Received: 4 May 2022 | Revised: 7 November 2022 | Accepted: 10 November 2022

DOI: 10.1111/geb.13620

PERSPECTIVE

Global Ecology and Biogeography A Journal of Macroecology

WILEY

Power laws and plant trait variation in spatio-temporally heterogeneous environments

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Funding information
National Science Foundation, Grant/Award Number: CAREER #2042453

Handling Editor: Adam Algar

Abstract

A challenge: Variation is ubiquitous in nature across all spatial and temporal scales and underlies prominent ecological and evolutionary theories. Although understanding the causes and consequences of trait variation is a central goal of trait-based ecology, the scaling of trait variance across space and time (variance scaling) is unresolved.

A solution: We argue that characterizing trait variance across spatio-temporal scales using a combination of prominent power laws can elucidate the role of environmental variability in trait variation and potential mechanisms driving trait patterns. In particular, the species–time–area relationship and Taylor's power law help to establish a generalizable framework for developing and testing variance scaling theory. Finally, we outline priority research questions and tractable systems for answering them. Successional forests, long-term forest monitoring networks and censuses of short-lived taxa are ideal for coupling high-resolution environmental data with measurements of trait variance across scales to test the models proposed here.

Main conclusions: Characterizing the behaviour of variance across spatio-temporal scales is feasible and a prerequisite for developing a predictive theory of trait-based ecology.

KEYWORDS
climatic variability, community assembly, environmental heterogeneity, functional ecology, species–area relationship, Taylor's power law, trait-based variance

1 | THE SCALING OF FUNCTIONAL TRAITS IS UNRESOLVED

Trait variation is an inherent property of ecological communities and is central to the search for general ecological principles. Trait variation is a key component of community assembly (McGill et al., 2006) and species coexistence (Adler et al., 2013) and predicts the resilience of organisms and ecosystems to environmental change (Mori et al., 2013). Despite the proliferation of trait-based ecological research, estimating the extent of trait variation, its spatial and temporal structure and its consequences for community and ecosystem properties remains challenging (Westerband et al., 2021), and we are still far from a predictive theory of trait variation (Enquist et al., 2015; Maitner et al., 2021).

This disconnect between the quantity of research on trait variation and our inability to predict trait variation across scales is surprising because increasing variance in population densities and species richness with increasing scale describes two of the most ubiquitous empirical patterns in ecology (Rosenzweig, 1995; Xiao et al., 2015). Here, we use trait variation in a broad sense (e.g., community trait variation) and trait variance in a mathematical sense, while recognizing the many metrics used to quantify variance (e.g., convex hull volumes). Increasing variance with scale is a universal phenomenon, and variance scaling (i.e., how variance changes with scale) is studied extensively across disparate fields (e.g., physics, mathematics, geography). In trait-based ecology, variance scaling is, in some ways, implicit because the field was developed around the central premise that interactions between organismal traits and their environments explain variation in population trends and species occurrences (Salguero-Gómez et al., 2018). In other ways, variance scaling is explicit because we know trait variation is substantial within and among communities (Kraft et al., 2008; Lamanna et al., 2014; Messier et al., 2010; among many others), and much of the global trait variation is often found at small spatial scales (e.g., Cornwell & Ackerly, 2009; Kraft et al., 2008; Westoby et al., 2002), although this pattern appears system and trait dependent (e.g., Götzenberger et al., 2012).

Trait variation is the outcome of a combination of ecological, evolutionary and developmental factors, and the spatio-temporal scale of environmental variability determines whether selection will favour phenotypic plasticity, adaptation or some combination (van Tienderen, 1991). As a result, measurements of trait variance across scales are commonly used to detect underlying drivers of diversity and community assembly. Although trait dispersion studies provide phenomenological evidence of mechanisms that maintain diversity at local and biogeographical scales, they are not generalizable or predictive (Adler et al., 2013). Identifying how trait variation is influenced by environmental variability offers a promising alternative.

2 | ENVIRONMENTAL VARIABILITY IN SPACE AND TIME

We argue that environmental variability is central to understanding variance scaling because the magnitude of environmental variability changes with scale. In other words, an increase in spatial and temporal scales is often associated with an increase in environmental variability, which, in turn, should influence trait variance, not only trait means. Environmental variability encompasses spatial and temporal variation, which play important roles in ecological and evolutionary processes that promote variability across and within natural communities, including natural selection, coexistence (Chesson, 2000), the evolution of specialization (Levins, 1968), persistence (Fjeldså et al., 2012) and diversification (Rosenzweig, 1995). Spatial environmental variability (environmental heterogeneity; *sensu* Ricklefs, 1977) is related to the spatial complexity or structure of the habitat and variability in resources and niches (Stein et al., 2014). Temporal environmental variability considers the variation of resources and environmental conditions over time (Menge & Sutherland, 1976). The effects of spatial and temporal environmental variability on species diversity are well studied across scales (MacArthur & MacArthur, 1961; Rosenzweig, 1995; Stein et al., 2014), whereas the influence of environmental variability on trait variation across scales is less understood (Biswas et al., 2016; Blonder et al., 2018; Price et al., 2017; Stark et al., 2017).

