

REPORT

Characterizing tree trait variance over spatiotemporal scales

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Abstract

Beyond the study of the mean, functional ecology lacks a concise characterization of trait variance patterns across spatiotemporal scales. Traits are measured in different ways, using different metrics, and at different spatial (and rarely temporal) scales. This study expands on previous research by applying a ubiquitous and widely used empirical model—Taylor's Power Law—to functional trait variance with the goal of identifying general patterns of trait variance scaling (the behavior of trait variance across scales). We compiled data on tree seedling communities monitored over 10 years across 213 2 m² plots and functional trait data from a subtropical forest in Puerto Rico. We examined trait-based Taylor's Power Law at nested spatial and temporal scales. The scaling of variance with the mean was idiosyncratic across traits suggesting that the drivers of variation are likely to differ across traits that may make variance scaling theory elusive. However, slopes varied more in space than through time, suggesting that spatial environmental variability may have a larger role in driving trait variance than temporal variability. Empirical models that characterize taxonomic patterns across spatiotemporal scales, like Taylor's Power Law, can provide an insight into the scaling of functional traits, a necessary next step toward a more predictive trait-based ecology.

KEYWORDS

Puerto Rico, seed mass, seedling censuses, specific leaf area, Taylor's Power Law, wood specific gravity

INTRODUCTION

A key first step to building a more predictive ecology is to understand how biological patterns change with scale (Chase et al., 2018; Levin, 1992; Wiens, 1989). All natural systems show variability over spatiotemporal scales and the phenotypic composition of communities is no exception (Asner et al., 2017; Smith et al., 2013). The magnitude of trait variation across species in a community depends on the spatial and temporal scales examined, yet a consensus on whether trait variance (in the mathematical sense)

varies systematically over space or time is lacking (Jarzyna & Jetz, 2018; Smith et al., 2013; Zhang et al., 2018). Without a clear understanding of trait variation patterns across spatial and temporal scales, the predictability and generalizability of functional approaches remain limited.

In a recent paper, Hulshof and Umaña (2022) call for the characterization of trait variation across spatiotemporal scales by taking advantage of existing empirical models used to characterize taxonomic patterns. Taylor's Power Law is of particular interest, given that it can integrate variation across temporal and spatial scales (Adler et al., 2005;

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Taylor, 1961; White et al., 2010). Taylor's Power Law describes the proportional relationship between (population) mean and variance where the slope typically varies between 1 and 2 (Taylor, 1961). This is a fundamental relationship reported across taxa and biomes (Cobain et al., 2019; Döring et al., 2015; Taylor et al., 1988) but has been rarely applied to other dimensions of biodiversity beyond taxonomic units (but see Ulrich et al., 2021; Xu, 2016). The underlying explanations for Taylor's Power Law (at least for populations) range from biological mechanisms, including the role of fluctuating immigration and population growth rates (Anderson et al., 1982; Cohen et al., 2013; Taylor & Taylor, 1977) to purely statistical mechanisms where the skewness of the population distribution in space or time is sufficient for explaining the pattern of mean–variance scaling (Cohen & Xu, 2015; Xiao et al., 2015). We extend this relationship to traits by comparing trait means and variances of plant communities monitored over time and across a large area. In this trait-based extension, the existence of trait-based Taylor's Power Law—a power-function increase in trait variance with trait means—regardless of the trait could point to statistical mechanisms where the pattern should be more visible in more skewed trait distributions. Alternatively,

trait-dependent mean–variance scaling could point to biological processes related to trait selection and niche space in spatiotemporally heterogeneous environments.

We suggest that the slope of this relationship will vary as a result of biological processes and spatiotemporal environmental variability (Hulshof & Umaña, 2022), such that at increasing spatiotemporal scales (greater environmental variability) the relationship between log-transformed trait mean and log-transformed trait variance should exhibit steeper positive slopes (Hulshof & Umaña 2022; Kalyuzhny et al., 2014) (Figure 1). A key assumption underlying the integration of spatiotemporal scales into this existing empirical model is that environmental variability increases with both area and time. Larger areas generally encompass a mosaic of environmental conditions, which is reflected by greater spatial heterogeneity, and longer time spans should encompass greater climatic variability. This increasing environmental variability should thus promote the colonization of species with “novel” functions able to take advantage of the increased number of niches contained in larger areas and longer periods (Armstrong & McGehee, 2008; Chesson & Warner, 1981) and ultimately lead to greater variance in functional composition.

