Title: Temporal turnover in species' ranks can explain variation in Taylor's slope for ecological timeseries

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Abstract:

The scaling exponent relating the mean and variance of the density of individual organisms in space (i.e. Taylor's slope: z_{space}) is well studied in Ecology, but the analogous scaling exponent for temporal datasets (z_{time}) is underdeveloped. Previous theory suggests the narrow distribution of z_{time} (e.g. typically 1 - 2) could be due to interspecific competition. Here, using 1,694 communities time series, we show that z_{time} can exceed 2, and reaffirm how this can affect our inference about the stabilizing effect of biodiversity. We also develop new theory, based on temporal change in the ranks of species abundances, to help account for the observed z_{time} distribution. Specifically, we find that communities with minimal turnover in species' rank abundances are more likely to have higher z_{time}. Our analysis provides a deeper mechanistic understanding of how species-level variability affects our inference about the stability of ecological communities.

Introduction

Our understanding of the temporal variability of populations or communities, which is of long-standing interest in ecology (Anderson *et al.* 1982; Bahram *et al.* 2015), often centers around a scaling relationship between the mean and variance of species' abundances (aka Taylor's Law, 1961). In a pioneering meta-analysis in 1961, L.R. Taylor proposed a general scaling relationship, referred to as Taylor's (power) law (hereafter TL), relating the variance (v) of population density with its mean (m): $v = am^z$, for values of a>0, z being called TL slope or exponent. This scaling relationship is ubiquitously observed for many taxa in nature (e.g., bacteria, fish, plants, insects, voles, etc.), and has also been applied outside of ecological systems (Eisler *et al.* 2008; Kalyuzhny *et al.* 2014; Taylor 2019). Although Taylor's law was originally developed for the analysis of spatial variation of population density (Taylor 1961), it is also highly relevant, but less often studied, in the context of temporal analyses of communities (reviewed by Cobain et al. 2019). In spatial analyses of density variation (TL_{space}), z_{space} is an index of the degree of patchiness of the population density of a single species among sites (i.e. metapopulations). Whereas, in temporal analyses of density variation (TL_{time}), z_{time} is an index of temporal aggregation of the abundance fluctuations of multiple species in a community (i.e., from the same site). The z_{time} exponent has been useful for assessing population persistence (Pertoldi *et al.* 2008; Kalyuzhny *et al.* 2014), the stability of crop yields (Döring *et al.* 2015), and fluctuations in fish stocks (Kuo *et al.* 2016; Xu *et al.* 2019; Segura *et al.* 2021).

Currently, understanding the importance of mean-variance fluctuation scaling (i.e. z_{time}) for making inferences from community dynamics is limited by uncertainty in i) the distribution of z_{time} in natural communities, ii) how z_{time} variability affects interpretations of community stability, and iii) the mechanisms underlying z_{time} variability. We address each of three gaps (referred to below as G1-G3). First, existing studies of natural communities have documented a limited range of variation in z_{time} (Cobain *et al.* 2019; Xu & Cohen 2019), but with the increasing availability of long-term community time series we can improve our inference about the distribution of z_{time} in nature.

Second, there is longstanding theory about how variation in z_{time} is relevant for interpreting community stability (Cottingham *et al.* 2001; Kilpatrick & Ives 2003; Kalyuzhny *et al.* 2014; Cobain *et al.* 2019; Zhao *et al.* 2019), but these interpretations are somewhat sensitive to mean variance scaling. Importantly, when z is greater than 1, the expected temporal variance of the total community abundance is less than that of a single population for that same mean abundance (Fig. 1), meaning that species-level variance increases nonlinearly in relation to mean abundances. This reduced variance arises because of the statistical averaging of independently varying population time series, which is known as the portfolio effect concept (hereafter PE) (Doak *et al.* 1998; Schindler *et al.* 2015). PE has been widely used to quantify the importance of species diversity for overall community stability (i.e., inverse of community variability, CV), but its interpretation depends on z_{time} for that community (Cottingham *et al.* 2001). For example, the magnitude of the PE is negligible when z_{time}~1, and increases with z_{time} (Fig. 1E, red line). This means that estimates of community stability (i.e. 1/CV), for a given species richness, decrease with the increase in z_{time} for a community (Fig. 1E, black line). Importantly, the consistently negative relationship between stability and z over a wide range of species diversity (Fig. 2A) means that the expected slope of the relationship between species richness and stability decreases substantially as z_{time} increases (Fig. 2A, inset). Often, PEs are estimated by comparing the overall community variability with the average variability of constituent populations, or, in a spatial context, by comparing the CV of overall the meta-population abundance with the average CVs of the subpopulations (Schindler *et al.* 2010). However, Anderson et al. (2003) showed that the above-mentioned approach is appropriate only for z_{time}=2, and they provided an alternate approach accounting for the potential heterogeneity of z among communities.

Third, existing theory can explain why z_{time} often varies between 1 and 2 (Taylor & Woiwod 1982; Tokeshi 1995; Xiao *et al.* 2015), but provides no general mechanistic explanation for the entire empirically observed range of z_{time}. For spatial TL context, several proposed mechanisms that explain variation in z_{space} have considered density dependence (Perry 1994), density-independent and stochastic population growth (Cohen *et al.* 2013), population synchrony (Cohen & Saitoh 2016), and random sampling from skewed distribution (Cohen & Xu 2015). Whereas for z_{time} proposed mechanisms have considered interspecific competition (Kilpatrick & Ives 2003), environmental variability (Cohen & Saitoh 2016), correlated reproduction (Ballantyne & J. Kerkhoff 2007), sampling error (Kalyuzhny *et al.* 2014), and limited sampling effort (Giometto *et al.* 2015). However, all of these previous studies have focused on explaining why z_{time} is typically less than 2, and only a few previous studies have provided a mechanistic explanation for why it can be greater than 2. In spatial models, z_{space} can be greater than 2 due to synchrony among metapopulations (Reuman *et al.* 2017) especially when they are rare (Ghosh *et al.* 2020a), and due to growing stochasticity (Cohen *et al.* 2013) or unexpected changes in a smoothly autocorrelated environment (Cohen 2014). In the case of z_{time}, only one previous study of a fish community found that environmental variability can lead to a size-based Taylor's slope greater than 2 (Cobain *et al.* 2019).

In this paper, we will address each of those three aforementioned gaps. First (for **G1**), we estimate the distribution of z_{time} (hereafter z) in nature by compiling thousands of long-term (>20 years) community time series (>15 species). Second (for **G2**), we use this dataset to explore the consequence of variation in z for interpreting stability in general, and the portfolio effect in particular. Third (for **G3**), we propose a novel and general mechanism that can help explain the wide range of z observed in natural communities. Our mechanism is based on how species' rank-abundance distribution in a community change over time (MacArthur 1957; McGill *et al.* 2007). Although the rank-abundance curves are widely studied in ecology (Whittaker 1965), their temporal turnover has not been previously explored in the context of explaining variation in mean-variance scaling among communities (i.e. variability in z).