At small spatial scales, environmental heterogeneity can affect the persistence of different species among patches (Chesson, 2000) through mechanisms that are themselves dependent on spatial variation (e.g., spatial storage effect, growth–density covariance; Amarasekare, 2003). That is, homogeneous patches are expected to favour a single species or multiple functionally similar species reflecting competitive hierarchies or shared adaptations to abiotic conditions (Kraft et al., 2014; Mayfield & Levine, 2010). Based on coexistence theory and the environmental heterogeneity hypothesis, greater environmental heterogeneity at small scales provides opportunities for resource partitioning, stabilizing coexistence among species, leading to greater species richness and, presumably, trait variation (Amarasekare, 2003; Chesson, 2000; Levins, 1968; Questad & Foster, 2008; Ricklefs, 1977; Rosenzweig, 1995; Spaak & De Laender, 2021; Stark et al., 2017). Yet, negative effects of environmental heterogeneity on trait variation can also emerge at small scales, owing to increased extinction risk (Kadmon & Allouche, 2007), or across trophic levels (Deraison et al., 2015). At larger spatial scales (i.e., regional to continental), environmental heterogeneity often increases, leading to increased species richness (Udy et al., 2021) and trait variation (Kang et al., 2018; Ribeiro et al., 2022; Vanneste et al., 2019). In this case, trait variation at biogeographical scales can reflect eco-evolutionary drivers of species distributions (Figueiredo et al., 2019; Violle et al., 2014), allowing the recasting of biodiversity theories, such as the latitudinal diversity gradient, in terms of environmental variability and its effects on trait variation across scales (e.g., Lamanna et al., 2014). We are only beginning to understand the importance of environmental heterogeneity on species coexistence and trait variation at smaller scales (Adler et al., 2013; Bergholz et al., 2017; Yoshiyama et al., 2009), and there is evidence that environmental heterogeneity influences trait variation at regional and biogeographical scales, too. Nevertheless, the contribution of environmental heterogeneity to species sorting and coexistence is likely to be scale dependent (Field et al., 2009; Stein et al., 2014). Understanding how environmental heterogeneity affects trait-based assembly of species from local to biogeographical scales is therefore necessary.

Climatic variability is a temporal case of environmental heterogeneity. The climatic variability hypothesis predicts greater physiological and morphological trait variation and broader physiological tolerance with increasing climatic variability (Addo-Bediako et al., 2000; Janzen, 1967). At small temporal scales (e.g., hours, days), organisms partition their niches according to temporal microclimates. Temporal microclimatic variation can be an important driver of trait variation through increased phenotypic plasticity, species diversity and coexistence (De Frenne et al., 2021). For example, forest patches with less canopy cover experience greater temporal microclimatic variability than closed-canopy forests (Chen et al., 1999), which results in greater variation in traits related to light interception in open-canopy forests, promoting niche partitioning and alleviating competitive interactions (Pronk et al., 2007). Over longer time scales (e.g., decadal), temporal fluctuations in the environment can increase total trait variation when three conditions are met: species respond differently to environmental variation; competition strength covaries with the environment; and functional trait strategies limit competition when conditions are unfavourable (the storage effect; Chesson, 2000). Moderate and extreme disturbances (e.g., hurricanes) can increase trait variation rapidly over time compared with mature, undisturbed forests, which are characterized by temporally stable environmental conditions (Swenson et al., 2012). Likewise, seasonality has been shown to increase trait variation in both terrestrial (Hulshof et al., 2013) and aquatic (Floury et al., 2018) Systems. At this temporal scale, ontogenetic or developmental changes can become a key source of trait variation. Shifts in functional traits during ontogeny have typically been associated with changes in environmental requirements as organisms grow, as has been shown in both animals (Werner & Gilliam, 1984) and plants (Niinemets, 2006). At even longer time-scales (e.g., centuries to millennia and longer), temporal fluctuations are an important driver of species evolution and the evolution of specialization and resource partitioning (Anderson et al., 2011; Levins, 1968). Precipitation seasonality, for example, predicted plant trait variation across tropical dry and wet forests in Mexico and Costa Rica, pointing to the evolution of temporal resource partitioning among coexisting species in seasonally dry forests (Hulshof et al., 2013). Furthermore, regional variation in plant traits was positively related to climatic variability (Diaz et al., 1998; Lamanna et al., 2014; Šímová et al., 2015; Swenson et al., 2012). Climatic variability can also drive plant trait variation at biogeographical scales, and the ubiquity of this pattern might be underappreciated (Wieczynski et al., 2019). Islands represent great examples of rapid diversification events that have resulted in large trait variation across different taxa over relatively large temporal scales (e.g., *Anolis* lizards, Hawaiian Ohi'a lehua birds, *Drosophila* flies). Taken together, evidence from coexistence theory and functional biogeography suggests that temporal environmental variation influences trait variation at both small (days, season) and large (decadal to geological) time-scales. Thus, measuring temporal environmental variation across days to millennia and determining its importance for trait variation is a pressing interdisciplinary challenge (Suárez-Castro et al., 2022).

3 | POWER LAWS FOR QUANTIFYING VARIANCE SCALING

The relative importance and strength of spatio-temporal environmental variability for patterns of trait variation across scales could be examined using a wide range of existing empirical models used for quantifying taxonomic variability in species richness, spatial and temporal autocorrelation and nonlinearities (Table 1). Doing so could lead to the development of a more generalizable and predictable trait-based framework. Power laws are especially compelling because they are ubiquitous in the natural world, from landslide size distributions to metabolic scaling. Two power laws in particular, the species–area relationship and Taylor's power law, are cornerstones of ecology. The species–area relationship indicates changes in variance (in species composition) with changes in scale and accounts for a large part of early ecological research (Preston, 1960; Rosenzweig, 1995). Taylor's power law measures variance in population densities with changes in scale (Hanski, 1987; Hurlbert, 1990; Taylor, 1961; Xiao et al., 2015) and is widely observed across disparate taxa and systems. We propose that variation in scaling exponents of these two power laws is influenced by spatio-temporal environmental variability, creating mechanistic linkages between environmental variability, trait variance and scale.

The species–area relationship (SAR) describes how species richness increases with spatial scale, is one of the most studied patterns in ecology (Rosenzweig, 1995) and can be approximated by the power function:

$$S = CA^z,$$

which is often expressed in the linear form: $\log S = \log C + z \times \log A$, where S is the number of observed species in area A, C is an empirically derived constant and z is the slope of the linear equation or spatial scaling exponent. The temporal analogue of the species–area relationship, the species–time relationship, describes how the number of species in a given area increases with the time span of sampling (Carey et al., 2007; Preston, 1960; Rosenzweig, 1995) but has received considerably less attention. It takes a similar form: $\log S = \log C + w \times \log T$, where S is the number of species observed in time T, and the scaling exponent is changed to w (Adler & Lauenroth, 2003; van der Gast et al., 2008). The species–time–area relationship (STAR) is defined by Adler et al. (2005) as:

$$\ln(S) = z_1 \ln(A) + w_1 \ln(T) + u \times \ln(A)\ln(T) + \ln(c)$$

where z_1 is the slope of the SAR at a temporal scale of one year, w_1 is the slope of the STR at a spatial scale of 1 m^2, u represents the interaction between area and time, and c is a constant has been extended to other dimensions of biodiversity (e.g., phylogenetic diversity; Swenson et al., 2013), including functional diversity (Alirezazadeh et al., 2021; de Camargo et al., 2019; Dias et al., 2020; Karadimou et al., 2016; Mazel et al., 2014; Smith et al., 2013; White et al., 2018; Whittaker et al., 2014). These studies report increased trait variation with increasing area, suggesting that increased environmental heterogeneity at larger spatial scales is key for determining patterns of trait variation not only for plant communities but also for other organisms. This is promising because it suggests a potential generality between area, environmental variability and trait variation that could be used to develop testable predictions (e.g., Table 2).

