

# 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:  $z_{\text{space}}$ ) is well studied in Ecology, but the analogous scaling exponent for temporal datasets ( $z_{\text{time}}$ ) is underdeveloped. Previous theory suggests the narrow distribution of  $z_{\text{time}}$  (e.g. typically 1 - 2) could be due to interspecific competition. Here, using 1,694 communities time series, we show that  $z_{\text{time}}$  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  $z_{\text{time}}$  distribution. Specifically, we find that communities with minimal turnover in species' rank abundances are more likely to have higher  $z_{\text{time}}$ . Our analysis provides a deeper mechanistic understanding of how species-level variability affects our inference about the stability of ecological communities.

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

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

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## 69 Introduction

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

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89 Currently, understanding the importance of mean-variance fluctuation scaling (i.e.  $z_{\text{time}}$ ) for  
90 making inferences from community dynamics is limited by uncertainty in i) the distribution of  
91  $z_{\text{time}}$  in natural communities, ii) how  $z_{\text{time}}$  variability affects interpretations of community stability,

92 and iii) the mechanisms underlying  $z_{\text{time}}$  variability. We address each of three gaps (referred to  
93 below as G1-G3). First, existing studies of natural communities have documented a limited range  
94 of variation in  $z_{\text{time}}$  (Cobain *et al.* 2019; Xu & Cohen 2019), but with the increasing availability  
95 of long-term community time series we can improve our inference about the distribution of  $z_{\text{time}}$   
96 in nature.

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98 Second, there is longstanding theory about how variation in  $z_{\text{time}}$  is relevant for interpreting  
99 community stability (Cottingham *et al.* 2001; Kilpatrick & Ives 2003; Kalyuzhny *et al.* 2014;  
100 Cobain *et al.* 2019; Zhao *et al.* 2019), but these interpretations are somewhat sensitive to mean  
101 variance scaling. Importantly, when  $z$  is greater than 1, the expected temporal variance of the  
102 total community abundance is less than that of a single population for that same mean abundance  
103 (Fig. 1), meaning that species-level variance increases nonlinearly in relation to mean  
104 abundances. This reduced variance arises because of the statistical averaging of independently  
105 varying population time series, which is known as the portfolio effect concept (hereafter PE)  
106 (Doak *et al.* 1998; Schindler *et al.* 2015). PE has been widely used to quantify the importance of  
107 species diversity for overall community stability (i.e., inverse of community variability, CV), but  
108 its interpretation depends on  $z_{\text{time}}$  for that community (Cottingham *et al.* 2001). For example, the  
109 magnitude of the PE is negligible when  $z_{\text{time}} \sim 1$ , and increases with  $z_{\text{time}}$  (Fig. 1E, red line). This  
110 means that estimates of community stability (i.e.  $1/\text{CV}$ ), for a given species richness, decrease  
111 with the increase in  $z_{\text{time}}$  for a community (Fig. 1E, black line). Importantly, the consistently  
112 negative relationship between stability and  $z$  over a wide range of species diversity (Fig. 2A)  
113 means that the expected slope of the relationship between species richness and stability decreases  
114 substantially as  $z_{\text{time}}$  increases (Fig. 2A, inset). Often, PEs are estimated by comparing the overall

115 community variability with the average variability of constituent populations, or, in a spatial  
116 context, by comparing the CV of overall the meta-population abundance with the average CVs of  
117 the subpopulations (Schindler *et al.* 2010). However, Anderson *et al.* (2003) showed that the  
118 above-mentioned approach is appropriate only for  $z_{\text{time}}=2$ , and they provided an alternate  
119 approach accounting for the potential heterogeneity of  $z$  among communities.

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121 Third, existing theory can explain why  $z_{\text{time}}$  often varies between 1 and 2 (Taylor & Woiwod  
122 1982; Tokeshi 1995; Xiao *et al.* 2015), but provides no general mechanistic explanation for the  
123 entire empirically observed range of  $z_{\text{time}}$ . For spatial TL context, several proposed mechanisms  
124 that explain variation in  $z_{\text{space}}$  have considered density dependence (Perry 1994),  
125 density-independent and stochastic population growth (Cohen *et al.* 2013), population synchrony  
126 (Cohen & Saitoh 2016), and random sampling from skewed distribution (Cohen & Xu 2015).  
127 Whereas for  $z_{\text{time}}$  proposed mechanisms have considered interspecific competition (Kilpatrick &  
128 Ives 2003), environmental variability (Cohen & Saitoh 2016), correlated reproduction  
129 (Ballantyne & J. Kerkhoff 2007), sampling error (Kalyuzhny *et al.* 2014), and limited sampling  
130 effort (Giometto *et al.* 2015). However, all of these previous studies have focused on explaining  
131 why  $z_{\text{time}}$  is typically less than 2, and only a few previous studies have provided a mechanistic  
132 explanation for why it can be greater than 2. In spatial models,  $z_{\text{space}}$  can be greater than 2 due to  
133 synchrony among metapopulations (Reuman *et al.* 2017) especially when they are rare (Ghosh *et*  
134 *al.* 2020a), and due to growing stochasticity (Cohen *et al.* 2013) or unexpected changes in a  
135 smoothly autocorrelated environment (Cohen 2014). In the case of  $z_{\text{time}}$ , only one previous study  
136 of a fish community found that environmental variability can lead to a size-based Taylor's slope  
137 greater than 2 (Cobain *et al.* 2019).