Materials & Methods

We compiled long-term abundance (or biomass when abundance was not available for 379 plant communities) annual time series (20 to 57 years) data from a public database (Ghosh *et al.* 2023) for 1,694 communities in total, and for multiple taxa (e.g., birds, fish, terrestrial and freshwater invertebrates, phytoplankton, plants with a minimum of 15 species sampled annually). We included species that were present for at least for 70% of the total sampling period, thus, following other studies (Sasaki & Lauenroth 2011; Valencia *et al.* 2020), we focused on the dynamics of dominant species in communities. For each of the 1,694 communities, we computed the average correlation between years (r), and five additional metrics using the *ecofolio* R-package (Anderson *et al.* 2013). They are temporal Taylor's slope (z), community-level temporal synchrony among species as variance ratio, VR, (Loreau & de Mazancourt 2008), temporal community stability (as CV^{-1}), and two types of portfolio effects (Anderson *et al.* 2013), PE, considering without (i.e. based on an average-CV based approach) and with mean-variance scaling. We also computed net tail-dependence among species' ranks (i.e. dependence between lower ranks minus dependence between higher ranks, rarest species got lowest rank) between any two years of the whole study period, using *partial Spearman correlation* approach (Ghosh *et al.* 2020a, b).

We addressed the first gap (**G1)** by evaluating the wide variation in z for the largest collection of such long-term natural communities. We also simulated communities with different combinations of richness (varying from 30 to 70) and z (varying from 1 to 3) to test whether the two types of PE differ from each other when z is not equal to 2. We later used both of these empirical and simulated communities to address **G2** and verified how the average-CV based approach overestimated PE when z<2, and underestimated when z>2 (results in Figs. 2B-3, see Box 1 for theoretical expectations). We also developed a rank abundance curve (RAC) turnover model to provide a general mechanism behind the wide variation in z found for natural communities (addressing **G3**). We then used the model to help us understand potential explanations for the observed variation of zin nature (results are shown in Figs. 4D, 5).

To develop the model, we simulated three types of communities with the same number of species (R) and the same between-year correlation (r). They are - type I, Fig. 4A: having more dependence among the dominant group of species (i.e., consistent upper ranks in RAC and more turnover in lower ranks), type II, Fig. 4B: having more dependence among the not-so-common or rare group of species (i.e., consistent lower ranks in RAC and more turnover in upper ranks), and type III, Fig. 4C: having no dependence in any specific group (i.e., complete and random annual turnover among species ranks). "Copula", a mathematical tool and a rank-based approach, has been used to compute tail-dependence (i.e., dependence in the extremely high or low values) among two correlated ecological variables in past studies (Ghosh *et al.* 2020a, b, c, 2021; Walter *et al.* 2022). Copulas make the marginal distribution uniform so that the dependence information remains unique on its own. For example, with the same sample set (x_i, y_i); $i = 1, 2, ..., R$ one can generate type I, type II, and type III dependence using three particular single-parameter "copula" families: Survival Clayton, Normal, Clayton, respectively (see *iRho* function from *copula* R-package for details (Yan 2007)). We used this approach in the community matrix, M, (with abundance or biomass for R number of species that are sampled for N years; species along columns and years along rows) so that the Spearman correlation between any two years are the same. Specifically, we first constructed such a community from Clayton family that has dependence in lower ranks (type II), and then we permuted M in such a way to eliminate the tail-dependence structure but preserve the same between-year correlation, r (up to sampling error). In doing so, this permutation generated a Normal copula (type III). Then, we again permuted the community matrix M to get upper tail-dependence (i.e., dependence in upper ranks) preserving between-year correlations and leading to the Survival Clayton copula (i.e. a 180-degree rotation of Clayton family). We generated 1,000 surrogates for each type of community (see Simulation_zmorethan2.R script from the Zenodo repo: https://doi.org/10.5281/zenodo.8373892). A similar algorithm was previously used in Spatial Taylor's law context to generate surrogate communities with the same correlation but different dependence structures among sites (Ghosh *et al.* 2020a).

Given this set of community types, we hypothesized that the third type (i.e. Fig. 4: Case III) would lead to z values within the commonly observed range of 1 and 2, irrespective of the value of the r. However, we also suspected that any tail-dependencies in the ranks (e.g. lower or upper tail dependencies in Case 1 and II) could expand the range of z both below 1 and above 2 (i.e., for the Case I, II). To explore this, we simulated for a given year-to-year correlation, r, three types of communities each with 1,000 surrogates (or replicates), and species richness R =40 where we tracked species abundance for N =22 years. Therefore, each replicate community type has the same year-to-year correlation, r, and we varied r over a range from 0.2 to 0.9 (results shown in Fig. 4D). R and N for this simulation are chosen to have same median values for richness and timeseries length found in our dataset, so that we can compare the results.

Results

Our data compilation confirms that most of communities had values of z within the commonly reported range from previous studies (i.e., between 1 to 2), but also reveals that nearly 5% of communities had values of z outside that range (Fig. 3A), addressing **G1**. Consistent with previous theory, and confirmed with simulated community timeseries (Fig. 2A), stability was higher for communities having z<2 than the communities with z>2 (Fig. 3B, addressing **G2**). The positive effect of diversity (i.e. richness) on stability was weaker (slope is less steep) for communities with z>2. This result highlights the potential need to account for heterogeneity in z values when comparing the stability among communities. We additionally find that such heterogeneity is important for interpreting stabilizing mechanisms of community stability, such as the portfolio effect (for **G2**). Simulated communities show the limitations of previous approaches (i.e. based on average-CVs following Box 1**)** that overestimate PE for z<2 (Fig. 2B, solid lines), and the underestimate PE for z>2 (Fig. 2B, dashed lines). As expected, these approaches converge to the same answer when z=2, and so the relevance of this improved method depends on how often the mean-variance scaling exponent in natural communities deviates from 2. Consistent with this previous theory, our empirical estimates of PE were higher without accounting for the mean-variance scaling (Fig. 3C), because the majority of communities had z<2. Comparing these two approaches (i.e. with and without accounting for mean-variance scaling) clearly shows larger values for PE without mean-variance scaling (i.e. green points, n=1,610, above the diagonal line, Fig. 3D) for z<2, whereas communities with z>2 had larger PE when accounting for mean-variance scaling (i.e. pink points, n=80, below the diagonal line, Fig. 3D).

Our model of RAC turnover provides new insight into explaining the wide variation observed in in our empirical dataset (Figs. 4D, 5), addressing **G3**. The simulation from RAC turnover model, as depicted in Fig. 4D, shows communities exhibiting high annual turnover among all species had z values within the expected range (black solid points ~1.5 showed the mean of 1,000 estimates, Case III). Moreover, we find that communities with high turnover for any particular group (rare: Case I, dominant: Case II) show a much wider range of z. For above-average year-to-year correlation (r>0.5), communities where rare species change their ranks more frequently are more likely to have z less than 1 (Case I, follow blue dotted lines in Fig. 4D after the crossing at r=0.5). Whereas, communities in which dominant species changed their ranks more frequently are more likely to have z greater than 2 (Case II, follow red dotted lines in Fig. 4D beyond r=0.5). The patterns are opposite below r=0.5, where Case I and Case II have a higher probability to have z>2, and z<1, respectively. Our repeated simulation for different combinations of richness (R), and time series length (N) gives similar general finding, and is robust to the choice of both R and N.