We propose that variation in slopes among trait variance–area or variance–time relationships can help us to differentiate ecological mechanisms that promote trait variation across spatio-temporal scales. For example, if the role of large-scale processes, such as long-distance dispersal and evolution, becomes dominant over that of small-scale processes (e.g., interspecific competition for resources),

TABLE 1 Empirical models for quantifying various aspects of trait variance scaling

Model	Description	Application
Negative binomial distribution	The mean, *x*, and the aggregation parameter, *k*, are related to variance, s^2, by: $s^2 = x + x^2/k$. Importantly, the parameter *k* can be expressed as a function of measurement scale, *L*: $k = \alpha \times L^\beta$ (Taylor et al., 1979)	Estimation of *k* at different scales could be used to calculate an expected trait variance at one scale based on an observed variance at another. The negative binomial distribution could also be used to understand how trait variance mediates differences in abundances across species, environments and scales (Warton et al., 2015)
Moran's *I*	Spatial or temporal correlation in environmental variables is likely to underlie spatial or temporal correlation of trait values, or synchrony, a phenomenon known as the "Moran effect", measured by Moran's *I* (Ranta et al., 1997). Moran's *I* computes the deviation between a variable as a function of spatial distance and decomposes spatial autocorrelation into positive and negative components that reflect large- and fine-scale processes	Moran's *I* computes the deviation between a variable (e.g., species occurrences) as a function of spatial distance (Legendre & Fortin, 1989; Ranta et al., 1997) and decomposes spatial autocorrelation into positive and negative components that reflect large- and fine-scale processes. Moran's *I* could thus be used to understand the behaviour and mechanistic drivers of trait variance by comparing environmental variability with trait variability across scales (e.g., Biswas et al., 2016)
Jensen's inequality	If function $f(x)$ is nonlinear, the average of the function is not equal to the function of the average: $\overline{f(x)} \neq f(\bar{x})$ (Jensen, 1906). Jensen's inequality implies that environmental variance can have substantial and predictable biological consequences on ecological variables (including populations, species and traits) that cannot be inferred from average environmental conditions (Ruel & Ayres, 1999)	Jensen's inequality has important implications for the prediction of how increasing environmental variability will impact performance and optimal trait variance and for estimation of the error involved in averaging traits across different scales (Denny, 2017). Thus, Jensen's inequality could quantify the effect of environmental variability on both the mean and the variance of trait values without the need to manipulate environmental variability (e.g., Wetzel et al., 2016)
Species–time–area relationship (STAR)	The linear form of the species–area relationship is described by: $\log S = \log C + z \times \log A$, where *S* is the number of species in area *A*, *C* is an empirically derived constant and *z* is the slope or spatial scaling exponent. The species–time relationship takes a similar form	We argue that variation in slopes among trait variance–area or variance–time relationships is indicative of ecological mechanisms that promote trait variation and is driven by environmental variability across spatio-temporal scales
Taylor's power law	Taylor's power law (Taylor, 1961) states that variance, s^2, is proportional to the mean, *x*, raised to an empirically determined exponent, *b*: $s^2 = ax^b$	The magnitude of *a* is dependent on scale, and the exponent *b* can quantify changes in variance with changes in scale (Horne & Schneider, 1995)

TABLE 2 Summary of priority research questions including processes that might lead to deviations from expected, with predictions and examples of tractable systems for testing variance scaling theory

Question	Prediction	Tractable systems
Is trait variance correlated with environmental variability?	Environmental variability impacts the slope and intercept of trait-based power laws	Long-term monitoring of successional communities; regions of complex microenvironments; censuses of short-lived taxa
Species–time–area relationship (STAR): Do space and time interact in the accumulation of trait variance; can space and time be substituted for one another?	Existing evidence suggests that spatial environmental variability is more influential for predicting trait variance than temporal environmental variability	Successional forest dynamics plots [e.g., the tropical dry forest San Emilio ForestGEO plot, subtropical wet forests of the Luquillo long-term ecological research (LTER) site and Cedar Creek, among others] and the long-term monitoring of aquatic and terrestrial taxa
Taylor's power law: Does environmental variability alter the slope of Taylor's power law?	Environmental variability should result in greater trait variance for a given mean and thus decrease *b*, the slope of Taylor's power law	Short-lived taxa (e.g., annual plants, insects, aquatic taxa) and other systems for which trait means and variances can be measured at high sampling intensities
Deviations: How does intraspecific variation impact trait-based power law slopes?	Fine-scale environmental variability should result in greater trait variance and thus shallower trait-based STAR slopes and steeper Taylor's power law slopes	Regions with complex microenvironmental variability (e.g., H. J. Andrews LTER and other areas of topographically complex terrain)
Deviations: How do different metrics of trait variance behave with increasing spatial and temporal scales?	The additive nature of species count data seems key to resolving metric consensus, and Hill numbers appear promising because they are intuitive and facilitate comparisons across different dimensions of biodiversity	Metric consensus will require simulations and statistical approaches using data from a broad range of taxa and tractable systems

we should expect to observe a positive slope between trait variance and increasing spatial scale (Figure 1). Likewise, increasing temporal scales should result in greater trait variance, resulting in shallower (less positive) trait variance–area slopes (Figure 1). On the contrary, if small-scale processes (e.g., interspecific competition) that limit trait variation dominate over large-scale processes, we should expect the opposite pattern.

