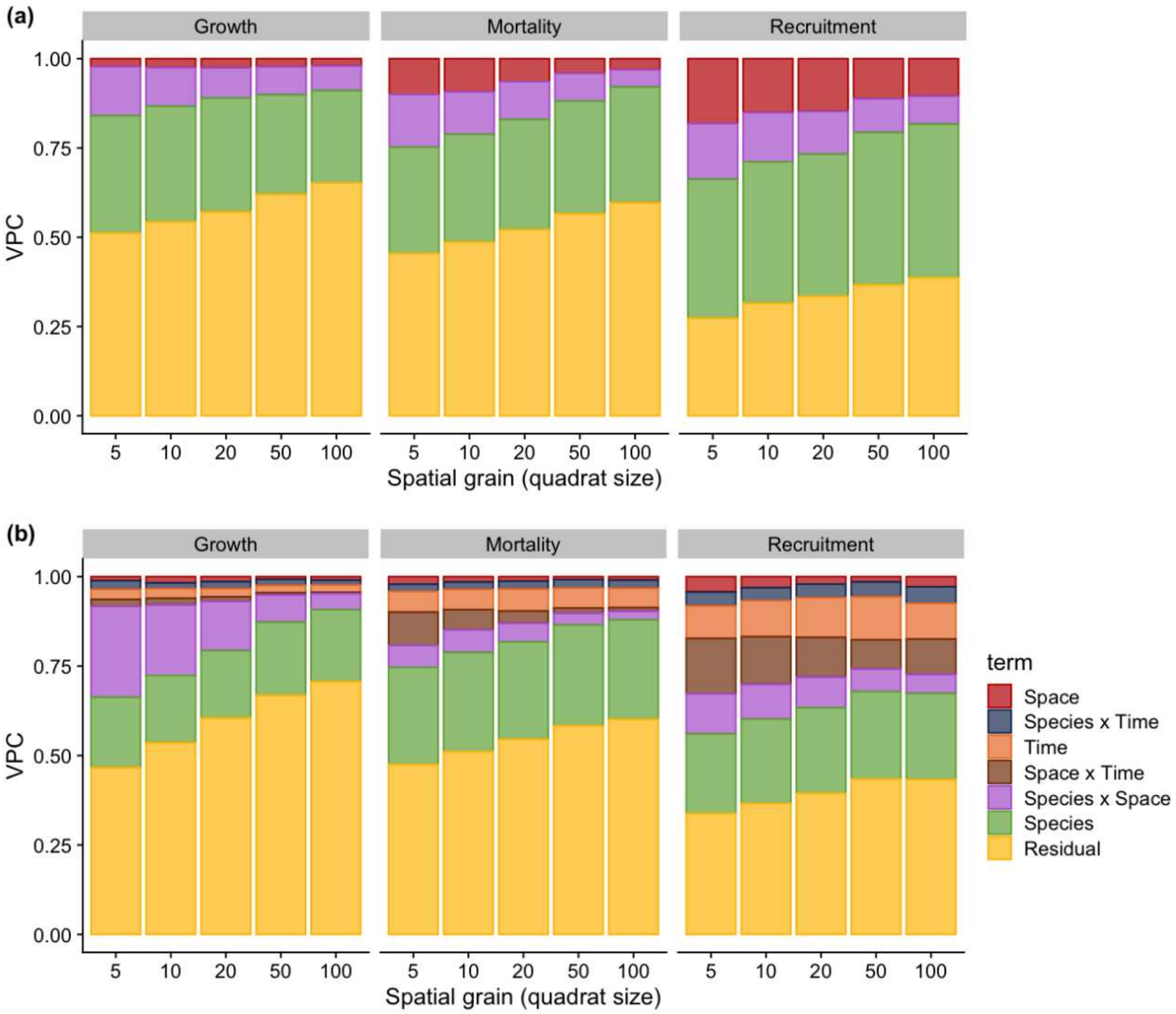

Figure 3. Average variance partition coefficients (VPCs) of each organising principle (OP) across five spatial grain sizes (quadrats from 5x5 m to 100x100 m) for the vital rates growth, mortality, and recruitment: (a) reduced models without temporal OPs for all 21 forests plots, and (b) full models with temporal OPs for the five (sub)tropical forest plots with enough censuses (Barro Colorado Island, Fushan, Lambir, Luquillo, and Pasoh).