When analysing empirical community time series, we found that the year-to-year correlation, r, was often greater than 0.5. This range of r led to our expectation, from the above-mentioned simulation result, that communities showing more dependence in species' upper ranks (Case I from Fig. 4D) would likely to have z<1, whereas, communities with more dependence in species' lower ranks (Case II from Fig. 4D) would likely to have z>2. Indeed, our empirically observed distribution of the net tail-dependence of communities is broadly in line with our modeling outcomes (Fig. 5D). Specifically, we find higher z values to be associated with communities that also show more dependence in lower ranks. In our analysis of the natural communities, we interpret more negative values to indicate stronger dependence in upper ranks (i.e. dominant species), and less negative to positive values mean increasing contribution of dependence in lower ranks (i.e. rare species). Overall, the qualitative match between our simulation results in Fig. 4 and our analysis of empirical analysis in Fig. 5 support our predictions. Specifically, communities with high annual turnover over their entire rank-abundance distribution tend to have z-values within the range of 1 and 2, whereas communities with high annual turnover in just their most dominant or more rare species can have z-values less than 1 or greater than 2.

In our compilation of community timeseries, the species richness varies from 15 to 89 (median=40 species, Fig. 5A), the length of timeseries sampled varies from 20 to 57 years (median=22 years), the correlations between years are typically >0.5 (Fig. 5B), and the synchrony among species (as measured by the variance ratio) is typically <0.75 (Fig. 5C). The Variance Ratio (VR) has a range of (0, 1). VR values close to 0 implies less synchrony and values of 1 indicate perfect synchrony. Though most data lies in the bottom-left box of Fig. 5C with low synchrony (VR<0.5, 1<z<2), there are also some communities with z>2 but low synchrony (in the top-left box).

Discussion

Overall, our data compilation, analysis, and simulation model allows us to explore how heterogeneity in z can affect inferences about stability-diversity relationships and the portfolio effect (PE) (Fig. 3), and provides a novel explanation for the wide distribution of temporal Taylor's slope (z) observed in ecological communities (Fig. 4). Previous work has established that strong positive relationships between richness and stability are only expected when z<2 (Fig. 3B), and that variability in z among communities can mask how we estimate the contribution of PE to community stability (Fig. 3C-D). Although the majority of empirical observations of communities find z between 1 and 2 (Fig. 3A), large values of z are common enough to affect inferences about the causes of stability variation. For example, measuring the PE without considering the mean-variance scaling relationship can lead to substantial overestimates of stability when z<2, and increasingly large underestimates when z>2 (Fig. 2B). As the statistical averaging effect is likely a fundamental mechanism of stability (Zhao *et al.* 2022), it is essential to make accurate assessments in order to support conservation and management efforts.

Several previous mechanisms have been proposed to explain variability in z, and have speculated about causal drivers of community stability. Interspecific competition and environmental variability, for example, can explain some variation in z that can impact stability (Kilpatrick & Ives 2003; Cobain *et al.* 2019). For example, negative interactions among species (e.g. competition) is a commonly proposed mechanism for explaining why abundant species are less variable than expected given their mean abundance, leading to communities with $z<2$ (Kilpatrick and Ives 2003). Here, our proposed mechanism can explain z values both less than and greater than 2 (Fig. 4). This implies there can be multiple reasons for the observed range of z values in natural communities, and also multiple explanations, beyond simply competition, for why communities can both have low synchrony and have z-values less than and greater than two (Fig. 5C).

Our simulations demonstrate how high turnover among all species' ranks (reordering all species) can yield communities with z-values in the range of [1, 2], whereas group-specific turnover, namely rank-inconsistency only for the dominant species or rare species throughout the years, can yield communities with z values outside the range of [1, 2]. Few previous studies have connected species abundance distribution with Taylor's law (Ma 2015; Cohen 2020), but doing so can reveal how changes in rank abundance distribution (Fig. 5) can impact our assessment of community stability (Fig. 3). Our results show that monitoring the RACs for rare vs. dominant groups of species can help explain the broad range of z observed in nature. There is a long history of tracking RACs to understand community dynamics in response to global change drivers (Collins *et al.* 2008; Avolio *et al.* 2015, 2019; Jones *et al.* 2017). Our work suggests we need a better understanding of the reasons for temporal variation in RACs and z. For a specific richness, RAC can change due to both species reordering and changes in eveness without reordering ((Collins *et al.* 2008; Avolio *et al.* 2015, 2019; Jones *et al.* 2017)). A previous study

(Wohlgemuth *et al.* 2016) highlighted the role of species reordering rather than evenness in maintaining ecosystem functioning. Our study also highlights that changes in species reordering, rather than eveness, is most likely to affect z and hence how we make inferences from observed community dynamics (Figs. 1, 2, and 5).

Earlier studies also showed that environmental variability (e.g., temperature, soil quality, drought) can affect the dynamics of species turnover, and hence the temporal variation in the identity of dominant and rare species in a community (Ulrich *et al.* 2016; Castillioni *et al.* 2020). Changes in the dominance structure of communities is expected due to differences in species environmental tolerance and competitive ability in a given environment (Shurin 2007). Reordering of the identity of species in rank-abundance curves is also likely when a community responds to environmental change (e.g., forb vs grass (Hoover *et al.* 2014)). For example, in a long-term study on desert grassland, the reordering of which species were dominant varied through time in response to both pulse (wildfire) and press (changes in Pacific decadal oscillation) climatic perturbations (Collins *et al.* 2020). There is overwhelming evidence that environmental change can drive community dynamics that substantially alter RACs (McCarthy *et al.* 2018). However, more work is clearly needed to test the hypotheses about how climatic change, for example, can alter the tail-dependence in species' ranks, and whether mean-variance relationships are stable in relation to their temporal Taylor's slope (i.e. z). A recent study (Tippett & Cohen 2020) showed seasonal variation in variance-to-mean relationship for all-India daily rainfall pattern (low during peak monsoon, high during otherwise). Such mean-variance relationships in climatic factors might affect communities' mean-variance scaling relationship in a similar way.

In conclusion, we have shown that considering Taylor's law can improve our understanding of community variability, stability, portfolio effects, and species abundance distribution over time. There are several important insights from our study. First, identifying the causes of mean-variance scaling of population abundances is important for the longstanding challenge of understanding relationships between diversity and stability of communities (McCann 2000). Importantly, greater species richness does not necessarily ensure more temporal stability if abundant species are more variable than expected, such that communities have $z>2$ (Fig. 3B). Second, identifying the importance of portfolio effects as a stabilizing mechanism of communities can be both over- or underestimated if the mean-variance scaling relationship is not carefully considered (Zhao *et al.* 2022). Third, we establish a novel and general biological mechanism that can help explain observed wide variation in z (i.e., <1 or >2) seen in natural communities. We confirm our hypothesis with simulated (i.e., from the *RAC-turnover model*; Fig. 4) and empirical data (i.e., from 1,694 long-term natural communities; Fig. 5) that temporal turnover in RACs via species-reordering is an important factor determining the value of z. This finding is consistent with earlier studies that showed global change drivers can reshape RACs via species reordering (Avolio *et al.* 2015, 2022), and could be crucial for better understanding the mechanism behind the community response to global change drivers.