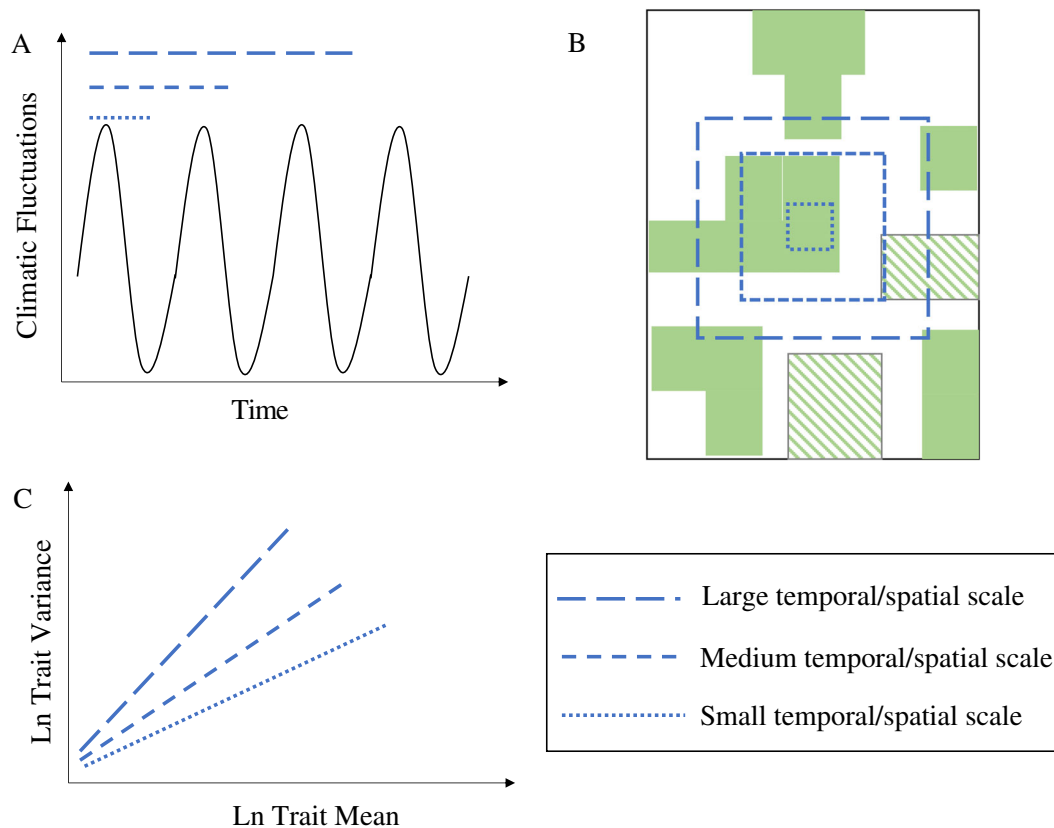


FIGURE 1 Schematic diagram depicting the predictions of the effect of increasing temporal and spatial scales on Taylor's Power Law: the relationship between log-transformed trait variance and the mean. (A) Temporal heterogeneity increases with scale. (B) Spatial heterogeneity increases with scale (colors/patterns indicate different habitat types). (C) Prediction: steeper slopes as spatial and temporal scales increase.

In this study, we examined trait-based Taylor's Power Law relationships by integrating decade-long annual census data from seedling plots located in a subtropical wet forest in Puerto Rico with species-level trait data. We focus on three commonly measured functional traits, specific leaf area, seed mass, and wood specific gravity, representing key dimensions of resource acquisition and reproductive strategies important for determining the assembly of tropical forest communities (Díaz et al., 2016). We used seedling census data, instead of adult data, because seedling dynamics are faster and can be monitored over shorter periods (e.g., annually), while adult censuses in this forest take place approximately every 5 years and turnover rates are much slower. The questions that framed our study were: Is it possible to use community trait mean values to predict community trait variance values? Does the relationship between log-transformed trait mean and log-transformed trait variance change systematically as spatial and temporal scales increase? Are these patterns trait dependent? Trait-based Taylor's Power Law relationships revealed variable trends across functional traits that generally showed more stable patterns across temporal than spatial scales. Generalities in trait variation patterns may point to unifying principles acting across space and time, aiding in the development of a predictive theory of variance scaling.