Emerging research suggests that there is merit in exploring trait variance–area and variance–time relationships further. Variance partitioning analyses indicate that both intra- and interspecific foliar trait variance increase with spatial scale (Messier et al., 2010). Indeed, larger patches had greater trait variance among herbaceous plants (Forsyth & Gilbert, 2021), although the opposite was true for seed size in fragmented forest patches (May et al., 2013). In tropical bird communities and global mammal communities, trait variance increased with increasing area, approximating a power law (de Camargo et al., 2019; Mazel et al., 2014). This suggests that trait variation is sampled rapidly as area increases and that species become functionally redundant such that much more area is required to detect functionally rare species (see Umaña et al., 2017). Thus, as area increases, the range of resources also increases, but some resources are more available and over-used while other resources are rare and under-used (Karadimou et al., 2016). In contrast, trait variation across temporal scales tends to be relatively stable (de Camargo et al., 2019; White et al., 2018). In temporally variable environments, functionally redundant species should show asynchronous responses to environmental fluctuations (via the storage effect), thus buffering against large fluctuations in species and functional diversity (the insurance hypothesis; Loreau et al., 2003) across temporal scales. However, Karadimou et al. (2016) suggested that the increase in trait variance with increasing area or time is much more nuanced and depends on the skewness of abundance distributions (i.e., many more rare species than common ones), the location of species in trait space (i.e., at the centre or periphery of trait space) and the metric used (i.e., functional richness, evenness and divergence). For example, evidence for increasing trait variance with increasing area appears to be less common when functional divergence is used as the metric of trait variance, and there seems to be more support for decreasing or invariant functional divergence with increasing area (Suárez-Castro et al., 2022). We expect future work to shed more light on these variance metric-dependent complexities.

These studies are promising, even if they appear contradictory, because they suggest that there are extrinsic constraints on the total trait variance of an ecological system and that spatial environmental variability is more influential than temporal environmental variability (as suggested by Snyder, 2008) for predicting trait variance. Preston's original work suggests that spatial and temporal biodiversity patterns (and, presumably, spatial and temporal trait variance patterns) should be closely linked, that there should be an area–time interaction and that space and time can be substituted for one another (Preston, 1960). Thus, research should focus on determining whether space and time interact in the accumulation of trait variance, whether this is determined by environmental variability (in space or time) and whether space and time can be substituted for one another such that one might use spatial heterogeneity in trait variance to predict temporal heterogeneity in trait variance and vice versa (Table 2). The linkage between spatial and temporal scaling exponents is especially compelling because it might provide insight into underlying community dynamics that traditional trait dispersion studies across scales cannot convey.

A non-trivial challenge in resolving the scaling of trait variance with increasing area or time is achieving metric consensus. Trait variance can be measured through different metrics, including variance *sensu stricto*, coefficient of variance, community-weighted variance, functional dispersion, evenness, richness, Rao's Q index, convex hull

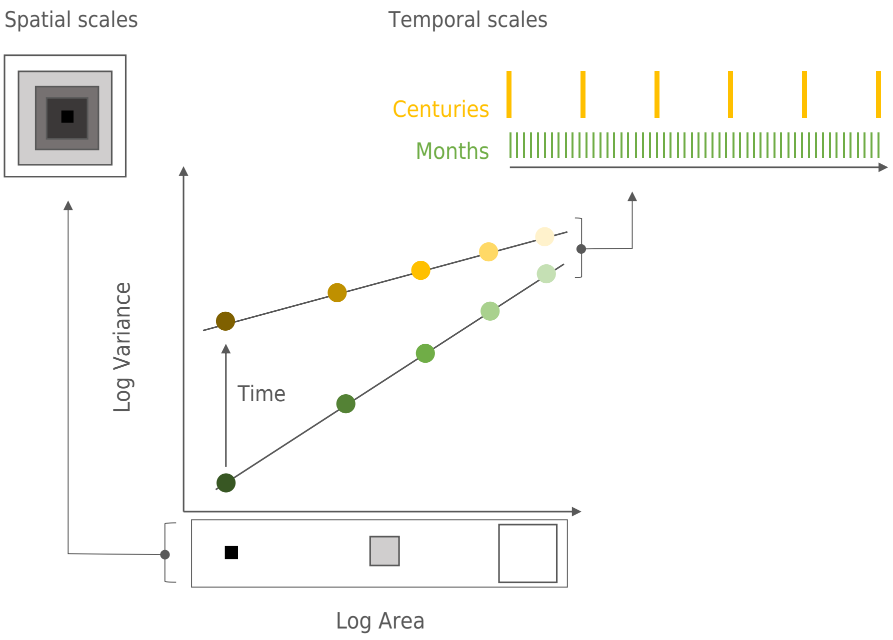

FIGURE 1 A positive slope between trait variance and increasing spatial scale emerges when large-scale processes, such as dispersal and speciation, become dominant over small-scale processes in generating trait variation. Temporal environmental variability should increase variance differentially at small spatial scales, resulting in shallower trait variance–area slopes. Differences in the intensity of colours represent differences in spatial scales, while the differences between green and orange patterns represent differences in temporal scales.

volume, etc. These metrics exhibit different behaviours and depend on species abundance and richness, which is likely to lead to discrepancies across metrics when evaluating the trait variance–time or variance–area relationships. In addition, the additive nature of species count data and the underlying point processes (i.e., the distribution of individuals in space) underlie the species–area relationship, but this might not apply to many trait variance metrics. One approach is to use a unified set of taxonomic and functional (and phylogenetic) diversity indices based on Hill numbers, as Mazel et al. (2014) have done, which fulfils statistical constraints of replication and is intuitive. This also makes it easier to compare slopes among different dimensions of biodiversity (e.g., taxonomic, functional). Another approach is to fit different point process models, to generate null communities and to compare simulated communities with observed ones at varying scales, as was done by Wang et al. (2013). Although more theoretical work is needed, the spatio-temporal accumulation of trait variance is intriguing, with implications for both ecological theory and biodiversity conservation.