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Competing interests: The authors declare that they have no competing interests.

Figures:

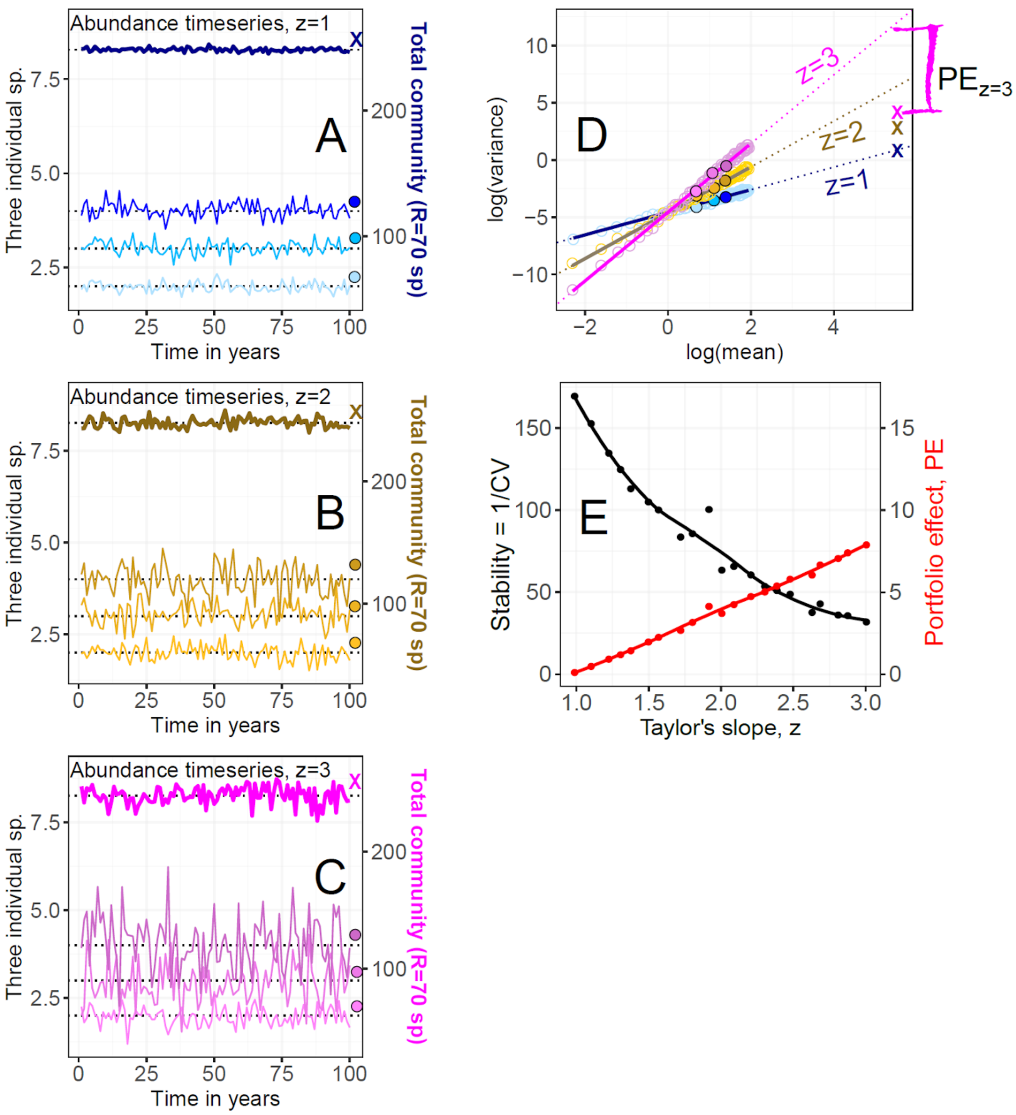

Figure 1: The concept of temporal Taylor's law: in ecological communities population abundance has a variance to mean scaling relationship. Temporal variance can fluctuate with an exponent (z) to the temporal mean - in log scale, the relationship would be a fitted straight line of slope z. Taylor's slope (z) can be below <2, A or >2, C, with z=2 often considered as a limiting case, B. A-C show three representative species among a total of 70 species in the community

(thinner lines) and total community abundance timeseries on the top (thicker lines). Species are very weakly related in each of these simulated communities (synchrony or variance ratio < 0.025). Due to the fluctuation scaling relationship, the variance of total community abundance is often lower (symbol X) than the predicted value on the dotted line for a given community mean, D. Higher value of z results in a larger difference, and lowers community stability (i.e., the inverse of variability in total community abundance timeseries), E.

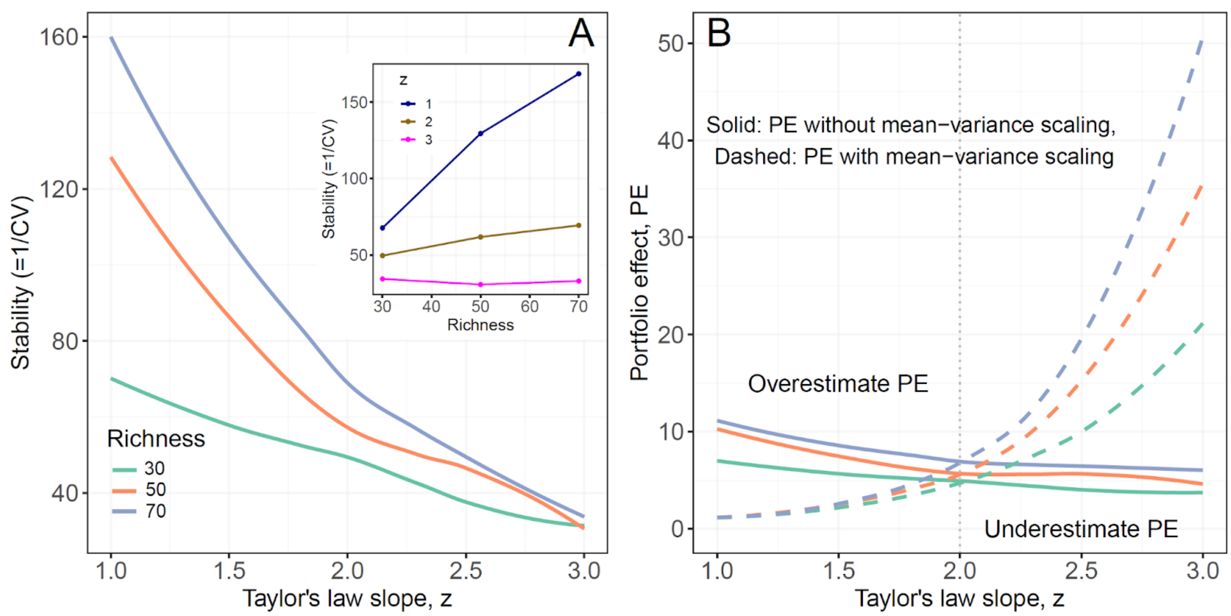

Figure 2: Temporal Taylor's law slope, z, affects stability (A) and portfolio effect (B) for three different levels of richness: R=30, 50, and 70. The diversity-stability relationship has a steeper positive slope for lower z, but a weaker positive slope at higher z (inset, A). Within the feasible set of [1, 2] portfolio effect (PE) computed based on average-CV (i.e., without mean-variance scaling, solid lines, B) gives an overestimate of accurate measure of PE (i.e. considering mean-variance scaling, dashed lines, B). For z>2, PE without mean-variance scaling underestimates the true effort. At z=2, both measures are exactly the same.

