

Umaña María Natalia (Orcid ID: 0000-0001-5876-7720)  
Hulshof Catherine M. (Orcid ID: 0000-0002-2200-8076)

Journal: Ecology

Manuscript type: Report

Handling Editor: Joseph B. Yavitt

## Characterizing tree trait variance over spatiotemporal scales

Maria Natalia Umaña<sup>1</sup> and Catherine M. Hulshof<sup>2</sup>

<sup>1</sup> Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109, USA

<sup>2</sup> Department of Biology, Virginia Commonwealth University, Richmond, VA, 23284, USA

Corresponding author: Maria Natalia Umaña. E-mail: [maumana@umich.edu](mailto:maumana@umich.edu)

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

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1002/ecy.4126](https://doi.org/10.1002/ecy.4126)

This article is protected by copyright. All rights reserved.

## **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 2m<sup>2</sup> 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 the drivers of variation likely differ across traits which may make variance scaling theory elusive. However, slopes varied more in space than through time, suggesting 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 insight into the scaling of functional traits, a necessary next step towards 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 in building a more predictive ecology is to understand how biological patterns change with scale (Wiens 1989, Levin 1992, Chase et al. 2018). All natural systems show variability over spatiotemporal scales and the phenotypic composition of communities is no exception (Smith et al. 2013, Asner et al. 2017). The magnitude of trait variation across species in a community depends on spatial and temporal scales examined, yet consensus on whether trait variance (in the mathematical sense) varies systematically over space or time is lacking (Smith et al. 2013, Jarzyna and Jetz 2018, 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 (2023) 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 (Taylor 1961, Adler et al. 2005, 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 (Taylor et al. 1988, Döring et al. 2015, Cobain et al. 2019) but has been rarely applied to other dimensions of biodiversity beyond taxonomic units (but see Xu 2016, Ulrich et al. 2021). 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 (Taylor and Taylor 1977, Anderson et al. 1982, Cohen et al. 2013) 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 and 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 and Umaña 2023), 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 (Kalyuzhny et al. 2014, Hulshof and Umaña 2023) (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 (Chesson and Warner 1981, Armstrong and McGehee 2008) and ultimately lead to greater variance in functional composition.

In this study, we examine 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 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 which 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  $2 \times 1$  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,  $\text{cm}^2 \text{g}^{-1}$ ), seed mass (SM, g), and wood specific gravity (WSG,  $\text{g cm}^{-3}$ ) were collected from all woody species in the 16-ha plot following standardized protocols (Cornelissen et al. 2003, Swenson and Enquist 2008) (Appendix S1: see Section S1 and Table S1) (Data available in Swenson and 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 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 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 1-

census temporal grain we had 10 values per plot, but for the 10-censuses temporal grain we had 1 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 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, Table S2). For SLA and SM, log-transformed variance and 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, 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 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 approaches a constant. For WSG, slopes were negative indicating that trait variance decreases in a power-function fashion as the trait mean increases.

When integrating data across space, slopes change in a systematic manner; for SLA, slopes increased, and for SM and WSG, slopes decreased with increasing area (Figure 3B, Table S3).

## **Discussion**

Characterizing patterns of trait variation over spatiotemporal scales is a necessary step towards 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 reveals 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 likely reflects 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 varies several orders of magnitude and exhibits greater skewness among co-occurring species (Rees and Venable 2007). For example, in our study site, mean WSG per plot ranged between 0.26 and 0.82 g cm<sup>-3</sup> 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 (Taylor et al. 1988, Döring et al. 2015). In addition, variance-mean slopes greater than one found for both SLA and SM indicate that as mean trait values increase, subsequent increases in variance become 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 which are, in comparison, less energetically costly (Niinemets and Kull 1999). Thus, varying  $1\text{cm}^2$  for a leaf that is small and thick (low SLA) incurs greater energetic costs compared to 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 indicate 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 which 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 means were generally stable across time (for SLA and WSG) but showed systematic variation across space. Stable variance-mean slopes across temporal scales contradicts 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 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 interpret 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 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), indicates 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, encompasses 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 tend to dominate disturbed areas, while species with low SLA are common in more mature forests (Grime 1979, Westoby 1998). In contrast, the shallower (positive) slopes at larger areas found for SM, indicate that changes in trait variance becomes smaller with increasing area. This likely occurs because the range of SM values is mostly, if not completely, encompassed by larger spatial scales. In other words, there seems to be an upper limit to the total variance of SM in this system. This pattern points to upper constraints on the

Author Manuscript

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., (Leffler and Enquist 2002, Freschet et al. 2011, Hulshof et al. 2013). Finally, for WSG we observed declining variance-mean slopes at increasing areas, but the slopes were negative. This indicates that trait variance decreases in a power-function fashion with mean values and the decreasing rate is faster as area increases. 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 reveal 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 were 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 (Tippett and Cohen 2016, Cohen et al. 2016). Further, the high variation for some traits (e.g., SLA) at the relatively constrained spatial and temporal scales examined here, suggest that small-scale processes like those emerging from species interactions are key drivers of trait variation. This finding has implications for trait sampling strategies and, more broadly, for understanding 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.