Organising principles across a global species richness gradient

While the *species* OP was the most important component of vital rates variance partitioning throughout the forests, we also found that the importance of the *species* OP decreased with species richness for recruitment and growth, but not for mortality (Fig. 4). The decrease in *species* VPC for growth and recruitment was led by a decrease in the *species* standard deviation (Fig. S5.4). This result was robust to the presence of rare species (Fig. S5.5). The other OPs showed no significant changes with species richness (Fig. 4).

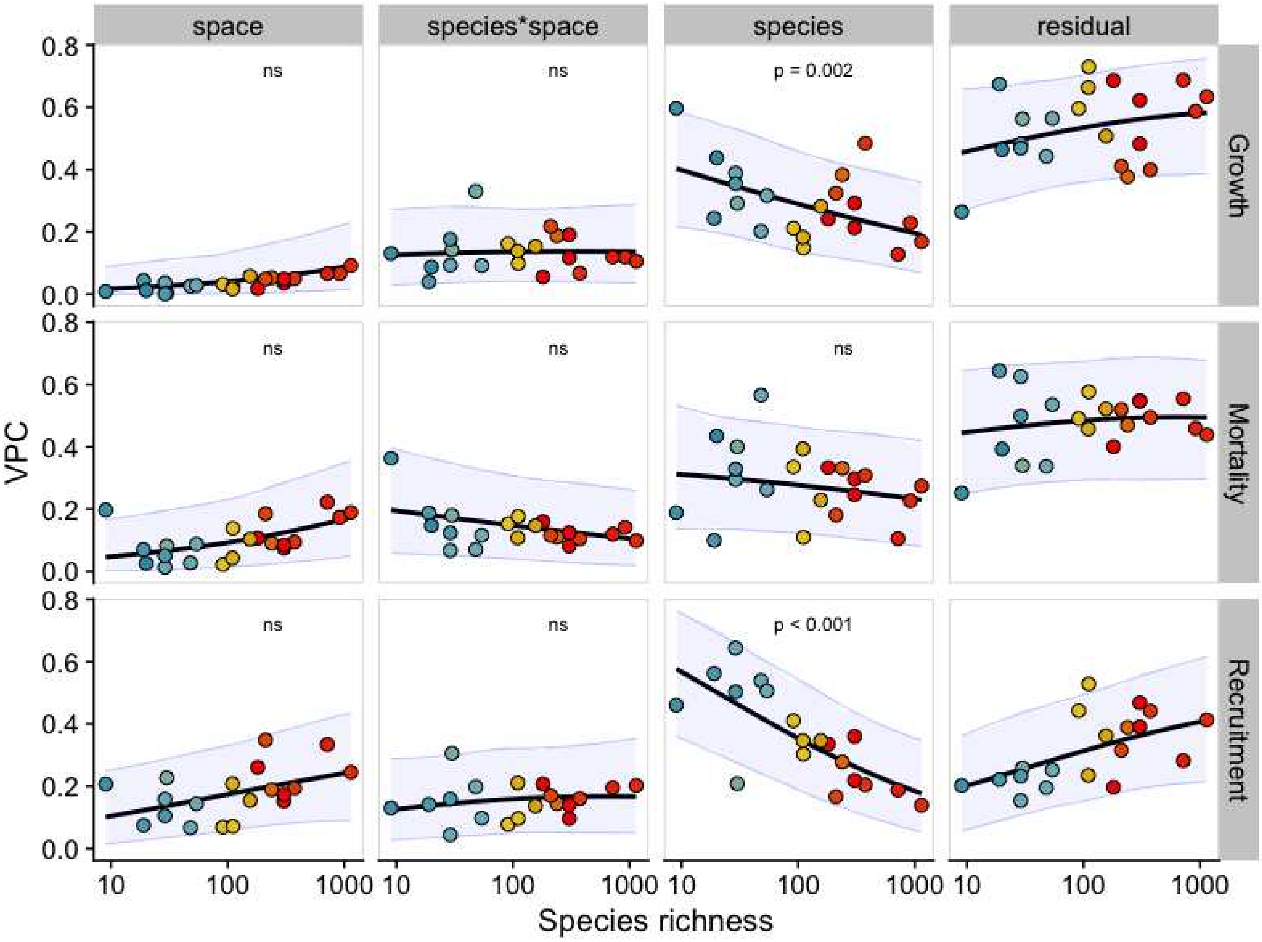

Figure 4. Variance partition coefficients (VPCc) for the organising principles (OPs) *species*, *space*, *species x space* and residual against rarefied species richness. OPs were estimated with the reduced model (eq. 1) without temporal OPs. Black lines are fitted relationships obtained from dirichlet regressions of VPCs against species richness; shaded blue areas are the 95% prediction intervals. p-values are shown only for the significant values after Bonferroni correction (alpha=0.016). Residual VPCs are reference categories and thus were not tested for significance. Each forest plot (dots) is colored by absolute latitude as in Fig. 1a. Species richness on the x-axis is at the logarithmic scale with base 10.

Discussion

Innumerable mechanisms operate and interact in forests and leave fingerprints of their integrated effects in tree vital rates, i.e., growth, survival, and recruitment, which together drive forest dynamics. Here, we used a conceptual and statistical framework to identify organising principles (OPs, Table 1) and quantify the associated variability among vital rates for more than 2.9 million trees of approx. 6,500 species in 21 forests across the globe. This, in turn, allows a first assessment of the relative importance of mechanisms that are underlying each OP offering a first step in narrowing down which of the mechanisms are critical for structuring global forests. In the following sections, we summarise our most striking findings, discuss some potentially important mechanisms, and provide recommendations for an agenda to study tree vital rates.

Species is a major source of variability in tree vital rates