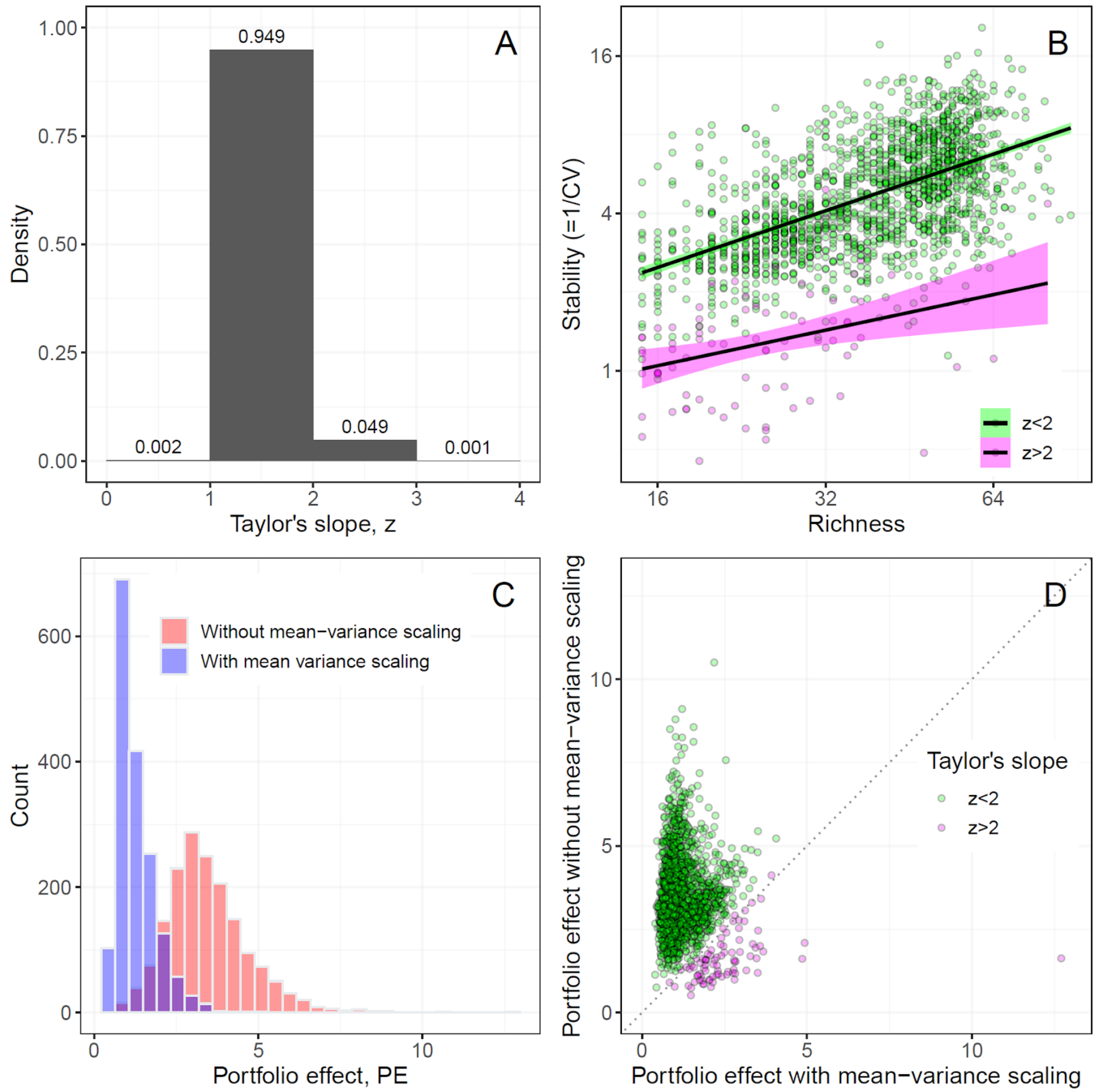

Figure 3: Empirical observations verify the concepts of Fig 2. The majority of the communities had temporal Taylor's law slope (z) <2 (n=1610), and 5% of communities had z>2 (n=84) (A). Stability, the inverse of variability in total community abundance (=1/CV), was lower for communities with z>2 and the stability-diversity relationship had a weaker positive slope compared to communities that had z<2 (B). Distributions of portfolio effects computed with and

without mean-variance relationship are depicted in C. For communities having z>2, the portfolio effect due to mean-variance scaling was higher (pink points below the dotted 1:1 line) than the portfolio effect if mean-variance scaling had not been considered. On the other hand, for communities with z<2, the pattern was opposite (green points above the dotted 1:1 line), i.e., a higher estimate for portfolio effect happened without considering mean-variance scaling.