In addition to the species–area relationship, the positive relationship between the mean and variance of population densities is one of the most widely observed empirical patterns in ecology (Hanski, 1987; Taylor, 1961; Xiao et al., 2015), and exhaustive reviews have been published on this topic (e.g., Hurlbert, 1990). Taylor's power law (Taylor, 1961) states that variance, s^2, is proportional to the mean, x, raised to an empirically determined exponent, b:

$$s^2 = ax^b.$$

The magnitude of a is dependent on the sampling scale (spatial or temporal), and the exponent b can quantify changes in variance with changes in scale (Horne & Schneider, 1995). In general, the empirical scaling exponent (slope) varies between one and two (Kendal, 2004), which, we argue, is driven by spatio-temporal environmental variability. Although Taylor argued that aggregation was key to understanding the mechanisms underlying the variance–mean relationship (and b is strongly tied to spatial aggregation; He & Gaston, 2003), others have argued that demographic and environmental stochasticity can produce similar patterns (Arruda-Neto et al., 2012; Kendal & Jørgensen, 2011) and can arise from statistical constraints (Cohen & Xu, 2015; Xiao et al., 2015). However, variation in b, a measure of aggregation, cannot be attributed to numerical constraints alone and is likely to have ecological significance (Xiao et al., 2015).

We propose that stable, homogeneous environments should favour lower trait variance reflecting habitat or resource specialization (Levins, 1968). In contrast, temporally variable and spatially heterogeneous environments should favour greater trait variance. Specifically, increasing spatio-temporal variability with scale should result in steeper slopes between $\log_{10}$-transformed mean and $\log_{10}$-transformed variance. This prediction assumes that increasing environmental variability (in space or time) increases the influence of evolutionary processes promoting diversification or source–sink dynamics over local-scale mechanisms. Thus, when regional processes become more important than local-scale processes (e.g., interspecific competition) with increasing spatio-temporal scales, the slope between means and variances should increase (Figure 2, $b = 2$). That is, for a given mean, variances should be greater (Kilpatrick & Ives, 2003). In contrast, at small spatio-temporal scales, variances should be smaller for a given mean (Figure 2, $b = 1$), limiting the degree of trait overlap (Kilpatrick & Ives, 2003), because strong interspecific competition should lead to a reduction of niche widths. Hanski (1987) argued that the slope of Taylor's power law is influenced by dispersal and the degree of correlation among local population dynamics such that the slope is greater for dispersal-limited species patchily distributed among different habitats, resulting in greater variance in abundance (i.e., lower synchrony) for a given mean. In a trait-based context, spatio-temporal environmental variability should promote greater asynchrony and thus greater trait variance, reflecting a larger total trait space for a given mean. Thus, the slope of Taylor's power law might be a suitable measure of changes in trait and niche space (Oliver et al., 2012) with increasing environmental variability across scales.

Taylor's power law has been applied predominantly to population means and variances, and the relationship between trait means and variances and spatio-temporal scales is much less studied (Blonder et al., 2018; Shi et al., 2019; Ulrich et al., 2021; White et al., 2018). However, the variance–mean relationship seems to hold for functional traits, and variation in scaling coefficients appears environmentally driven. Across crops as diverse as maize, wheat, tomato and soybean, crop yield variance increased with mean crop

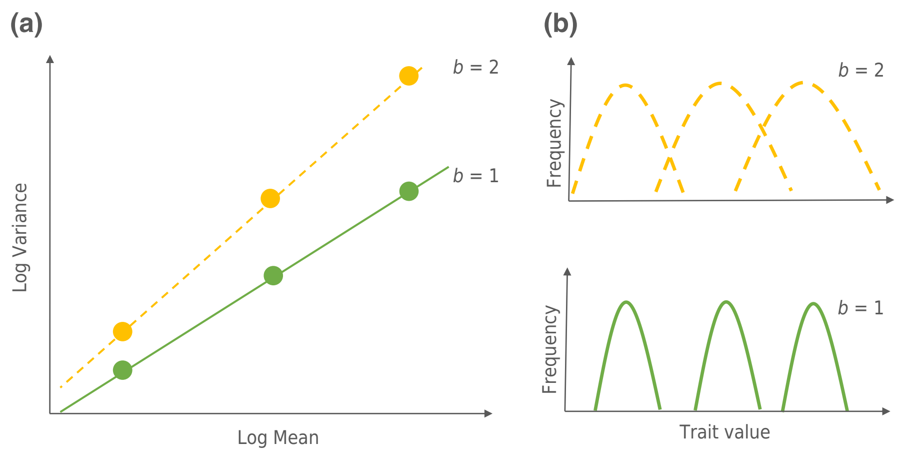

FIGURE 2 (a) Stable, homogeneous environments should favour lower trait variance, reflecting strong hierarchical competition, density dependence or the evolution of specialization (slope $b = 1$, in green). In comparison, spatio-temporal environmental variability should favour greater trait variance (slope $b = 2$, in orange). Thus, (b) for a given mean, variances should be greater with increasing spatio-temporal environmental variability.

yield according to Taylor's power law, and this relationship persisted across scales (across species, environments and globally; Döring et al., 2015). Additionally, the variance–mean relationship of metabolic rates across tropical tree communities followed Taylor's power law (Xu et al., 2021), as did measures of leaf asymmetry (Wang et al., 2018). In another example, trait means and variances were well described by Taylor's power law for wood density, plant height, fruit size, leaf thickness, foliar C/P ratio and foliar C/N ratio, but not for seed size, specific leaf area or leaf tannin and phenol content (Ulrich et al., 2021). In their study, the scaling exponent, *b*, varied across traits and exhibited environmentally driven variation. Although the spatial extent of their study was large (across latitude), we suggest that future work should examine trait variance–mean scaling explicitly across spatial and temporal scales.