We found that *species* was the most important OP for all vital rates, explaining on average between 29 and 36% of the demographic variance across the globe (Fig. 1, reduced models). Species in interaction with space added another 13-15% variance explained, meaning that a total of 42- 51% of demographic variation can be partitioned towards species differences and species-specific responses to spatial heterogeneity (Table 1). In contrast, *space* and *time* explained relatively little variability in vital rates (Fig. 1, 2). Our results, therefore, suggest that - at least at the temporal and spatial scales covered by our datasets - spatio-temporally varying factors alone contribute less to demographic variance than evolutionary history and adaptations to the environment. Grouping individuals into species thus creates a globally important cluster of demographic variation that appears consistently most important across a wide range of forests.

Our results on the importance of species support numerous ongoing research agendas. Efforts to include more realistic representation of species strategies in global vegetation models appear to be a promising route (Fisher *et al.*, 2018; Anderegg *et al.*, 2022), regardless of whether forest dynamics are studied in local tree neighbourhoods or larger spatial units (Fig. 3). We expect that accounting for species differences can explain up to ~36% of demographic variation, while additionally accounting for small-scale species–environment associations (Messier et al., 2010; Lasky et al., 2014) might further improve this to almost half of the variation explained. More critically, however, our work shows that there are clear limits to the improvement more realistic representations of species can bring. Studies including species strategies typically rely on functional traits (Rubio & Swenson, 2022) or demographic trade-offs (Rüger *et al.*, 2020; Russo *et al.*, 2021), i.e. simplifications that explain only about half of the among-species variation (e.g., Visser *et al.*, 2016). Nevertheless, the global importance of species in clustering demographic variance and its consistency across spatial scales indicates that endeavours seeking to better map species differences may have been underestimated compared to those focussing on spatial and temporal effects.