METHODS

Study site and census data

We compiled census and functional trait data from tree communities distributed along a 16-ha permanent plot located in a subtropical wet forest of northeastern Puerto Rico (18°200' N, 65°490' W) (Thompson et al., 2002). We used data on 213 2 × 1 m seedling plots monitored annually for survival and recruitment from 2007 to 2016 (Appendix S1: see Section S1, and Figure S1; data available in Zimmerman, 2018). The study site has a long history of natural and anthropogenic disturbance including hurricanes and fruit plantations that have altered the functional composition and dynamics of this forest (Thompson et al., 2002; Umaña et al., 2023).

Functional traits

Species-level specific leaf area (SLA, cm²/g), seed mass (SM, g), and wood specific gravity (WSG, g/cm³) were collected from all woody species in the 16-ha plot following standardized protocols (Cornelissen et al., 2003; Swenson & Enquist, 2008; Appendix S1: see Section S1 and Table S1; data available in Swenson & Umaña, 2015).

Data analysis

To fit a trait-based Taylor's Power Law, we calculated plot-level trait unweighted means and variances based on species composition of tree seedling communities and fit power laws to trait variance at increasing spatial and temporal scales. Across spatial scales, we calculated trait variance and the mean across species with increasing radial distance from one plot until all plots were encompassed. We repeated this same procedure for each of the 213 seedling plots across all censuses from 2007 to 2016. That is, at each spatial scale in a given census, we calculated the community mean and variance per trait. Next, we defined 10 major categories to obtain the same number of slopes for temporal (10 years) and spatial scales. The categories were defined using different radial distances as follows: (1) less than 50 m; (2) between 51 and 100 m; (3) between 101 and 150 m; and so on every 50 m (we also ran the analyses applying different categories, but the results were largely consistent with those presented here). For each spatial category, we calculated the slopes between the log-transformed trait variance and log-transformed trait mean. Then, we calculated the correlation between slopes and spatial categories.

Across temporal scales, we first calculated trait variance and the mean across species per seedling plot for nested temporal scales beginning with periods of a single census (census period t_1 , t_2 , t_3 , etc.), followed by periods of two consecutive censuses (census period t_1-t_2 , t_2-t_3 , t_3-t_4 , etc.) and so on until a period encompassing all 10 censuses (census period t_1 to t_{10}). Because this procedure resulted in a variable number of data points for each temporal grain (e.g., for the one-census temporal grain we had 10 values per plot, but for the 10-censuses temporal grain we had one value per plot), we calculated the mean value across all census combinations per temporal grain, so that for each temporal grain we had a single value for trait variance and the mean per plot. Next, we calculated the slopes between the log-transformed trait variance and log-transformed trait mean at different time spans and accumulated areas. Then, we calculated the correlation between slopes and temporal grain.

RESULTS

Temporal trait-based Taylor's Power Law

The statistical significance of temporal Taylor's Power Law was dependent on the trait (Figure 2A,B; Appendix S1: Table S2). For SLA and SM, log-transformed variance and