The disparate sampling methodologies and prevalent data aggregation in trait-based ecology are real challenges for examining variation in slopes of Taylor's power law at varying spatial and temporal scales. Based on simulation studies, recommendations for testing Taylor's power law might preclude the use of existing trait data from global databases. To study variance in population densities, for example, the total number of organisms within a sample should be >15, and the density of organisms between samples should vary by at least two orders of magnitude (Clark & Perry, 1994). How these constraints translate to trait applications should be determined. Individual-centric sampling approaches (as advocated by Baraloto et al., 2010; Clark et al., 2011; Kraft et al., 2014; Swenson, Worthy, et al., 2020; Yang et al., 2018) might be necessary. Alternatively, instead of individual researchers measuring traits on thousands of individuals and species across multiple sites, trait sampling networks could bypass some of these challenges by coordinating a standard set of trait variance measurements world-wide; for example, by developing a sampling protocol for regionally and globally distributed plot networks (e.g., National Ecological Observatory Network, ForestGEO, among others). These dual approaches could quantify Taylor's power law definitively and determine the influence of environmental variability on trait variation across scales.

Another challenge is that some traits will not be responsive to environmental variation (e.g., Kraft et al., 2015; Thuiller et al., 2010; Wright et al., 2010), probably owing to physiological constraints limiting trait variation or because the functions linked to those traits are not relevant for acquiring the resources changing along a given gradient; therefore, it is important to identify traits that are linked mechanistically to changing environmental factors and to use a combination of traits (e.g., via multivariate trait axes) to capture the multidimensionality of niches (Kraft et al., 2015; Muscarella & Uriarte, 2016). Failure to do so might result in patterns that deviate from and obscure the expected power-law relationship. Additionally, when deviations do occur, further investigation into the underlying processes (e.g., phenotypic plasticity) could reveal important mechanisms contributing to variance scaling. For example, the finding that much of the global variation in traits is found locally (e.g., Cornwell & Ackerly, 2009; Kraft et al., 2008; Westoby et al., 2002) suggests that multiple viable strategies co-occur (Brown et al., 2022; Umaña et al., 2021) and might be a result of underlying (albeit unmeasured) microenvironmental heterogeneity. High trait variation at local spatial scales would result in shallower-than-expected slopes between trait variance and scale. Nevertheless, deviations from the expected power-law relationship serve as useful test cases for understanding the ecological and evolutionary drivers of trait variation.

4 | TRACTABLE SYSTEMS FOR QUANTIFYING VARIANCE SCALING

We identify three tractable systems for quantifying slopes of trait-based STAR and Taylor's power law: successional forests, long-term monitoring networks and censuses of short-lived taxa. We focus our selection on three criteria. First, measurable traits should be strongly linked to organismal fitness and population dynamic processes. Second, environmental variables should be quantified at scales appropriate to the organism(s) of interest. Third, both trait and environmental variation should be measurable at nested spatial and temporal scales. In particular, we propose that measurements of organismal traits coupled with measurements of abiotic variables could determine: (1) whether trait variance is correlated with environmental variability and whether environmental variability alters the slope or intercept of the variance–time–area relationship or Taylor's power law, as predicted by theory; (2) the proportion of trait variance explained by spatial or temporal environmental variability at each scale (as in Liu et al., 2013); and (3) the scale at which spatial or temporal environmental variability has the greatest impact on trait variation.

First, successional forests encompass environmental variability in both space and time, ideal for quantifying the relationship between trait variance and scale. During succession, environmental conditions influence and are influenced by changes in plant composition and structure. The most evident feature of succession is the marked shift in species and functional composition through time resulting from interspecific trade-offs between resource use and acquisition (Grime, 2006; Pacala & Rees, 1998) that promote coexistence (Amarasekare, 2003). These successional dynamics result in faster shifts in species composition and traits in successional forests compared with old-growth or less-disturbed forests (Swenson et al., 2012). At early successional stages, species specialize on recently disturbed environments (e.g., high light) and tend to be superior colonizers (e.g., high fecundity, recruitment or dispersal). In comparison, late successional dominants specialize on undisturbed patches and resist invasion by early successional species. The interplay between succession and disturbance thus creates a mosaic of aggregated patches of different ages, ensuring the coexistence of species with differing functional strategies and promoting greater trait variation at increasing spatial scales (Falster et al., 2017). Therefore, the slopes of trait-based STAR and Taylor's power law should change more abruptly in communities undergoing succession (Box 1).

Examples of successional systems can be found in both temperate and tropical regions. One such system is the mosaic of secondary successional tropical dry forests across the Pacific lowlands of

BOX 1 Trait variance across spatio-temporal scales during succession

The successional process represents a particular case where temporal and spatial environmental variation are magnified at small scales. Succession involves the gradual change in species (and trait) composition related to changes in light availability and other resources (Grime, 2006). By taking advantage of the models discussed in the main text (the trait variance–time–area relationship and Taylor's power law), we can characterize patterns of trait variation during succession. Here, we describe potential scenarios related to the trait variance–time–area model.

Although shifts in resource-acquisition strategies during succession depend on the system (tropical dry forests vs. tropical wet forests), generalities in trait variation still occur. For example, early and late successional stages tend to be dominated by a single type of species (i.e., in tropical wet forests, pioneer acquisitive species dominate early successional stages, whereas shade-tolerant conservative species dominate late stages). In contrast, intermediate stages exhibit a combination of species reflecting diverse resource acquisition strategies (including both acquisitive and conservative strategies). This should result in a peak of trait variance at intermediate levels of succession (Figure 3a,b).

By implementing the trait variance–time model, we expect to find a positive relationship between $\log_{10}$-transformed temporal grain and trait variance that would indicate an accumulation of species and traits as succession progresses, with a saturation point following intermediate stages. One difference between this pattern and the pattern described for non-disturbed forests (Figure 1) is that the scale for observing change would be shorter for the forest undergoing succession (Figure 3c).

The trend describing the trait variance–area relationship should thus deviate from the predictions presented for old-growth forests (Figure 1). Succession increases environmental heterogeneity at small spatial scales, when a mosaic of forest patches at different successional stages constitutes the sampled community (Figure 3b,d). Thus, small-sized forest patches can exhibit a wide range of trait variance reflecting differences in successional ages among patches and obscuring expected power-law distributions (Video S1). In increasingly larger patches, however, trait variance should converge, encompassing the total trait variance of the entire landscape (Figure 3d).