**Acknowledgments:** We thank Nathan G. Swenson for his comments on an earlier version of the manuscript, John Bithorn, Jimena Forero-M, Chris Nytech, Setch Rifkin, Sarah Stankavich, Jill Thompson, Maria Uriarte, Jess Zimmerman, and the LTER volunteers for conducting the seedling censuses and collecting trait data. This study was based on work supported by the National Science foundation under Grants BSR-8811902, DEB-9411973, DEB-9705814, DEB-0080538, DEB-0218039, DEB-0620910, DEB-1239764, DEB-1546686, DEB-1831952, DEB-0614659 and 11222325. MNU was supported by DEB-2016678, CMH was supported by NSF CAREER-2042453.

**Author contributions:** CMH and MNU conceived the idea. MNU performed the analyses and wrote the first draft of the manuscript, CMH contributed substantially to editing.

**Conflicts of interest:** the authors declare no conflicts of interest.

### **Literature cited**

- Adler, P. B., E. P. White, W. K. Lauenroth, D. M. Kaufman, A. Rassweiler, and J. A. Rusak. 2005. Evidence for a general Species-Time-Area Relationship. *Ecology* 86:2032–2039.
- Anderson, R. M., D. M. Gordon, M. J. Crawley, and M. P. Hassell. 1982. Variability in the abundance of animal and plant species. *Nature* 296:245–248.
- Armstrong, R. A., and R. McGehee. 2008. Competitive exclusion. 1980 115:151–170.
- Asner, G. P., R. E. Martin, C. B. Anderson, K. Kryston, N. Vaughn, D. E. Knapp, L. P. Bentley, et al. 2017. Scale dependence of canopy trait distributions along a tropical forest elevation gradient. *New Phytologist* 214:973–988.
- de Camargo, U., T. Roslin, and O. Ovaskainen. 2019. Spatio-temporal scaling of biodiversity in acoustic tropical bird communities. *Ecography* 42:1936–1947.
- Chase, J. M., B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, et al. 2018. Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters* 21:1737–1751.
- Chesson, P., and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist* 117:923–943.

- Cobain, M. R. D., M. Brede, and C. N. Trueman. 2019. Taylor's power law captures the effects of environmental variability on community structure: An example from fishes in the North Sea. *Journal of Animal Ecology* 88:290–301.
- Cohen, J. E., and M. Xu. 2015. Random sampling of skewed distributions implies Taylor's power law of fluctuation scaling. *Proceedings of the National Academy of Sciences of the United States of America* 112:7749–7754.
- Cohen, J. E., M. Xu, and W. S. F. Schuster. 2013. Stochastic multiplicative population growth predicts and interprets Taylor's power law of fluctuation scaling. *Proceedings of the Royal Society B: Biological Sciences* 280.
- Coley, P. D., J. P. Bryant, and S. F. Chaping. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Díaz, S., J. Kattge, J. H. C. Cornelissen, I. J. Wright, S. Lavorel, S. Dray, B. Reu, et al. 2016. The global spectrum of plant form and function. *Nature* 529:1–17.
- Döring, T. F., S. Knapp, and J. E. Cohen. 2015. Taylor's power law and the stability of crop yields. *Field Crops Research* 183:294–302.
- Enquist, B. J., J. H. Brown, and G. B. West. 1998. Allometric scaling of plant energetics and population density. *Nature* 395:163–165.
- Freschet, G. T., A. T. C. Dias, D. D. Ackerly, R. Aerts, P. M. Van Bodegom, W. K. Cornwell, M. Dong, et al. 2011. Global to community scale differences in the prevalence of convergent over

divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography* 20:755–765.

Grime, J. P. 1979. *Plant strategies and vegetation processes*. First edition. John Wiley and Sons., Chichester, UK.

Hulshof, C. M., C. Violle, M. J. Spasojevic, B. McGill, E. Damschen, S. Harrison, and B. J. Enquist. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science* 24:921–931.