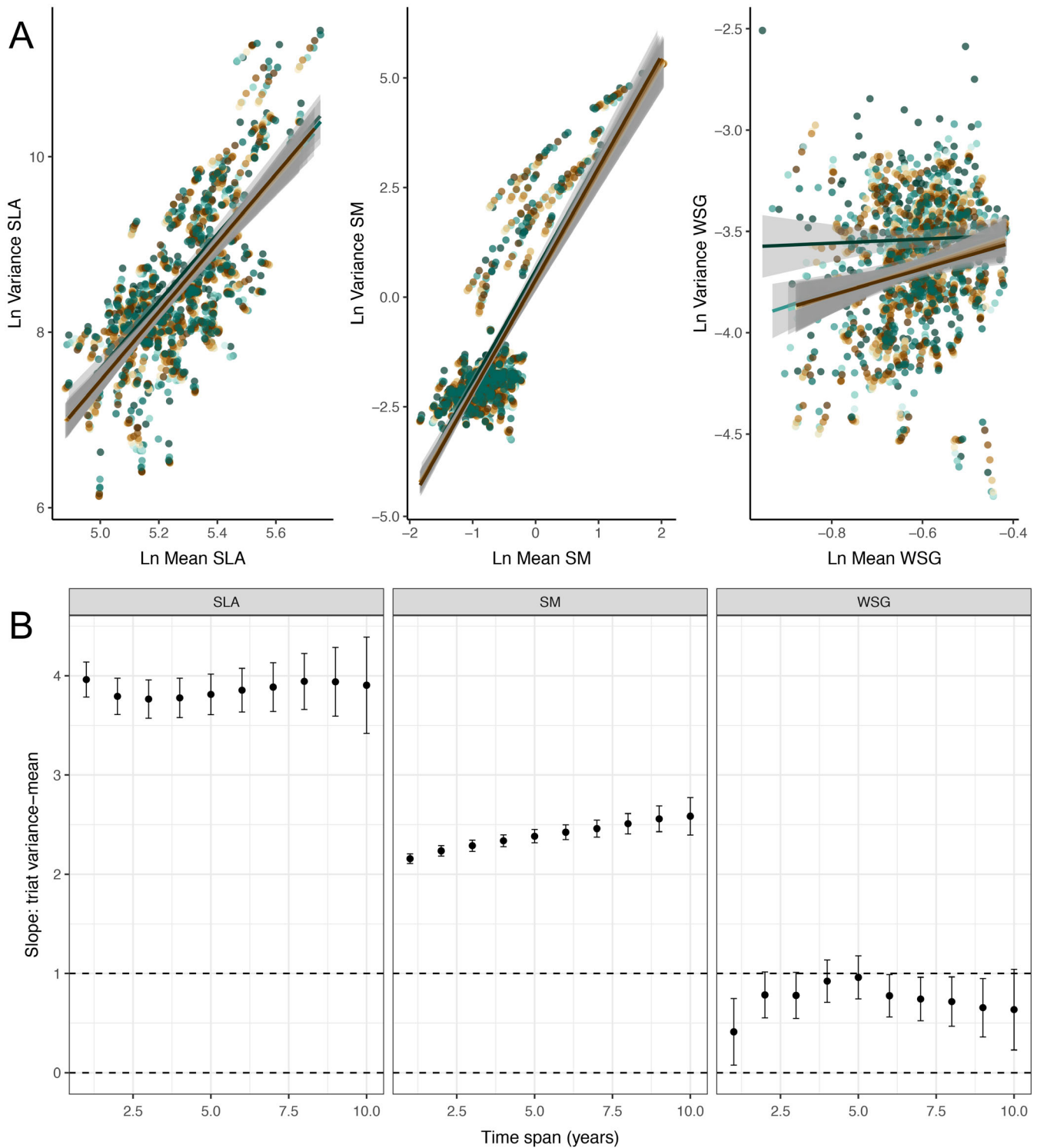


FIGURE 2 Trait-based Taylor's Power Law across increasing temporal grain for 213 seedling plots in Puerto Rico monitored annually over 10 years. Brown colors indicate a larger accumulated time or area using 10 spatial grain categories (1: less than 50 m; 2: 51 and 100 m; 3: 101 and 150 m; and so on every 50 m in radius distance). (A) Relationship between log-transformed trait variance and log-transformed trait means. (B) Variation in slopes between log-transformed trait variance and log-transformed trait means at increasing temporal grains. The shaded gray areas in the top plot and the error bars in the bottom plots represent the 95% confidence intervals. SLA, specific leaf area (cm^2/g); SM, seed mass (g); WSG, wood specific gravity (cm^3/g).

the mean were positively related, and the slopes were greater than 1, in line with expectations from Taylor's Power Law (Figure 2A). However, for WSG this relationship

was generally flat with slopes ranging between 0.10 and 0.76. With increasing temporal extent, we observed relatively constant slopes for SLA and WSG and a positive trend for

SM (Figure 2B; Appendix S1: Table S3). The only exception was the WSG slope at a 1-year time span (slope = 0.10), which was associated with an outlying point; one plot showed extremely low variance.