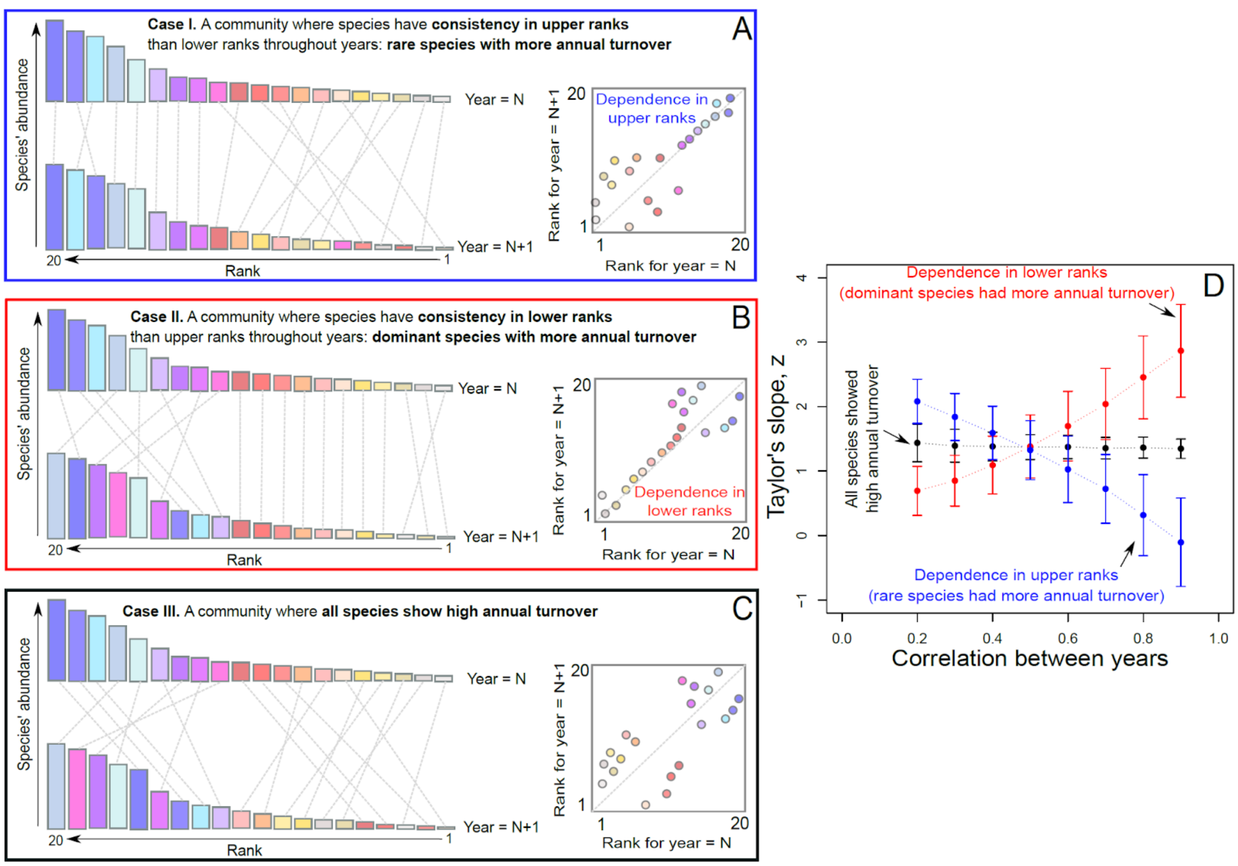

Figure 4: Mechanism explaining variation in temporal Taylor's law slope (z) for ecological communities when species show a positive year-to-year correlation (r>0) in the *RAC-turnover model* (see *Materials & Methods*). In a community where some dominant species are always dominant throughout the years (so consistent in high rank-abundances) but rare species show a more annual turnover, z could be <1 or >2 depending on the value of r (Case I: A, the blue line

in D). In an opposite scenario, in a community where some rare species are always rare throughout the years (so consistent in low rank-abundances) but dominant species show a more annual turnover, z could also be <1 or >2 depending on the value of r (Case II: B, the red line in D). When in a community all species would fluctuate in their annual rank abundance, $1<z<2$ would happen, irrespective of r values (Case III: C, the black line in D). Simulation with surrogate communities (40 species were simulated for 22 years to match the median values of sampled richness and years from empirical communities) shows dependence in either rank (lower or upper) can make $z<1$ or $z>2$, whereas turnover for all species always results in $1<z<2$; for details see *Materials & Methods*. The bars are due to two standard deviations for the estimates from 1,000 surrogate communities, and plotted around the mean (solid points).

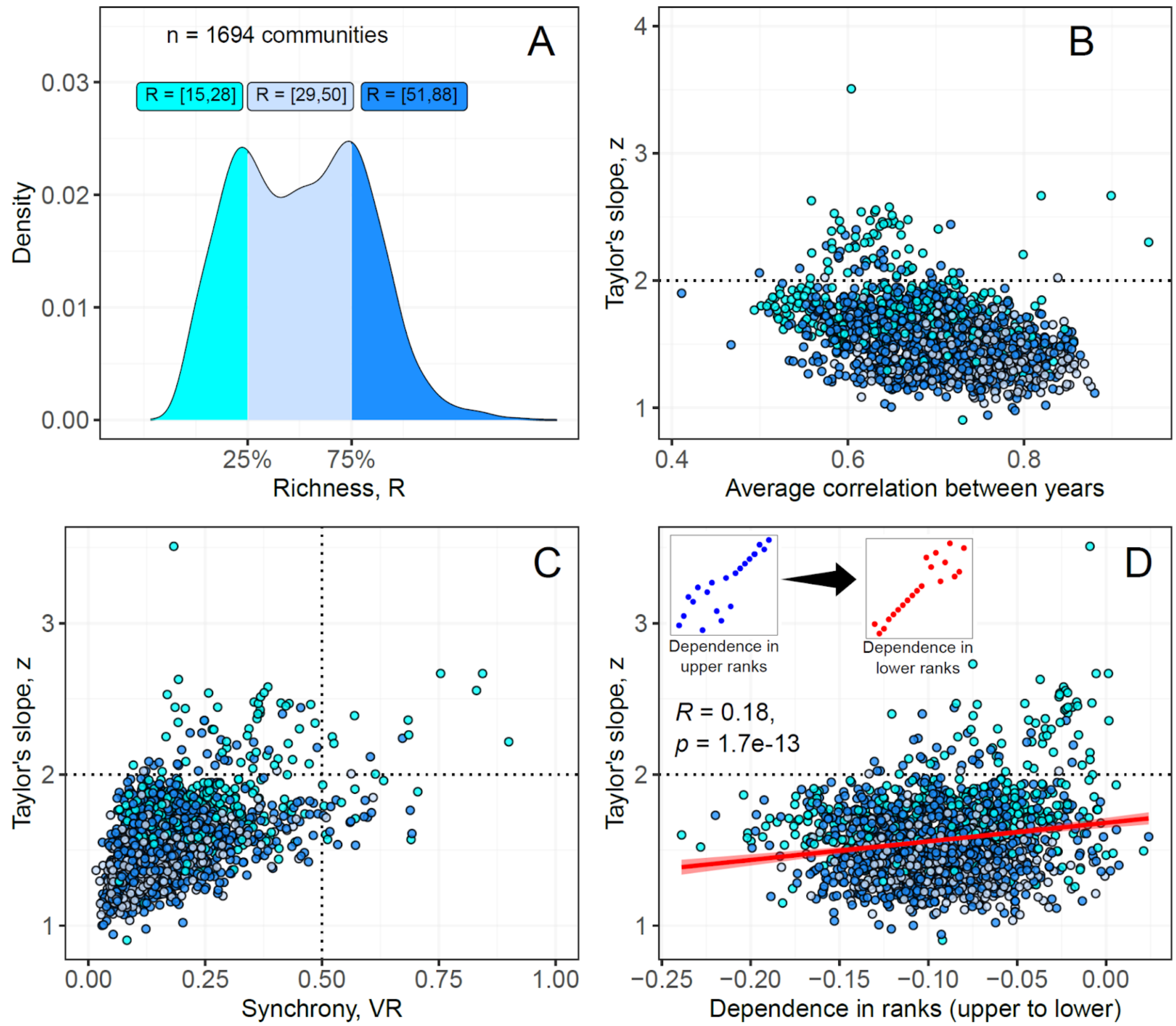

Figure 5: Empirical observations show results consistent with the mechanism from Fig. 4. A total of 1,694 communities have richness in between [15, 88], A, an on-average correlation between years r>0.5, B, and interspecific synchrony (variance ratio) <0.75, C. Range of r indicates z can be greater than 2 if ranks of rare species were consistent throughout years as shown for the red line in Fig. 4D. Empirical communities also show z>2 is possible as consistency or dependence increases in the lower ranks (Pearson correlation, R, from the linear regression is significantly positive, shown in panel D).