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139 In this paper, we will address each of those three aforementioned gaps. First (for **G1**), we  
140 estimate the distribution of  $z_{\text{time}}$  (hereafter  $z$ ) in nature by compiling thousands of long-term (>20  
141 years) community time series (>15 species). Second (for **G2**), we use this dataset to explore the  
142 consequence of variation in  $z$  for interpreting stability in general, and the portfolio effect in  
143 particular. Third (for **G3**), we propose a novel and general mechanism that can help explain the  
144 wide range of  $z$  observed in natural communities. Our mechanism is based on how species'  
145 rank-abundance distribution in a community change over time (MacArthur 1957; McGill *et al.*  
146 2007). Although the rank-abundance curves are widely studied in ecology (Whittaker 1965),  
147 their temporal turnover has not been previously explored in the context of explaining variation in  
148 mean-variance scaling among communities (i.e. variability in  $z$ ).

149

## 150 **Materials & Methods**

151 We compiled long-term abundance (or biomass when abundance was not available for 379 plant  
152 communities) annual time series (20 to 57 years) data from a public database (Ghosh *et al.* 2023)  
153 for 1,694 communities in total, and for multiple taxa (e.g., birds, fish, terrestrial and freshwater  
154 invertebrates, phytoplankton, plants with a minimum of 15 species sampled annually). We  
155 included species that were present for at least for 70% of the total sampling period, thus,  
156 following other studies (Sasaki & Lauenroth 2011; Valencia *et al.* 2020), we focused on the  
157 dynamics of dominant species in communities. For each of the 1,694 communities, we computed  
158 the average correlation between years ( $r$ ), and five additional metrics using the *ecofolio*  
159 R-package (Anderson *et al.* 2013). They are temporal Taylor's slope ( $z$ ), community-level  
160 temporal synchrony among species as variance ratio, VR, (Loreau & de Mazancourt 2008),

161 temporal community stability (as  $CV^{-1}$ ), and two types of portfolio effects (Anderson *et al.*  
162 2013), PE, considering without (i.e. based on an average-CV based approach) and with  
163 mean-variance scaling. We also computed net tail-dependence among species' ranks (i.e.  
164 dependence between lower ranks minus dependence between higher ranks, rarest species got  
165 lowest rank) between any two years of the whole study period, using *partial Spearman*  
166 *correlation* approach (Ghosh *et al.* 2020a, b).

167

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

178

179 To develop the model, we simulated three types of communities with the same number of species  
180 ( $R$ ) and the same between-year correlation ( $r$ ). They are - type I, Fig. 4A: having more  
181 dependence among the dominant group of species (i.e., consistent upper ranks in RAC and more  
182 turnover in lower ranks), type II, Fig. 4B: having more dependence among the not-so-common or  
183 rare group of species (i.e., consistent lower ranks in RAC and more turnover in upper ranks), and

