

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

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24 Abstract

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

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47 Introduction

48 Our understanding of the temporal variability of populations or communities, which is of
49 long-standing interest in ecology (R. M. Anderson et al. 1982; Bahram, Peay, and Tedersoo
50 2015), often centers around a scaling relationship between the mean and variance of species'
51 abundances (aka Taylor's Law, 1961). In a pioneering meta-analysis in 1961, L.R. Taylor
52 proposed a general scaling relationship, referred to as Taylor's (power) law (hereafter TL),
53 relating the variance (v) of population density with its mean (m): $v = am^z$, for values of $a > 0$, z
54 being called TL slope or exponent. This scaling relationship is ubiquitously observed for many
55 taxa in nature (e.g., bacteria, fish, plants, insects, voles, etc.), and has also been applied outside
56 of ecological systems (Eisler, Bartos, and Kertész 2008; R. A. J. Taylor 2019; Kalyuzhny et al.
57 2014). Although Taylor's law was originally developed for the analysis of spatial variation of
58 population density (L. R. Taylor 1961), it is also highly relevant, but less often studied, in the
59 context of temporal analyses of communities (reviewed by Cobain et al. 2019). In spatial
60 analyses of density variation (TL_{space}), z_{space} is an index of the degree of patchiness of the
61 population density of a single species among sites (i.e. metapopulations). Whereas, in temporal
62 analyses of density variation (TL_{time}), z_{time} is an index of temporal aggregation of the abundance
63 fluctuations of multiple species in a community (i.e., from the same site). The z_{time} exponent has
64 been useful for assessing population persistence (Pertoldi, Bach, and Loeschcke 2008;
65 Kalyuzhny et al. 2014), the stability of crop yields (Döring, Knapp, and Cohen 2015), and
66 fluctuations in fish stocks (Kuo et al. 2016; Xu, Kolding, and Cohen 2019; Segura et al. 2021).

67 Currently, understanding the importance of mean-variance fluctuation scaling (i.e. z_{time})
68 for making inferences from community dynamics is limited by uncertainty in i) the distribution
69 of z_{time} in natural communities, ii) how z_{time} variability affects interpretations of community

70 stability, and iii) the mechanisms underlying z_{time} variability. We address each of three gaps
71 (referred to below as G1-G3). First, existing studies of natural communities have documented a
72 limited range of variation in z_{time} (Xu and Cohen 2019; Cobain, Brede, and Trueman 2019), but
73 with the increasing availability of long-term community time series we can improve our
74 inference about the distribution of z_{time} in nature.

75 Second, there is longstanding theory about how variation in z_{time} is relevant for
76 interpreting community stability (Cottingham, Brown, and Lennon 2001; Kilpatrick and Ives
77 2003; Kalyuzhny et al. 2014; Zhao et al. 2019; Cobain, Brede, and Trueman 2019), but these
78 interpretations are somewhat sensitive to mean variance scaling. Importantly, when z is greater
79 than 1, the expected temporal variance of the total community abundance is less than that of a
80 single population for that same mean abundance (Figure 1), meaning that species-level variance
81 increases nonlinearly in relation to mean abundances. This reduced variance arises because of the
82 statistical averaging of independently varying population time series, which is known as the
83 portfolio effect concept (hereafter PE) (Doak et al. 1998; Schindler, Armstrong, and Reed 2015).
84 PE has been widely used to quantify the importance of species diversity for overall community
85 stability (i.e., inverse of community variability, CV), but its interpretation depends on z_{time} for
86 that community (Cottingham, Brown, and Lennon 2001). For example, the magnitude of the PE
87 is negligible when $z_{\text{time}} \sim 1$, and increases with z_{time} (Figure 1e, red line). This means that estimates
88 of community stability (i.e. $1/\text{CV}$), for a given species richness, decrease with the increase in z_{time}
89 for a community (Figure 1e, black line). Importantly, the consistently negative relationship
90 between stability and z over a wide range of species diversity (Figure 2a) means that the
91 expected slope of the relationship between species richness and stability decreases substantially
92 as z_{time} increases (Figure 2a, inset). Often, PEs are estimated by comparing the overall