Box 1: Quantifying portfolio effect, PE, for a community considering with or without mean-variance fluctuation relationship

Let us consider we are monitoring a community with n number of species for N years, where mean, m_i, and variance, v_i, of species abundance or biomass are related via temporal Taylor's law slope z:

$$v_i = a m_i^z ;\ i = 1, 2, \ldots, n \ldots\ldots\ldots\ldots (1)$$

Portfolio effect, PE is defined as the CV of a single species timeseries compared to the CV of the total community abundance (or biomass) timeseries.

$$PE = CV_{sp} / CV_{com} \ldots\ldots\ldots\ldots (2)$$

Following the recipe given by Anderson et al. (Anderson *et al.* 2013), we computed PE in two ways: (i) type I: based on the average CV of species in the community as PE_{avgCV} and (ii) type II: considering the effect of the mean-variance relationship as PE_{mv}.

Both types of PE have the same denominator, i.e., CV for total community timeseries

$$CV_{com} = \frac{\sqrt{m_1^z + m_2^z + \ldots\ldots + m_n^z}}{m_1 + m_2 + \ldots + m_n} = \frac{\sqrt{\sum_{i=1}^{n} m_i^z}}{\sum_{i=1}^{n} m_i} \ldots\ldots\ldots\ldots (3)$$

For type I average-CV based approach, CV_{sp} is computed as the average of individual species' CV that leads to following relationship for PE:

$$PE_{avgCV} = CV_{sp} \,/\, CV_{com} = \left(\frac{1}{n} \sum_{i=1}^{n} \frac{\sqrt{m_i^z}}{m_i} \right) \times \frac{1}{CV_{com}} = \frac{1}{nCV_{com}} \sum_{i=1}^{n} m_i^{(z/2)-1} \quad \ldots\ldots\ldots\ldots (4)$$

For type II mean-variance scaling approach, CV_{sp} is computed as the single species' CV, as if only one species equivalent to total community (abundance or biomass) is present. This leads to following relationship for PE:

$$PE_{mv} = CV_{sp} \,/\, CV_{com} = \left(\frac{\sqrt{\left(\sum_{i=1}^{n} m_i\right)^z}}{\sum_{i=1}^{n} m_i} \right) \times \frac{1}{CV_{com}} = \frac{1}{CV_{com}} \left(\sum_{i=1}^{n} m_i \right)^{(z/2)-1} \quad \ldots\ldots\ldots\ldots (5)$$

Now we will compare between two types of PE from Eqs. (4-5), for different values of z.

Case I: when $z = 2$, $PE_{avgCV} / PE_{mv} = 1$.

Case II: when z<2, to illustrate say, z=1:

then $PE_{avgCV} / PE_{mv} = \dfrac{\sum_{i=1}^{n} m_i^{-1/2}}{n\left(\sum_{i=1}^{n} m_i\right)^{-1/2}}$, i.e., $PE_{avgCV} > PE_{mv}$ (see (Ramanujan 1915)). This inequality indicates if we do not consider the fluctuation scaling relationship, average CV based method will overestimate stability.

Case III: when z>2, to illustrate say, z=4: then

$PE_{avgCV} / PE_{mv} = 1/n$, i.e., $PE_{avgCV} < PE_{mv}$. This inequality indicates if we do not consider the fluctuation scaling relationship, average CV based method will underestimate stability.

Both Case II and case III can be verified trivially with mathematical induction and also consistent with the metapopulation context (spatial Taylor's law; (Anderson *et al.* 2013)).

References

Anderson, R.M., Gordon, D.M., Crawley, M.J. & Hassell, M.P. (1982). Variability in the abundance of animal and plant species. *Nature*, 296, 245–248.

Anderson, S.C., Cooper, A.B. & Dulvy, N.K. (2013). Ecological prophets: quantifying metapopulation portfolio effects. *Methods in Ecology and Evolution*.

Avolio, M.L., Carroll, I.T., Collins, S.L., Houseman, G.R., Hallett, L.M., Isbell, F., *et al.* (2019). A comprehensive approach to analyzing community dynamics using rank abundance curves. *Ecosphere*, 10.

Avolio, M.L., Komatsu, K.J., Koerner, S.E., Grman, E., Isbell, F., Johnson, D.S., *et al.* (2022). Making sense of multivariate community responses in global change experiments. *Ecosphere*, 13.

Avolio, M.L., Pierre, K.J.L., Houseman, G.R., Koerner, S.E., Grman, E., Isbell, F., *et al.* (2015). A framework for quantifying the magnitude and variability of community responses to global change drivers. *Ecosphere*, 6, art280.

Bahram, M., Peay, K.G. & Tedersoo, L. (2015). Local-scale biogeography and spatiotemporal variability in communities of mycorrhizal fungi. *New Phytol.*, 205, 1454–1463.

Ballantyne, F., IV & J. Kerkhoff, A. (2007). The observed range for temporal mean-variance scaling exponents can be explained by reproductive correlation. *Oikos*, 116, 174–180.

Castillioni, K., Wilcox, K., Jiang, L., Luo, Y., Jung, C.G. & Souza, L. (2020). Drought mildly reduces plant dominance in a temperate prairie ecosystem across years. *Ecol. Evol.*, 10, 6702–6713.

Cobain, M.R.D., Brede, M. & Trueman, C.N. (2019). Taylor's power law captures the effects of environmental variability on community structure: An example from fishes in the North Sea. *J. Anim. Ecol.*, 88, 290–301.

Cohen, J.E. (2014). Taylor's law and abrupt biotic change in a smoothly changing environment. *Theor. Ecol.*, 7, 77–86.

Cohen, J.E. (2020). Species-abundance distributions and Taylor's power law of fluctuation scaling. *Theor. Ecol.*, 13, 607–614.

Cohen, J.E. & Saitoh, T. (2016). Population dynamics, synchrony, and environmental quality of Hokkaido voles lead to temporal and spatial Taylor's laws. *Ecology*, 97, 3402–3413.

Cohen, J.E. & Xu, M. (2015). Random sampling of skewed distributions implies Taylor's power law of fluctuation scaling. *Proc. Natl. Acad. Sci. U. S. A.*, 112, 7749–7754.

Cohen, J.E., Xu, M. & Schuster, W.S.F. (2013). Stochastic multiplicative population growth predicts and interprets Taylor's power law of fluctuation scaling. *Proceedings of the Royal Society B: Biological Sciences*.

Collins, S.L., Chung, Y.A., Baur, L.E., Hallmark, A., Ohlert, T.J. & Rudgers, J.A. (2020). Press–pulse interactions and long-term community dynamics in a Chihuahuan Desert grassland. *J. Veg. Sci.*, 31, 722–732.

Collins, S.L., Suding, K.N., Cleland, E.E., Batty, M., Pennings, S.C., Gross, K.L., *et al.* (2008). Rank clocks and plant community dynamics. *Ecology*, 89, 3534–3541.

Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72–85.

Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264–276.

Döring, T.F., Knapp, S. & Cohen, J.E. (2015). Taylor's power law and the stability of crop yields. *Field Crops Research*.

Eisler, Z., Bartos, I. & Kertész, J. (2008). Fluctuation scaling in complex systems: Taylor's law and beyond. *Adv. Phys.*, 57, 89–142.