184 type III, Fig. 4C: having no dependence in any specific group (i.e., complete and random annual  
185 turnover among species ranks). “Copula”, a mathematical tool and a rank-based approach, has  
186 been used to compute tail-dependence (i.e., dependence in the extremely high or low values)  
187 among two correlated ecological variables in past studies (Ghosh *et al.* 2020a, b, c, 2021; Walter  
188 *et al.* 2022). Copulas make the marginal distribution uniform so that the dependence information  
189 remains unique on its own. For example, with the same sample set  $(x_i, y_i); i = 1, 2, \dots, R$  one  
190 can generate type I, type II, and type III dependence using three particular single-parameter  
191 “copula” families: Survival Clayton, Normal, Clayton, respectively (see *iRho* function from  
192 *copula* R-package for details (Yan 2007)). We used this approach in the community matrix,  $M$ ,  
193 (with abundance or biomass for  $R$  number of species that are sampled for  $N$  years; species along  
194 columns and years along rows) so that the Spearman correlation between any two years are the  
195 same. Specifically, we first constructed such a community from Clayton family that has  
196 dependence in lower ranks (type II), and then we permuted  $M$  in such a way to eliminate the  
197 tail-dependence structure but preserve the same between-year correlation,  $r$  (up to sampling  
198 error). In doing so, this permutation generated a Normal copula (type III). Then, we again  
199 permuted the community matrix  $M$  to get upper tail-dependence (i.e., dependence in upper ranks)  
200 preserving between-year correlations and leading to the Survival Clayton copula (i.e. a  
201 180-degree rotation of Clayton family). We generated 1,000 surrogates for each type of  
202 community (see `Simulation_zmorethan2.R` script from the Zenodo repo:  
203 <https://doi.org/10.5281/zenodo.8373892>). A similar algorithm was previously used in Spatial  
204 Taylor’s law context to generate surrogate communities with the same correlation but different  
205 dependence structures among sites (Ghosh *et al.* 2020a).

206

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

217

## 218 Results

219 Our data compilation confirms that most of communities had values of  $z$  within the commonly  
220 reported range from previous studies (i.e., between 1 to 2), but also reveals that nearly 5% of  
221 communities had values of  $z$  outside that range (Fig. 3A), addressing **G1**. Consistent with  
222 previous theory, and confirmed with simulated community timeseries (Fig. 2A), stability was  
223 higher for communities having  $z < 2$  than the communities with  $z > 2$  (Fig. 3B, addressing **G2**).  
224 The positive effect of diversity (i.e. richness) on stability was weaker (slope is less steep) for  
225 communities with  $z > 2$ . This result highlights the potential need to account for heterogeneity in  $z$   
226 values when comparing the stability among communities. We additionally find that such  
227 heterogeneity is important for interpreting stabilizing mechanisms of community stability, such  
228 as the portfolio effect (for **G2**). Simulated communities show the limitations of previous  
229 approaches (i.e. based on average-CVs following Box 1) that overestimate PE for  $z < 2$  (Fig. 2B,

230 solid lines), and the underestimate PE for  $z > 2$  (Fig. 2B, dashed lines). As expected, these  
231 approaches converge to the same answer when  $z = 2$ , and so the relevance of this improved  
232 method depends on how often the mean-variance scaling exponent in natural communities  
233 deviates from 2. Consistent with this previous theory, our empirical estimates of PE were higher  
234 without accounting for the mean-variance scaling (Fig. 3C), because the majority of communities  
235 had  $z < 2$ . Comparing these two approaches (i.e. with and without accounting for mean-variance  
236 scaling) clearly shows larger values for PE without mean-variance scaling (i.e. green points,  
237  $n = 1,610$ , above the diagonal line, Fig. 3D) for  $z < 2$ , whereas communities with  $z > 2$  had larger PE  
238 when accounting for mean-variance scaling (i.e. pink points,  $n = 80$ , below the diagonal line, Fig.  
239 3D).

240

241 Our model of RAC turnover provides new insight into explaining the wide variation observed in  
242 in our empirical dataset (Figs. 4D, 5), addressing **G3**. The simulation from RAC turnover model,  
243 as depicted in Fig. 4D, shows communities exhibiting high annual turnover among all species  
244 had  $z$  values within the expected range (black solid points  $\sim 1.5$  showed the mean of 1,000  
245 estimates, Case III). Moreover, we find that communities with high turnover for any particular  
246 group (rare: Case I, dominant: Case II) show a much wider range of  $z$ . For above-average  
247 year-to-year correlation ( $r > 0.5$ ), communities where rare species change their ranks more  
248 frequently are more likely to have  $z$  less than 1 (Case I, follow blue dotted lines in Fig. 4D after  
249 the crossing at  $r = 0.5$ ). Whereas, communities in which dominant species changed their ranks  
250 more frequently are more likely to have  $z$  greater than 2 (Case II, follow red dotted lines in Fig.  
251 4D beyond  $r = 0.5$ ). The patterns are opposite below  $r = 0.5$ , where Case I and Case II have a  
252 higher probability to have  $z > 2$ , and  $z < 1$ , respectively. Our repeated simulation for different

253 combinations of richness ( $R$ ), and time series length ( $N$ ) gives similar general finding, and is  
254 robust to the choice of both  $R$  and  $N$ .