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

98 Third, existing theory can explain why z_{time} often varies between 1 and 2 (L. R. Taylor
99 and Woivod 1982; Tokeshi 1995; Xiao, Locey, and White 2015), but provides no general
100 mechanistic explanation for the entire empirically observed range of z_{time} . For spatial TL context,
101 several proposed mechanisms that explain variation in z_{space} have considered density dependence
102 (Perry 1994), density-independent and stochastic population growth (Cohen, Xu, and Schuster
103 2013), population synchrony (Cohen and Saitoh 2016), and random sampling from skewed
104 distribution (Cohen and Xu 2015). Whereas for z_{time} proposed mechanisms have considered
105 interspecific competition (Kilpatrick and Ives 2003), environmental variability (Cohen and
106 Saitoh 2016), correlated reproduction (Ballantyne and J. Kerkhoff 2007), sampling error
107 (Kalyuzhny et al. 2014), and limited sampling effort (Giometto et al. 2015). However, all of
108 these previous studies have focused on explaining why z_{time} is typically less than 2, and only a
109 few previous studies have provided a mechanistic explanation for why it can be greater than 2. In
110 spatial models, z_{space} can be greater than 2 due to synchrony among metapopulations (Reuman et
111 al. 2017) especially when they are rare (Ghosh, Sheppard, Holder, et al. 2020), and due to
112 growing stochasticity (Cohen, Xu, and Schuster 2013) or unexpected changes in a smoothly
113 autocorrelated environment (Cohen 2014). In the case of z_{time} , only one previous study of a fish
114 community found that environmental variability can lead to a size-based Taylor's slope greater
115 than 2 (Cobain, Brede, and Trueman 2019).

116 In this paper, we will address each of those three aforementioned gaps. First (for **G1**), we
117 estimate the distribution of z_{time} (hereafter z) in nature by compiling thousands of long-term (>20
118 years) community time series (>15 species). Second (for **G2**), we use this dataset to explore the
119 consequence of variation in z for interpreting stability in general, and the portfolio effect in
120 particular. Third (for **G3**), we propose a novel and general mechanism that can help explain the
121 wide range of z observed in natural communities. Our mechanism is based on how species'
122 rank-abundance distribution in a community change over time (MacArthur 1957; McGill et al.
123 2007). Although the rank-abundance curves are widely studied in ecology (Whittaker 1965),
124 their temporal turnover has not been previously explored in the context of explaining variation in
125 mean-variance scaling among communities (i.e. variability in z).

126

127 **Materials & Methods**

128 We compiled long-term abundance (or biomass when abundance was not available for
129 379 plant communities) annual time series (20 to 57 years) data from a public database (Ghosh et
130 al. 2023) for 1,694 communities in total, and for multiple taxa (e.g., birds, fish, terrestrial and
131 freshwater invertebrates, phytoplankton, plants with a minimum of 15 species sampled annually).
132 We included species that were present for at least for 70% of the total sampling period, thus,
133 following other studies (Valencia et al. 2020; Sasaki and Lauenroth 2011), we focused on the
134 dynamics of dominant species in communities. For each of the 1,694 communities, we computed
135 the average correlation between years (r), and five additional metrics using the *ecofolio*
136 R-package (S. C. Anderson, Cooper, and Dulvy 2013). They are temporal Taylor's slope (z),
137 community-level temporal synchrony among species as variance ratio, VR, (Loreau and de
138 Mazancourt 2008), temporal community stability (as CV^{-1}), and two types of portfolio effects (S.

139 C. Anderson, Cooper, and Dulvy 2013), PE, considering without (i.e. based on an average-CV
140 based approach) and with mean-variance scaling. We also computed net tail-dependence among
141 species' ranks (i.e. dependence between lower ranks minus dependence between higher ranks,
142 rarest species got lowest rank) between any two years of the whole study period, using *partial*
143 *Spearman correlation* approach (Ghosh, Sheppard, Holder, et al. 2020; Ghosh, Sheppard, Reid,
144 et al. 2020).