Ghosh, S., Cottingham, K.L. & Reuman, D.C. (2021). Species relationships in the extremes and their influence on community stability. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 376, 20200343.

Ghosh, S., Matthews, B., Supp, S.R., van Klink, R., Pomati, F., Rusak, J.A., *et al.* (2023). Project BioDyn: compilation of long-term (>20yrs) community timeseries data from terrestrial and freshwater realms, https://zenodo.org/record/8233591.

Ghosh, S., Sheppard, L.W., Holder, M.T., Loecke, T.D., Reid, P.C., Bever, J.D., *et al.* (2020a). Copulas and their potential for ecology. In: *Advances in Ecological Research*. Elsevier, pp. 409–468.

Ghosh, S., Sheppard, L.W., Reid, P.C. & Reuman, D. (2020b). A new approach to interspecific synchrony in population ecology using tail association. *Ecol. Evol.*, 10, 12764–12776.

Ghosh, S., Sheppard, L.W. & Reuman, D.C. (2020c). Tail associations in ecological variables and their impact on extinction risk. *Ecosphere*, 11.

Giometto, A., Formentin, M., Rinaldo, A., Cohen, J.E. & Maritan, A. (2015). Sample and population exponents of generalized Taylor's law. *Proceedings of the National Academy of Sciences*, 112, 7755–7760.

Hoover, D.L., Knapp, A.K. & Smith, M.D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, 95, 2646–2656.

Jones, S.K., Ripplinger, J. & Collins, S.L. (2017). Species reordering, not changes in richness, drives long-term dynamics in grassland communities. *Ecol. Lett.*, 20, 1556–1565.

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

Kilpatrick, A.M. & Ives, A.R. (2003). Species interactions can explain Taylor's power law for ecological time series. *Nature*, 422, 65–68.

Kuo, T.-C., Mandal, S., Yamauchi, A. & Hsieh, C.-H. (2016). Life history traits and exploitation affect the spatial mean-variance relationship in fish abundance. *Ecology*, 97, 1251–1259.

Loreau, M. & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *Am. Nat.*, 172, E48–66.

MacArthur, R.H. (1957). ON THE RELATIVE ABUNDANCE OF BIRD SPECIES. *Proceedings of the National Academy of Sciences*, 43, 293–295.

Ma, Z.S. (2015). Power law analysis of the human microbiome. *Mol. Ecol.*, 24, 5428–5445.

McCann, K.S. (2000). The diversity–stability debate. *Nature*, 405, 228–233.

McCarthy, J.K., Mokany, K., Ferrier, S. & Dwyer, J.M. (2018). Predicting community rank-abundance distributions under current and future climates. *Ecography* , 41, 1572–1582.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., *et al.* (2007).

Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995–1015.

Perry, J.N. (1994). Chaotic dynamics can generate Taylor's power law. *Proc. Biol. Sci.*, 257, 221–226.

Pertoldi, C., Bach, L.A. & Loeschcke, V. (2008). On the brink between extinction and persistence. *Biol. Direct*, 3, 47.

Ramanujan, S. (1915). On the sum of the square roots of the first n natural numbers. *J. Indian Math. Soc.*, 173–175.

R Core Team. (2022). *R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.*

Reuman, D.C., Zhao, L., Sheppard, L.W., Reid, P.C. & Cohen, J.E. (2017). Synchrony affects Taylor's law in theory and data. *Proc. Natl. Acad. Sci. U. S. A.*, 114, 6788–6793.

Sasaki, T. & Lauenroth, W.K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities. *Oecologia*, 166, 761–768.

Schindler, D.E., Armstrong, J.B. & Reed, T.E. (2015). The portfolio concept in ecology and evolution. *Front. Ecol. Environ.*, 13, 257–263.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., *et al.* (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–612.

Segura, A.M., Wiff, R., Jaureguizar, A.J., Milessi, A.C. & Perera, G. (2021). A macroecological perspective on the fluctuations of exploited fish populations. *Mar. Ecol. Prog. Ser.*, 665, 177–183.

Shurin, J.B. (2007). How is diversity related to species turnover through time? *Oikos*, 116, 957–965.

Taylor, L.R. (1961). Aggregation, variance and the mean. *Nature*, 189, 732–735.

Taylor, L.R. & Woiwod, I.P. (1982). Comparative Synoptic Dynamics. I. Relationships Between Inter- and Intra-Specific Spatial and Temporal Variance/Mean Population Parameters. *J. Anim. Ecol.*, 51, 879–906.

Taylor, R.A.J. (2019). *Taylor's Power Law: Order and Pattern in Nature*. Academic Press.

Tippett, M.K. & Cohen, J.E. (2020). Seasonality of Taylor's law of fluctuation scaling in all-India daily rainfall. *npj Climate and Atmospheric Science*, 3, 1–7.

Tokeshi, M. (1995). On the mathematical basis of the variance-mean power relationship. *Popul. Ecol.*, 37, 43–48.

Ulrich, W., Soliveres, S., Thomas, A.D., Dougill, A.J. & Maestre, F.T. (2016). Environmental correlates of species rank - abundance distributions in global drylands. *Perspect. Plant Ecol. Evol. Syst.*, 20, 56–64.

Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A., *et al.* (2020). Synchrony matters more than species richness in plant community stability at a global scale. *Proc. Natl. Acad. Sci. U. S. A.*, 117, 24345–24351.

Walter, J.A., Castorani, M.C.N., Bell, T.W., Sheppard, L.W., Cavanaugh, K.C. & Reuman, D.C. (2022). Tail-dependent spatial synchrony arises from nonlinear driver-response relationships. *Ecol. Lett.*, 25, 1189–1201.

Whittaker, R.H. (1965). Dominance and Diversity in Land Plant Communities: Numerical relations of species express the importance of competition in community function and evolution. *Science*, 147, 250–260.

Wohlgemuth, D., Solan, M. & Godbold, J.A. (2016). Specific arrangements of species dominance can be more influential than evenness in maintaining ecosystem process and function. *Sci. Rep.*, 6, 39325.

Xiao, X., Locey, K.J. & White, E.P. (2015). A Process-Independent Explanation for the General Form of Taylor's Law. *Am. Nat.*, 186, E51–60.

Xu, M. & Cohen, J.E. (2019). Analyzing and interpreting spatial and temporal variability of the United States county population distributions using Taylor's law. *PLoS One*, 14, e0226096.

Xu, M., Kolding, J. & Cohen, J.E. (2019). Sequential analysis and design of fixed-precision sampling of Lake Kariba fishes using Taylor's power law. *Can. J. Fish. Aquat. Sci.*, 76, 904–917.

Yan, J. (2007). Enjoy the Joy of Copulas: With a Package copula. *J. Stat. Softw.*, 21, 1–21.

Zhao, L., Sheppard, L.W., Reid, P.C., Walter, J.A. & Reuman, D.C. (2019). Proximate determinants of Taylor's law slopes. *J. Anim. Ecol.*, 88, 484–494.

Zhao, L., Wang, S., Shen, R., Gong, Y., Wang, C., Hong, P., *et al.* (2022). Biodiversity stabilizes plant communities through statistical-averaging effects rather than compensatory dynamics. *Nat. Commun.*, 13, 7804.