255

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

272

273 In our compilation of community timeseries, the species richness varies from 15 to 89  
274 (median=40 species, Fig. 5A), the length of timeseries sampled varies from 20 to 57 years  
275 (median=22 years), the correlations between years are typically  $>0.5$  (Fig. 5B), and the

276 synchrony among species (as measured by the variance ratio) is typically  $<0.75$  (Fig. 5C). The  
277 Variance Ratio (VR) has a range of (0, 1). VR values close to 0 implies less synchrony and  
278 values of 1 indicate perfect synchrony. Though most data lies in the bottom-left box of Fig. 5C  
279 with low synchrony ( $VR < 0.5$ ,  $1 < z < 2$ ), there are also some communities with  $z > 2$  but low  
280 synchrony (in the top-left box).

281

## 282 Discussion

283 Overall, our data compilation, analysis, and simulation model allows us to explore how  
284 heterogeneity in  $z$  can affect inferences about stability-diversity relationships and the portfolio  
285 effect (PE) (Fig. 3), and provides a novel explanation for the wide distribution of temporal  
286 Taylor's slope ( $z$ ) observed in ecological communities (Fig. 4). Previous work has established  
287 that strong positive relationships between richness and stability are only expected when  $z < 2$  (Fig.  
288 3B), and that variability in  $z$  among communities can mask how we estimate the contribution of  
289 PE to community stability (Fig. 3C-D). Although the majority of empirical observations of  
290 communities find  $z$  between 1 and 2 (Fig. 3A), large values of  $z$  are common enough to affect  
291 inferences about the causes of stability variation. For example, measuring the PE without  
292 considering the mean-variance scaling relationship can lead to substantial overestimates of  
293 stability when  $z < 2$ , and increasingly large underestimates when  $z > 2$  (Fig. 2B). As the statistical  
294 averaging effect is likely a fundamental mechanism of stability (Zhao *et al.* 2022), it is essential  
295 to make accurate assessments in order to support conservation and management efforts.

296

297 Several previous mechanisms have been proposed to explain variability in  $z$ , and have speculated  
298 about causal drivers of community stability. Interspecific competition and environmental

299 variability, for example, can explain some variation in  $z$  that can impact stability (Kilpatrick &  
300 Ives 2003; Cobain *et al.* 2019). For example, negative interactions among species (e.g.  
301 competition) is a commonly proposed mechanism for explaining why abundant species are less  
302 variable than expected given their mean abundance, leading to communities with  $z < 2$  (Kilpatrick  
303 and Ives 2003). Here, our proposed mechanism can explain  $z$  values both less than and greater  
304 than 2 (Fig. 4). This implies there can be multiple reasons for the observed range of  $z$  values in  
305 natural communities, and also multiple explanations, beyond simply competition, for why  
306 communities can both have low synchrony and have  $z$ -values less than and greater than two (Fig.  
307 5C).

308

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

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

326

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

345

346 In conclusion, we have shown that considering Taylor's law can improve our understanding of  
347 community variability, stability, portfolio effects, and species abundance distribution over time.

348 There are several important insights from our study. First, identifying the causes of  
349 mean-variance scaling of population abundances is important for the longstanding challenge of  
350 understanding relationships between diversity and stability of communities (McCann 2000).

351 Importantly, greater species richness does not necessarily ensure more temporal stability if  
352 abundant species are more variable than expected, such that communities have  $z > 2$  (Fig. 3B).

353 Second, identifying the importance of portfolio effects as a stabilizing mechanism of  
354 communities can be both over- or underestimated if the mean-variance scaling relationship is not

355 carefully considered (Zhao *et al.* 2022). Third, we establish a novel and general biological  
356 mechanism that can help explain observed wide variation in  $z$  (i.e.,  $< 1$  or  $> 2$ ) seen in natural

357 communities. We confirm our hypothesis with simulated (i.e., from the *RAC-turnover model*;  
358 Fig. 4) and empirical data (i.e., from 1,694 long-term natural communities; Fig. 5) that temporal

359 turnover in RACs via species-reordering is an important factor determining the value of  $z$ . This  
360 finding is consistent with earlier studies that showed global change drivers can reshape RACs via

361 species reordering (Avolio *et al.* 2015, 2022), and could be crucial for better understanding the  
362 mechanism behind the community response to global change drivers.