Temporal variability acts mostly on recruitment and mortality and in interaction with space

In contrast to variability among species, temporal OPs played a minor role for variability in tree vital rates, as time interval alone was responsible for only 3-7% of total variability for plots with sufficient data. Although these data probably have the most comprehensive temporal coverage of large forest areas currently available, our findings might reflect the relatively short time frame

(20 to 40 years) and low temporal resolution of the inventory data (approximately 5 years). Nevertheless, variability between census intervals was detected in recruitment and to a lesser degree in mortality but was rather unimportant for growth (Fig. 2). A possible explanation is that growth rates fluctuate within shorter periods than our 5 year census interval can capture (Dobbertin, 2005), while recruitment and mortality may exhibit several bad or good years in a row (Schwartz *et al.*, 2020).

Temporal effects were most important in interaction with *space* which, for instance, could indicate gap dynamics that jointly affect vital rates of most trees (Kohyama, 1993). This interpretation is consistent with the result that the *space x time* interaction OP was more important for mortality and recruitment than for growth - as mortality in gaps is known to be “spatially contagious” with falling trees killing multiple neighbours (Araujo *et al.*, 2021), and the resulting gaps generally favour recruitment for many species (Brokaw, 1987). Additionally, some of the variability in the *space x time* OP could be the result of climatic events acting differently depending on local conditions, such as droughts that harm trees more in valleys than on ridges (Zuleta *et al.*, 2017).

Our results on temporal OPs support a research agenda that should analyse the importance of climatic and/or temporal effects on vital rates in interaction with spatial effects. Moreover, we advocate for datasets with higher temporal resolution and longer time series, which would allow us to capture larger but infrequent disturbances (Šamonil *et al.*, 2013), thereby revealing more of the demographic importance of environmental fluctuations and temporal niches (Fung *et al.*, 2020).

Small spatial grain variability is important

Spatial OPs were important for vital rate variability mostly in interaction with species for growth, and time for mortality and recruitment (Fig. 1 and 2), indicating the importance of spatial niches and patch dynamics (see previous section). Alone, *space* was the least important OP and only created considerable variability in models without time (Fig. 1).

Spatially acting mechanisms were best detected by dividing the plots into quadrats of 5x5 m (Fig. 3), indicating that trees interact and respond to local conditions at scales of a few metres, through mechanisms such as gap dynamics, competition, crown damage, and micro-topography (Schwartz *et al.*, 2020). Further decreasing the spatial grain would then move below the scale of tree crowns, and begin to merely assign quadrats to single trees, here reflected by residual variance. With increasing grain size, less variability is explained by spatial mechanisms. Consequently, vital rates become less predictable at larger spatial grain. Nevertheless, even at the largest quadrat size of 100x100 m, spatial OPs still explained a reasonable part of the variability, with the consequence that tree species seem to distinctly respond also to environmental heterogeneity over larger areas (de Knegt *et al.*, 2010), probably due to topography, water resources and soil nutrients (Russo *et al.*, 2005, 2008; Zuleta *et al.*, 2020).

Large proportion of unexplained variability in vital rates

Residual variance was consistently the dominant component of the vital rate VPCs across sites and in the temporal and spatial analyses. In multilevel models, residual variance represents the variance in the response that cannot be attributed to any of the grouping factors (here, the OPs). On one hand, this result encourages more detailed models that might include covariates that 'explain' differences among individual trees. For instance, both growth and mortality are known to differ across ontogeny, and thus the inclusion of tree size (e.g. dbh) as a covariate would most likely explain some of the residual variance (Hülsmann *et al.*, 2018). Moreover, functional traits at the individual level (Su *et al.*, 2020) and structures that explicitly deal with spatial (Wiegand *et al.*, 2017) and temporal autocorrelation may explain additional differences in individual vital rates. On the other hand, there are intrinsic limits to what can be explained by even the most detailed models, as the residual variance also includes inherent noise which, by definition, is unexplainable. The noise includes misattribution of species, mapping error or measurement error (Detto *et al.*, 2019) and chaotic behaviour known to exist in many biological systems (Benincà *et al.*, 2015). Nevertheless, individual (i.e., 'tree-level') covariates represent a promising avenue for extending our framework.