Spatial trait-based Taylor's Power Law

As with the temporal trends, the statistical significance of spatial Taylor's Power Law was dependent on the trait (Figure 3A,B). For SLA and SM, log-transformed variance and the mean were positively related, but for WSG the relationship was negative (Figure 3A). For SLA, slopes were always greater than 1 indicating a power-function type increase in trait variance with the mean. For SM, slopes ranged from 3.30 to 0.91 indicating that trait variance approached a constant. For WSG, slopes were negative, indicating that trait variance decreased in a power-function fashion as the trait mean increased. When integrating data across space, slopes changed in a systematic manner; for SLA, slopes increased, and for SM and WSG, slopes decreased with an increasing area (Figure 3B; Appendix S1: Table S3).

DISCUSSION

Characterizing patterns of trait variation over spatiotemporal scales is a necessary step toward a generalizable framework in trait-based ecology. In this study, we extended Taylor's Power Law to trait variance using seedling communities from a species-rich subtropical wet forest. While some results are consistent with previously reported taxonomic patterns—supporting the existence of Taylor's Power Law for some traits—the application of the trait dimension revealed additional complexities discussed in more detail below.

Notably, trait variance scaled positively with the mean for SLA and SM, yet the relationship between WSG variance and the mean was flat or negative (Figures 2 and 3). This is likely to reflect the degree of variation or skewness across trait types and energetic costs of trait variance; foliar traits are known to be more variable than wood traits (Kattge et al., 2011; Siefert et al., 2015) and SM generally varied several orders of magnitude and exhibits greater skewness among co-occurring species (Rees & Venable, 2007). For example, in our study site, mean WSG per plot ranged between 0.26 and 0.82 g cm⁻³, while SM ranged between 0.0007 and 13.2 g with a highly skewed distribution (Appendix S1: Table S1, Figure S2). This variation in the magnitude and skewness of traits may influence the visibility of Taylor's Power Law because when the range of log(mean) values

is large the relationship tends to be more visible (Döring et al., 2015; Taylor et al., 1988). In addition, variance–mean slopes greater than 1 found for both SLA and SM indicated that as the mean trait values increased, subsequent increases in variance became larger. In other words, gram for gram, variance is greater for larger SLA and SM values. This is intuitive for SLA considering the energetic costs of leaf construction. Low SLA values are indicative of greater cell wall concentrations and energetically expensive carbon-based secondary compounds like lignins and tannins (Coley et al., 1985). Whereas high SLA values are indicative of greater concentrations of structural compounds such as hemicellulose and cellulose that are, in comparison, less energetically costly (Niinemets & Kull, 1999). Thus, varying 1 cm² for a leaf that is small and thick (low SLA) incurs greater energetic costs compared with varying the same area for a leaf that is large and thin (high SLA). Independent of the mechanism underlying Taylor's Power Law, our results indicated that this may be a useful model for predicting trait variances based on trait means, but these predictions may vary depending on the trait. Predicting trait variances based on trait means has clear applications for improving ecosystem demography models that can incorporate species-level trait variances in addition to species mean trait values (e.g., ED2; Medvigy et al., 2009).

In addition, our analyses of Taylor's Power Law showed that variation in slopes between trait variance and the means were generally stable across time (for SLA and WSG) but showed systematic variation across space. Stable variance–mean slopes across temporal scales contradicted our expectation of increasing slopes at larger temporal scales (encompassing greater seasonality or climatic variability). It is possible the relatively short study period (10 years) did not encompass sufficient climatic variation to affect the relationship between trait variance and the means for SLA and WSG and/or that these traits were weakly affected by the temporal variation during the period studied. We recommend determining the validity of Taylor's Power Law for longer time periods including major temporal fluctuations to determine whether patterns detected in this study are general and point to fundamental drivers of global plant trait variation (e.g., Diaz et al., 2016). Interestingly, SM was the only trait that showed a positive trend over a longer time span, indicating that the variance for a given mean is larger at longer temporal scales than at shorter ones. We interpreted this as a combined effect of the high variation in magnitude of this trait, which increases the visibility of Taylor Power Law functions, and an increased climatic variability over time that in turn, increases the number of niches. For instance, as the studied forest undergoes secondary succession, the process generates a replacement