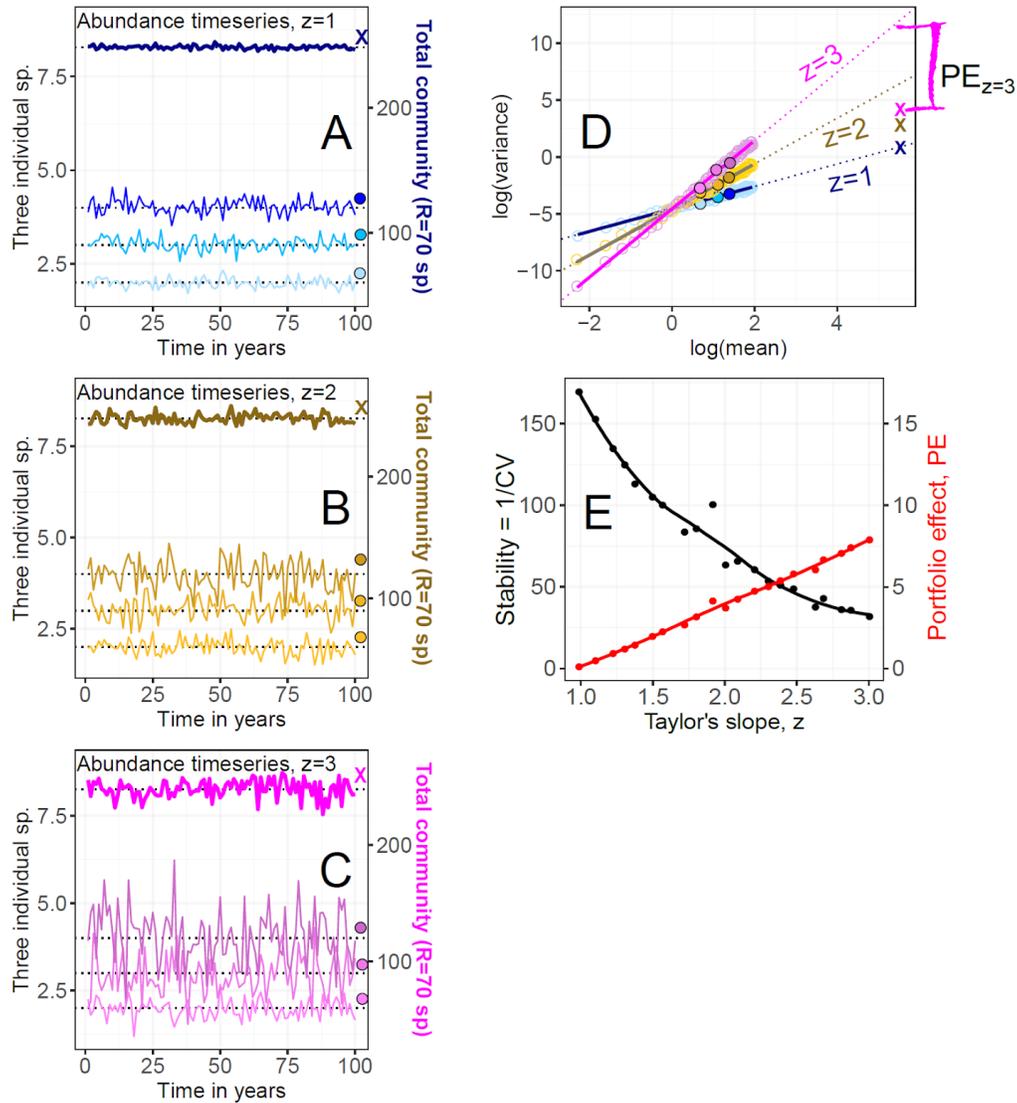
363

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369 **Figures:**

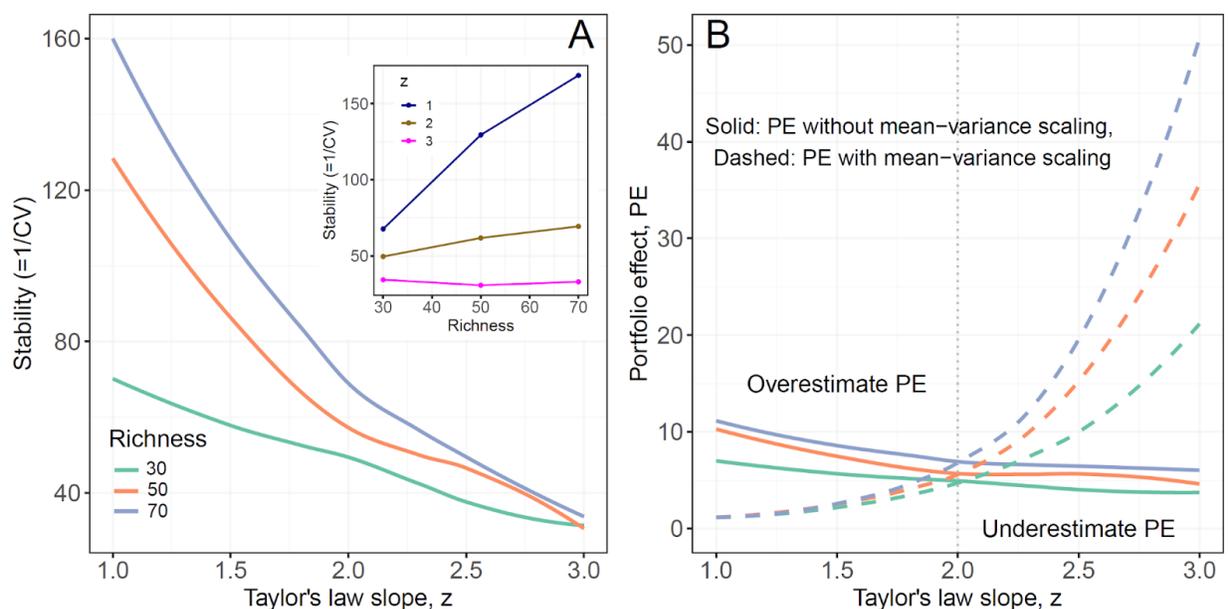


370

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

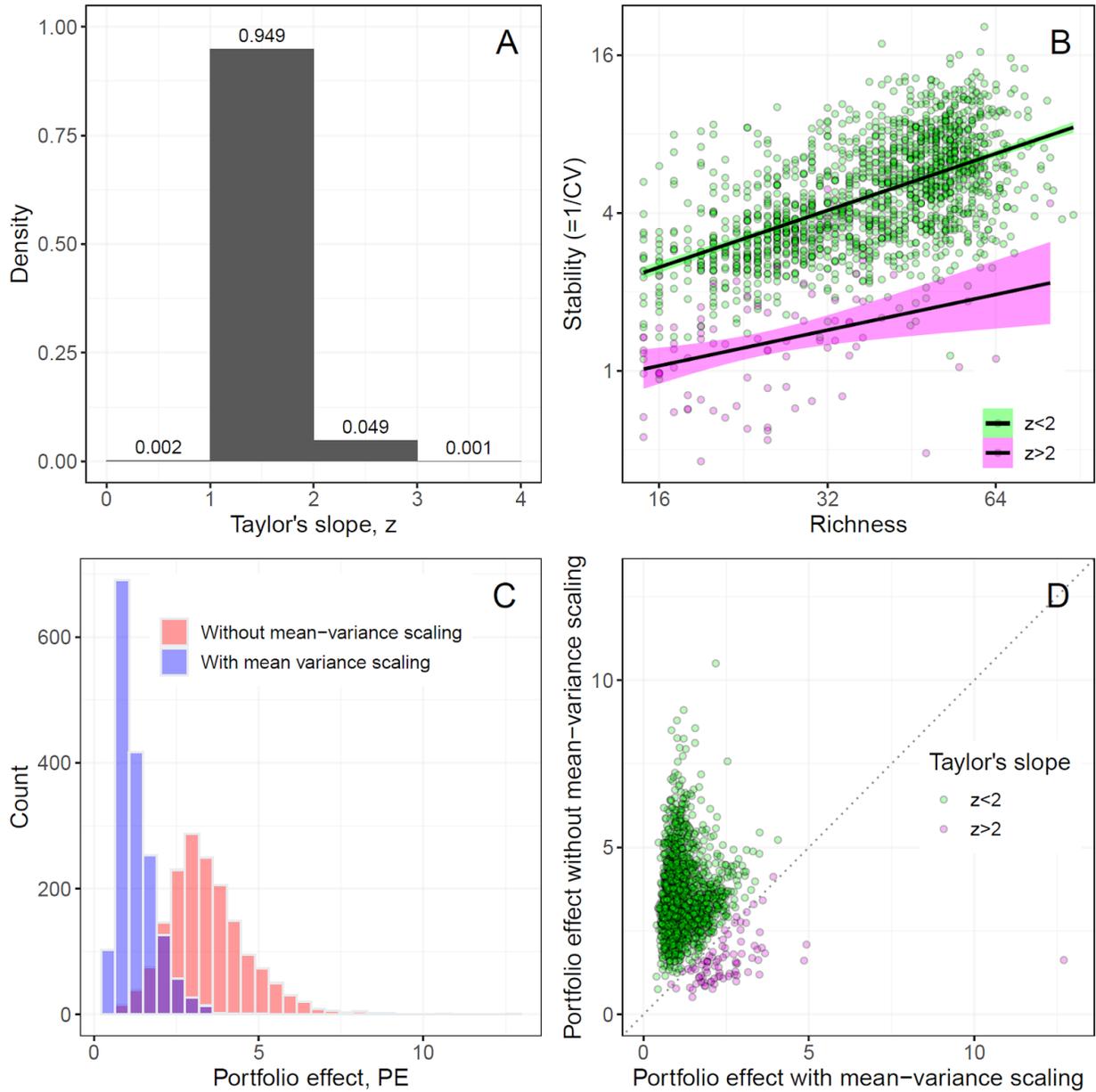
376 (thinner lines) and total community abundance timeseries on the top (thicker lines). Species are  
 377 very weakly related in each of these simulated communities (synchrony or variance ratio <  
 378 0.025). Due to the fluctuation scaling relationship, the variance of total community abundance is  
 379 often lower (symbol X) than the predicted value on the dotted line for a given community mean,  
 380 D. Higher value of  $z$  results in a larger difference, and lowers community stability (i.e., the  
 381 inverse of variability in total community abundance timeseries), E.