Mesoamerica. In Mexico, for example, plant trait variance was explained by spatial heterogeneity in environmental conditions across a chronosequence of different-aged patches (Lebrija-Trejos et al., 2010). Likewise, in Costa Rica, wood density variance and functional richness (integrating wood density, specific leaf area, foliar CNP and carbon isotope composition) peaked in intermediate-aged forests (Becknell & Powers, 2014). Chronosequences are useful for understanding temporal changes that occur during succession via the spatial heterogeneity created by different-aged patches. Although temporal scale is implicit in chronosequences, as in the above two studies, research from both regions suggests, first, that trait variance peaks when environmental heterogeneity peaks and, second, that this occurs during intermediate successional stages. However, because succession encompasses both spatial variation among different-aged patches and temporal variation within patches as successional processes occur, studies that measure both (such as in the San Emilio ForestGEO plot; Swenson, Hulshof, et al., 2020) are even better suited for quantifying variance scaling. Other systems that simultaneously consider spatial and temporal successional dynamics include the Cedar Creek Ecosystem Science Reserve (formerly the Cedar Creek Natural History Area), Minnesota. The spatial scales and environmental variation of the old-field chronosequence and the long-term fire-frequency experiment in oak-savanna woodlands of Cedar Creek present several opportunities for quantifying trait variance and environmental variation across spatio-temporal scales. For example, Willis et al. (2010) showed that increasing phylogenetic and functional turnover among plots with increasing spatial scale was explained by increasing environmental variation at larger scales. They argued that the steepness of the environmental gradient (and thus the magnitude of environmental variation) determined the strength of environmental filtering. In the context of trait-based power laws, the steepness of the environmental gradient is likely to impact the magnitude of the slope between trait variation and scale. Given two similar-sized patches, for example, the patch exhibiting a stronger environmental gradient should exhibit a steeper variance scaling slope because trait variation accumulates faster with increasing area as increasingly differing environmental conditions are encompassed. A less pronounced environmental gradient should therefore exhibit a shallower slope.

Another system meeting the above criteria is the successional subtropical wet forests of Luquillo, Puerto Rico. The Luquillo long-term ecological research (LTER) site is one of the longest continuously studied forests in the tropics, where research has focused on natural and anthropogenic disturbance and succession (Zimmerman et al., 2021). In this system, disturbance and land-use history drive patterns of trait and environmental variation across spatio-temporal scales (Swenson et al., 2012; Thompson et al., 2002; Umaña et al., 2021; Uriarte et al., 2009), which provides a useful backdrop for disentangling the effects of temporal versus spatial environmental variability. For example, Hogan et al. (2018) showed that population growth and species mortality were more temporally dynamic in Luquillo compared with other frequently disturbed tropical forests, suggesting that temporal environmental variability might be higher too. In comparison, spatial heterogeneity in soil moisture and light availability mediated seedling survival (Uriarte et al., 2018) and forest regeneration (Comita et al., 2009), suggesting that both spatial and temporal environmental variability are important determinants

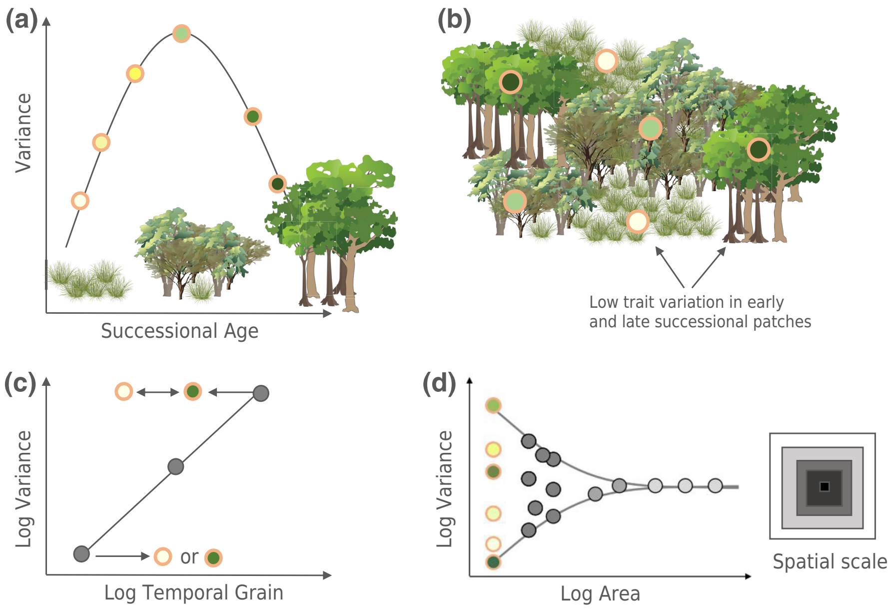

FIGURE 3 Succession integrates environmental variability in space and time. (a) Environmental heterogeneity is low at both early and late successional stages and high at intermediate stages, resulting in a unimodal pattern of trait variation with increasing age. (b) A mosaic of forests in varying successional stages is thus likely to obscure the expected power-law distribution between trait variation and (c) temporal grain or (d) spatial scale. Small forest patches can exhibit low to high values of trait variation (circles outlined in orange) depending on successional age (as depicted in a,b), converging on a single value at large spatial scales that reflects the total trait variation of the landscape. Plant symbols credit: Integration and application network (ian.umces.edu/media-library).

of community assembly. Quantifying the contributions of spatial and temporal environmental variability to variance scaling across nested scales could provide key insight into the relative role of spatial versus temporal processes on trait variation. Owing to the interplay of succession and disturbance that has resulted in a mosaic of different-aged forest patches, we predict that spatial environmental variation will have a greater effect than temporal environmental variation in this site owing to persistent legacies of past land use (as in Perring et al., 2018, among others). In addition to plants, animals (e.g., birds, bats) are also intrinsically linked to successional processes in secondary forests (Dent & Estrada-Villegas, 2021; Whittaker & Jones, 1994), and research has shown that community functional composition responds to both temporal and spatial environmental variation associated with succession and disturbance (Farneda et al., 2018; Matuoka et al., 2020). These systems offer additional opportunities to quantify variance scaling across taxa.