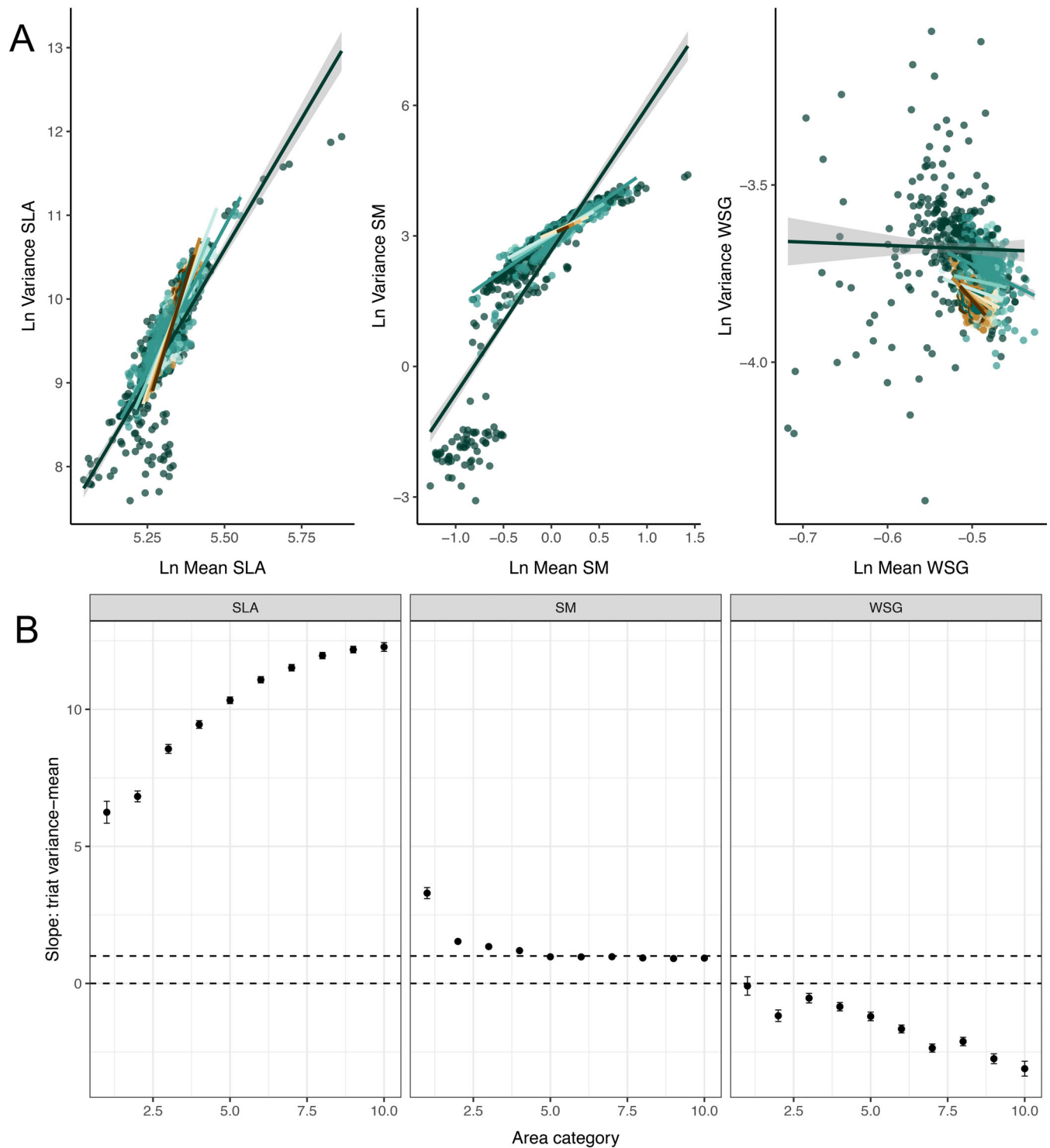


FIGURE 3 Trait-based Taylor's Power Law across increasing spatial grain for 213 seedling plots in Puerto Rico monitored annually over 10 years. (A) Relationship between log-transformed trait variance and log-transformed trait means. (B) Variation in slopes between log-transformed trait variance and log-transformed trait means at an increasing area grain categories. Colors and acronyms are the same as in Figure 2.

of species that exhibit different ecological strategies, with pioneer species that tend to have small SM being subsequently replaced by old growth species that exhibit large SM.