382



383

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

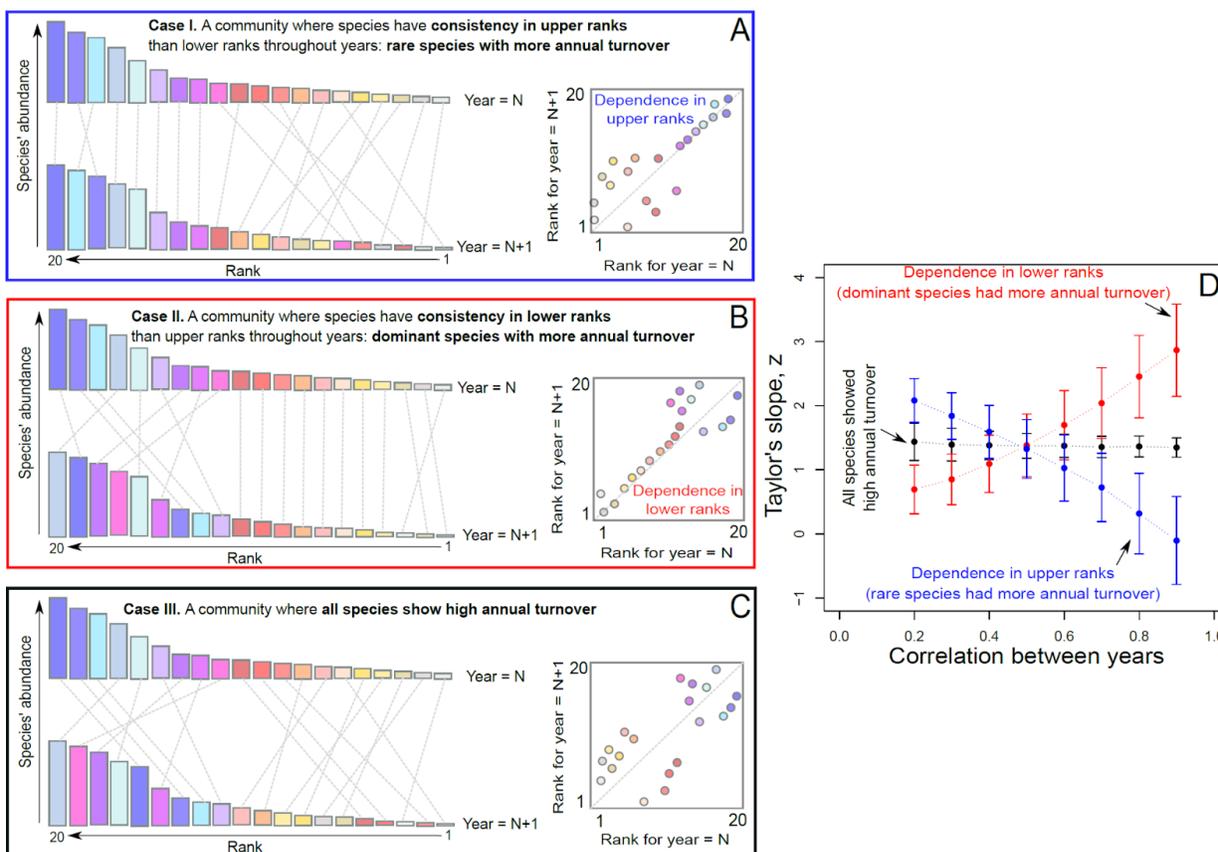


392

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

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

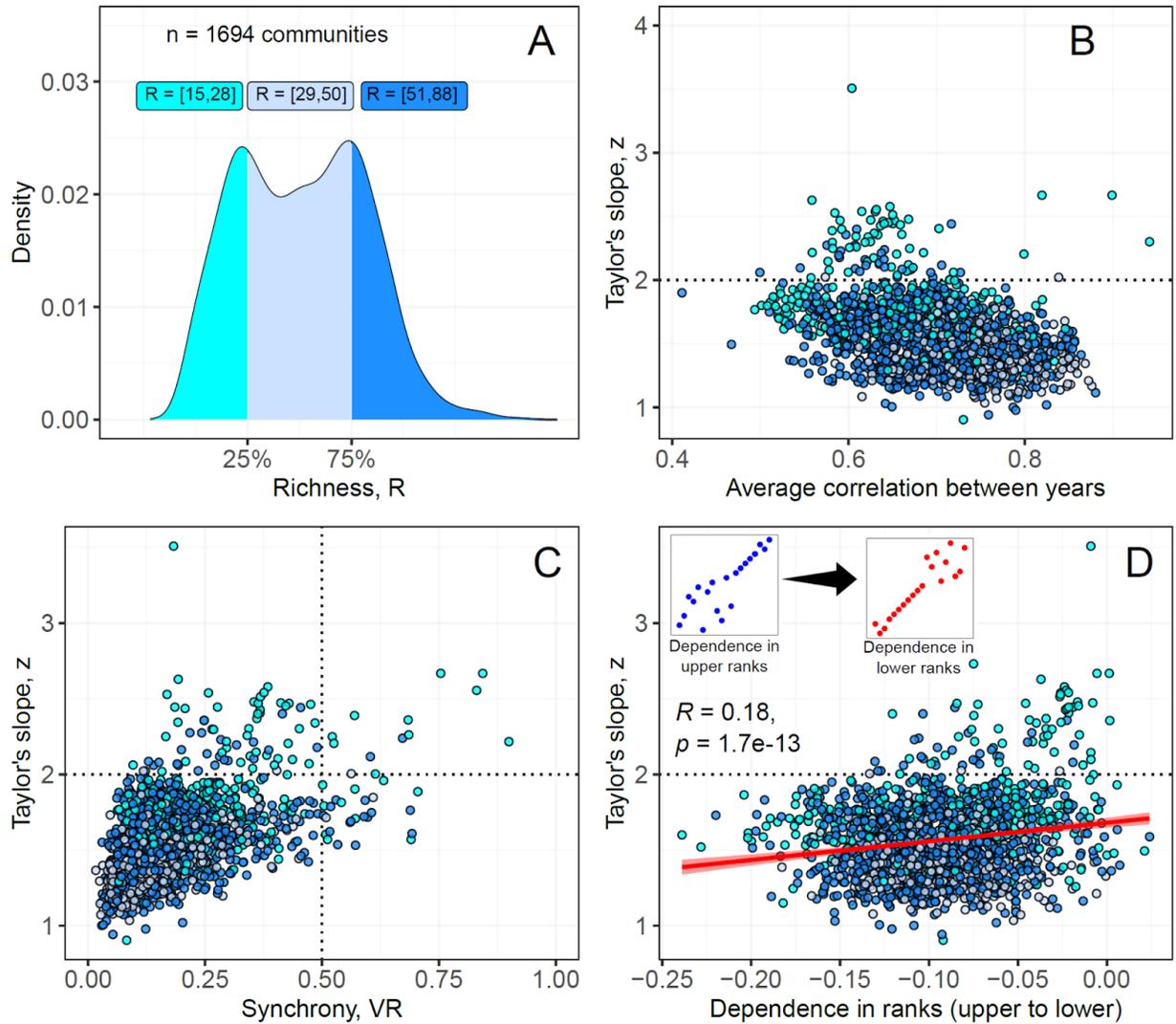
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404

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

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



420

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

428

429 **Box 1: Quantifying portfolio effect, PE, for a community considering with or without**  
 430 **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  $z$ :

$$v_i = am_i^z; i = 1, 2, \dots, n \dots \dots \dots (1)$$

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.

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

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

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

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

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

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  $PE$ :

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

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  $PE_{avgCV} / PE_{mv} = \frac{\sum_{i=1}^n m_i^{-1/2}}{n \left( \sum_{i=1}^n m_i \right)^{-1/2}}$ , 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)).

431

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