Jarzyna, M. A., and W. Jetz. 2018. Taxonomic and functional diversity change is scale dependent. *Nature Communications* 9.

Kalyuzhny, M., Y. Schreiber, R. Chocron, C. H. Flather, R. Kadmon, D. A. Kessler, and N. M. Shnerb. 2014. Temporal fluctuation scaling in populations and communities. *Ecology* 95:1701–1709.

Kattge, J., S. Díaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bonisch, E. Garnier, et al. 2011. TRY - a global database of plant traits. *Global Change Biology* 17:2905–2935.

Leffler, A. J., and B. J. Enquist. 2002. Carbon isotope composition of tree leaves from Guanacaste, Costa Rica: Comparison across tropical forests and tree life history. *Journal of Tropical Ecology* 18:151–159.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology : The Robert H . MacArthur Award Lecture. *Ecology* 73:1943–1967.

Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research: Biogeosciences* 114:1–21.

- Niinemets, Ü., and O. Kull. 1999. Biomass investment in leaf lamina versus lamina support in relation to growth irradiance and leaf size in temperate deciduous trees. *Tree Physiology* 19:349–358.
- Rees, M., and D. L. Venable. 2007. Why do big plants make big seeds? *Journal of Ecology* 95:926–936.
- Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* 18:1406–1419.
- Smith, A. B., B. Sandel, N. J. B. Kraft, and S. Carey. 2013. Characterizing scale-dependent community assembly using the functional-diversity-area relationship. *Ecology* 94:2392–02.
- Snyder, R. E. 2008. When does environmental variation most influence species coexistence? *Theoretical Ecology* 1:129–139.
- Swenson, Nathan G.; Umana, M. N. 2015. Data from: Interspecific functional convergence and divergence and intraspecific negative density dependence underlie the seed-to-seedling transition in tropical trees, Dryad, Dataset, <https://doi.org/10.5061/dryad.j2r53>
- Swenson, N. G., and B. J. Enquist. 2008. The relationship between stem and branch wood specific gravity and the ability of each measure to predict leaf area. *American Journal of Botany* 95:516–519.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature* 1:732–735.
- Taylor, L. R., J. N. Perry, I. P. Woiwod, and R. A. J. Taylor. 1988. Specificity of the spatial power-law exponent in ecology and agriculture. *Nature* 332:721–722.
- Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration and population mechanics. *Nature* 265:415–421.



- Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- Tippett, M. K., and J. E. Cohen. 2016. Tornado outbreak variability follows Taylor’s power law of fluctuation scaling and increases dramatically with severity. *Nature Communications* 7:4–10.
- Ulrich, W., B. Kusumoto, T. Shiono, and Y. Kubota. 2021. Latitudinal gradients and scaling regions in trait space: Taylor’s power law in Japanese woody plants. *Global Ecology and Biogeography* 30:1334–1343.
- Umaña, M. N., J. Needham, J. Forero-Montaña, C. J. Nytech, N. G. Swenson, J. Thompson, M. Uriarte, et al. *in press*. Demographic trade-offs and functional shifts in a hurricane-impacted tropical forest. *Annals of Botany*.
- Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, et al. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecological Monographs* 79:423–443.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- White, E. P., S. K. M Ernest, P. B. Adler, A. H. Hurlbert, and S. K. Lyons. 2010. Integrating spatial and temporal approaches to understanding species richness. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3633–3643.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.
- Xiao, X., K. J. Locey, and E. P. White. 2015. A process-independent explanation for the general form of Taylor’s law. *American Naturalist* 186:E51–E60.

Xu, M. 2016. Ecological scaling laws link individual body size variation to population abundance fluctuation. *Oikos* 125:288–299.

Zhang, H., H. Y. H. Chen, J. Lian, R. John, L. Ronghua, H. Liu, W. Ye, F. Berninger, and Q. Ye. 2018. Using functional trait diversity patterns to disentangle the scale-dependent ecological processes in a subtropical forest. *Functional Ecology* 32:1379–1389.

Zimmerman, J. 2018. LFDP phenology plot seedlings-16 ha plot ver 5347491. Environmental Data Initiative. <https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569>

## Figures

**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 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.

**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 area in the top plot and the error bars in the bottom plots represent the 95% confidence intervals. SLA: specific leaf area ( $\text{cm}^2 \text{g}^{-1}$ ); SM: seed mass (g); WSG: wood specific gravity ( $\text{cm}^3 \text{g}^{-1}$ ).

**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 increasing area grain categories. Colors and acronyms are the same as in Figure 2.