Globally, variability among species declines with species richness

Across plots, increasing species richness resulted in decreasing relative importance of the *species* OP in growth and recruitment (Fig. 4). This trend was robust to one of the most probable sources of bias, i.e., differences in species rarity between forest plots, and thus we consider that the decreasing relative importance of the *species* OP with species richness reflects a true ecological signal. Moreover, the decrease in the *species* VPC was determined by a decrease in the respective variance estimates, and not by an increase of variances related to the other OPs (Fig. S5.4). Similarly, Condit et al. (2006) found across ten tropical forests (seven in common with this study) that the range of mortality and growth rates among species decreased with higher species richness.

These results underpin that - in contrast to expectations of niche theory - the most diverse forests feature the lowest interspecific variation in vital rates. Following the rationale of niche theory, diverse forests should have more demographic niches than low-diversity forests, as more niches allow more species to have equivalent fitness thus favouring species coexistence (Chesson, 2000). The lack of evidence for wider demographic ranges in species-rich forests (this study, Condit *et al.*, 2006; Clark, 2010) suggests that demographic niches play a minor role for large-scale diversity patterns, hinting towards more neutral dynamics (Hubbell, 2006). However, coexistence is inherently high dimensional, and comparing mean species values across low dimensions (a few vital rates) only partly represents the full niche space (Clark, 2010). In summary, species in highly diverse forests present redundant vital rates that do not add to the diversity of demographic types, highlighting the challenges of studying and predicting changes in hyperdiverse systems.

Conclusions

As the mechanisms that influence vital rates can be grouped by the dimensions at which they operate and interact, patterns of how variance is partitioned along key dimensions can reveal how important various biotic and abiotic mechanisms are in influencing tree demography and hence forest dynamics. Here, we have shown that variance partitioning of vital rates among key ecological dimensions, i.e., species, space, and time, has the potential to provide a first step in identifying the structuring processes of global forest dynamics. We found that species differences were a major source of variability in tree vital rates, while temporal variability acted mostly on recruitment and in interaction with spatial variability. Small grain sizes captured most of the spatial variability, but there were still larger proportions of unexplained variability in vital rates. Most intriguing, we found that, globally, variability among species declined with species richness.

The proposed framework highlights the most promising avenues for future research both in terms of understanding the relative contributions of mechanisms to forest demography and diversity, and for predicting forest ecosystems. We hope future studies may benefit from using this approach as a conceptual and modelling baseline to narrow down which of the mechanisms are critical for structuring global forests.

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Author contributions

MSL, SM, MV, LH, PIP, AOA conceived the ideas and conceptualization of the study.

MSL, SM, MV, LH conceived and designed the analyses.

MSL, LH curated the data.

MSL performed the analyses.

MSL, SM, MV, LH wrote the initial draft.

MSL, SM, MV, LH, PIP, SD, HD wrote reviewed versions of the draft.

SA, KAA, NA, NAB, WYB, NC, CHCY, YYC, GC, KC, AD, SE, CENE, GG, IAUNG, CVSG, RH, WHH, AI, DJJ, DK, KK, YTL, JAL, JRM, YM, WJMS, MBM, MN, AN, GP, ReP, RoP, RPP, PS, IFS, ST, DT, JT, MU, AW, JZ, DZ contributed data and provided site-specific information.

All authors contributed to the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Data and code availability

The forest data that support the findings of this study are available from the ForestGEO network. For some of the sites, the data is publicly available at https://forestgeo.si.edu/explore-data.

Restrictions apply, however, to the availability of the data from other sites, which were used under license for the current study, and so are not publicly available. Data are however available from the authors upon reasonable request and with permission of the principal investigators of the ForestGEO sites. We provide an example of data preparation and analysis workflow from a forest plot with public available data and the code for all results and analyses on Zenodo repository (Leite, 2022).

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