Second, long-term monitoring networks (as in the above examples) are generally well suited for characterizing trait variance across scales using the models presented here. Detailed site and vegetation data coupled with ground- and satellite-based sensors provide opportunities for merging intensively sampled traits to spatial and temporal environmental variability measured at high resolutions and at nested scales, as in the National Ecological Observatory Network (NEON). The long-term measurement of canopy and subcanopy microclimates in H. J. Andrews Experimental Forest (a NEON and LTER site), for example, creates opportunities for identifying emergent trends between trait and environmental variation. Research has shown that forest structure mediates microclimate (Frey et al., 2016), influencing plant phenology (Ward et al., 2018) and, probably, trait variation. Long-term monitoring in other mountainous or topographically complex terrain (e.g., alpine landscapes) might help to identify the underlying drivers of trait-based power laws. Small-scale microclimatic variation in these systems promotes species richness and turnover by creating variation in assembly processes and selection pressures. For example, microenvironmental heterogeneity was an important driver of functional composition in alpine communities in Colorado (Blonder et al., 2018; Stark et al., 2017) and Norway (Opedal et al., 2015), suggesting that fine-scale environmental variation should result in greater trait variance at small scales, thus resulting in shallower trait-based STAR slopes and steeper Taylor's power law slopes. Although environmental variation can also promote trait variation within species through ecotypic differentiation, phenotypic plasticity or some combination of the two, small-scale microclimatic variation might preclude genetic differentiation when dispersal distances are larger than the scale of environmental variation. Thus, fine-scale environmental heterogeneity should favour phenotypic plasticity (Sultan, 1987). Because of this, topographically complex regions are important test beds for quantifying how intraspecific trait variation influences trait-based power law slopes.

Long-term monitoring of aquatic systems also meets the above criteria for measuring spatio-temporal variation in traits and the environment, and there is a rich history of doing so. Numerous studies have explored the responses of marine and freshwater communities and their functional composition over time. Some studies report that spatial environmental heterogeneity is more important for trait variation than temporal heterogeneity (e.g., Bremner et al., 2003; Hewitt et al., 2008; Pinel-Alloul et al., 1988). Other studies, however, report strong seasonal fluctuations in environmental conditions and trait variation (Edwards, 2016), strong temporal reductions in trait variation owing to disturbance (Edwards et al., 2013; Pomerleau et al., 2015) and increases in trait variation over time (Floury et al., 2018). Aquatic environments are likely to exhibit the trait-based power-law relationships proposed here and are ideal for determining the relative impact of temporal versus spatial environmental heterogeneity on trait variance of aquatic organisms.

Lastly, we propose that short-lived taxa are another focal group for examining ecological responses to environmental change at varying spatio-temporal scales. The shorter life spans and annual life-history strategies of many herbaceous plants, for example, relative to long-lived woody species, provide an opportunity to capture temporal dynamics over shorter time periods. Despite the advantages of studying shorter-lived plants, the herbaceous understorey has been largely neglected, particularly in the tropics (Gilliam, 2007; Murphy et al., 2017). The measurement of environmental resource gradients at increasing spatial and temporal scales, coupled with herbaceous plant distributions and dynamics, could shed light on variance scaling and the proximate mechanisms underlying its behaviour. In comparison, short-lived aquatic taxa (as in the examples above) might be even better positioned for addressing the questions posed here, particularly in laboratory settings (e.g., Bishop et al., 2022), because trait measurements can be linked to demographic processes and fine-scale spatio-temporal environmental variation across a wide range of taxa and environments (Martini et al., 2021). Quantification of variance scaling in these and other systems will require a combination of statistical and experimental approaches across gradients of environmental variability and mechanistic modelling of traits at nested spatio-temporal scales.

5 | THE PROMISE OF A UNIFIED THEORY OF TRAIT VARIATION

The demand for reliable predictions and, therefore, models is rapidly increasing in light of accelerating changes in spatio-temporal environmental variability. In the same way that geodiversity is used as a proxy for species diversity (Zarnetske et al., 2019), environmental variability might be a reliable proxy for functional diversity (Blonder et al., 2018; Stark et al., 2017), making it possible to identify functional diversity hotspots based on, for example, LiDAR-derived measures of environmental heterogeneity (i.e., canopy structural complexity or rugosity; Gough et al., 2019). Doing this, however, initially requires the establishment of quantitative linkages between environmental variability, trait variance and scale. Application of empirical models to quantify trait variance across scales could also aid in the discovery of general macroecological patterns, in addition to inferring the underlying mechanisms that vary with spatio-temporal environmental variability. The environmental heterogeneity and climatic variability hypotheses provide useful, albeit underused, frameworks for disentangling the proximate mechanisms underlying patterns of trait variance across scales. Empirical models, such as the STAR and Taylor's power law, can reveal additional generalities and facilitate prediction. Quantification of variance scaling does not require the development of new metrics. On the contrary, emerging evidence suggests that the broad characterization of trait variance using the models presented here would be worthwhile (Tables 1 and 2). Coordination of sampling efforts across nested spatio-temporal scales in combination with technological and methodological advancements could overcome inherent challenges of robust tests of the models presented here. In short, understanding the spatial and temporal dependencies of trait variance and its underlying determinants is a prerequisite for developing a unified theory of trait variation.

AUTHOR CONTRIBUTIONS

C.M.H. conceived the idea and wrote the first draft. M.N.U. contributed substantially to the ideas, organization, writing and editing of the manuscript. Both authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

This material is based upon work supported by the National Science Foundation under grant no. NSF CAREER #2042453 to C.M.H.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

No data were created or analysed in this manuscript.

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BIOSKETCH

Catherine M. Hulshof is a plant ecologist who uses empirical, theoretical and experimental approaches to understand community assembly processes across spatial and temporal scales. **María Natalia Umaña** is a forest community ecologist focused on addressing questions about community assembly and forest dynamics via the integration of information on intra- and interspecific trait data with demographic measurements.

SUPPORTING INFORMATION

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

How to cite this article: Hulshof, C. M., & Umaña, M. N. (2023). Power laws and plant trait variation in spatio-temporally heterogeneous environments. *Global Ecology and Biogeography*, *32*, 310–323. https://doi.org/10.1111/geb.13620