Across spatial scales, the slopes of Taylor's Power Law either consistently increased (SLA) or decreased (SM and WSG) (Figure 3B). The increasing slopes at larger spatial scales (observed for SLA), indicated that the

change in trait variance for a given mean is larger when larger areas are considered. This pattern is consistent with our expectations and could be the outcome of increased spatial environmental heterogeneity at larger spatial scales (Cobain et al., 2019; Ulrich et al., 2021). In this forest, the 16-ha plot where seedling plots were located encompassed substantial spatial heterogeneity associated with land-use history; the northern portion of the plot (3/4 parts) was used for fruit plantations and selective logging before 1940, while the southern portion (1/4) experienced less anthropogenic activity (Thompson et al., 2002). This spatial heterogeneity was accentuated after hurricanes (Georges and Hugo in 1991 and 1998, respectively) (Uriarte et al., 2009) and could explain some of the observed patterns in SLA: species with high SLA tended to dominate disturbed areas, while species with low SLA were common in more mature forests (Grime, 1979; Westoby, 1998). In contrast, the shallower (positive) slopes at larger areas found for SM, indicated that changes in trait variance became smaller with an increasing area. This is likely to occur because the range of SM values was mostly, if not completely, encompassed by larger spatial scales. In other words, there seemed to be an upper limit to the total variance of SM in this system. This pattern points to upper constraints on the magnitude of trait variation and potentially to ecosystem function (de Camargo et al., 2019; Ulrich et al., 2021) and may also help explain the large variation of traits reported at local scales (e.g., Freschet et al., 2011; Hulshof et al., 2013; Leffler & Enquist, 2002). Finally, for WSG we observed declining variance–mean slopes at an increasing areas, but the slopes were negative. This indicated that trait variance decreased in a power-function fashion with mean values and the decreasing rate was faster as the area increased. On an energetic basis, denser wood requires more carbon and is energetically more expensive per unit volume than lighter woods (Enquist et al., 1998). Together, the trends reported here for Taylor’s Power Law across spatial scales revealed systematic variation in slopes dependent on the type of trait, pointing to the roles of different biological processes and constraints.

Independently of the traits examined, variability in trait variance across time was always lower than variability in trait variance across space. This result has key implications for predicting species coexistence where spatial variability may have a greater influence on coexistence than temporal variability, at least for the relatively short period that was studied (Snyder, 2008). It would be important to examine these trends for periods including major climatic events such as hurricanes, and test if temporal variation remains minor relative to spatial variation (Cohen & Xu, 2015; Tippet & Cohen, 2016). Further, the

high variation for some traits (e.g., SLA) at the relatively constrained spatial and temporal scales examined here, suggested that small-scale processes like those emerging from species interactions were key drivers of trait variation. This finding has implications for trait sampling strategies and, more broadly, for understanding the spatial and temporal dynamics of plant communities worldwide.

Conclusion

The contrasting results across nested spatial and temporal scales shown here suggest a variable role of biological drivers associated with environmental heterogeneity underlying a trait-based analog of Taylor’s Power Law. In our study system (a small subtropical island once heavily deforested and increasingly frequented by storms), disturbance history plays an important role in driving patterns of trait and environmental variation across spatial scales (Thompson et al., 2002; Uriarte et al., 2009). Our findings point to fundamental relationships worth examining across other systems varying in spatiotemporal environmental variability. Two findings in particular, the upper constraint on trait variance and greater trait variance due to spatial relative to temporal scales, have broad implications for understanding species coexistence and ecosystem function. Characterizing patterns of trait variance promises to advance trait-based ecology and improve the predictability of ecological models. Integrating information over space and time will allow us to identify processes operating at different scales, resolve potential inconsistencies between spatial and temporal components, and understand the impact of ongoing increases in spatiotemporal environmental variability on natural systems worldwide.

AUTHOR CONTRIBUTIONS

Catherine M. Hulshof and Maria Natalia Umaña conceived the idea. Maria Natalia Umaña performed the analyses and wrote the first draft of the manuscript. Catherine M. Hulshof contributed substantially to editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Seedling data (Zimmerman, 2018) are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569>. The trait data (Swenson & Umaña, 2015) are available in Dryad: <https://doi.org/10.5061/dryad.j2r53>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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