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

156 To develop the model, we simulated three types of communities with the same number of
157 species (R) and the same between-year correlation (r). They are - type I, Figure 4a: having more
158 dependence among the dominant group of species (i.e., consistent upper ranks in RAC and more
159 turnover in lower ranks), type II, Figure 4b: having more dependence among the not-so-common
160 or rare group of species (i.e., consistent lower ranks in RAC and more turnover in upper ranks),
161 and type III, Figure 4c: having no dependence in any specific group (i.e., complete and random

162 annual turnover among species ranks). “Copula”, a mathematical tool and a rank-based
163 approach, has been used to compute tail-dependence (i.e., dependence in the extremely high or
164 low values) among two correlated ecological variables in past studies (Ghosh, Sheppard, Holder,
165 et al. 2020; Ghosh, Cottingham, and Reuman 2021; Ghosh, Sheppard, Reid, et al. 2020; Ghosh,
166 Sheppard, and Reuman 2020; Walter et al. 2022). Copulas make the marginal distribution
167 uniform so that the dependence information remains unique on its own. For example, with the
168 same sample set $(x_i, y_i); i = 1, 2, \dots, R$ one can generate type I, type II, and type III
169 dependence using three particular single-parameter “copula” families: Survival Clayton, Normal,
170 Clayton, respectively (see *iRho* function from *copula* R-package for details (Yan 2007)). We
171 used this approach in the community matrix, M , (with abundance or biomass for R number of
172 species that are sampled for N years; species along columns and years along rows) so that the
173 Spearman correlation between any two years are the same. Specifically, we first constructed such
174 a community from Clayton family that has dependence in lower ranks (type II), and then we
175 permuted M in such a way to eliminate the tail-dependence structure but preserve the same
176 between-year correlation, r (up to sampling error). In doing so, this permutation generated a
177 Normal copula (type III). Then, we again permuted the community matrix M to get upper
178 tail-dependence (i.e., dependence in upper ranks) preserving between-year correlations and
179 leading to the Survival Clayton copula (i.e. a 180-degree rotation of Clayton family). We
180 generated 1,000 surrogates for each type of community (see *Simulation_zmorethan2.R* script
181 from the Zenodo repo: <https://doi.org/10.5281/zenodo.8373892>). A similar algorithm was
182 previously used in Spatial Taylor’s law context to generate surrogate communities with the same
183 correlation but different dependence structures among sites (Ghosh, Sheppard, Holder, et al.
184 2020).

185 Given this set of community types, we hypothesized that the third type (i.e. Figure 4:
186 Case III) would lead to z values within the commonly observed range of 1 and 2, irrespective of
187 the value of the r . However, we also suspected that any tail-dependencies in the ranks (e.g. lower
188 or upper tail dependencies in Case 1 and II) could expand the range of z both below 1 and above
189 2 (i.e., for the Case I, II). To explore this, we simulated for a given year-to-year correlation, r ,
190 three types of communities each with 1,000 surrogates (or replicates), and species richness $R = 40$
191 where we tracked species abundance for $N = 22$ years. Therefore, each replicate community type
192 has the same year-to-year correlation, r , and we varied r over a range from 0.2 to 0.9 (results
193 shown in Figure 4d). R and N for this simulation are chosen to have same median values for
194 richness and timeseries length found in our dataset, so that we can compare the results.

195

196 **Results**

197 Our data compilation confirms that most of communities had values of z within the
198 commonly reported range from previous studies (i.e., between 1 to 2), but also reveals that nearly
199 5% of communities had values of z outside that range (Figure 3a), addressing **G1**. Consistent
200 with previous theory, and confirmed with simulated community timeseries (Figure 2a), stability
201 was higher for communities having $z < 2$ than the communities with $z > 2$ (Figure 3b, addressing
202 **G2**). The positive effect of diversity (i.e. richness) on stability was weaker (slope is less steep)
203 for communities with $z > 2$. This result highlights the potential need to account for heterogeneity
204 in z values when comparing the stability among communities. We additionally find that such
205 heterogeneity is important for interpreting stabilizing mechanisms of community stability, such
206 as the portfolio effect (for **G2**). Simulated communities show the limitations of previous
207 approaches (i.e. based on average-CVs following Box 1, *Supporting Information*) that

208 overestimate PE for $z < 2$ (Figure 2b, solid lines), and the underestimate PE for $z > 2$ (Figure 2b,
209 dashed lines). As expected, these approaches converge to the same answer when $z = 2$, and so the
210 relevance of this improved method depends on how often the mean-variance scaling exponent in
211 natural communities deviates from 2. Consistent with this previous theory, our empirical
212 estimates of PE were higher without accounting for the mean-variance scaling (Figure 3c),
213 because the majority of communities had $z < 2$. Comparing these two approaches (i.e. with and
214 without accounting for mean-variance scaling) clearly shows larger values for PE without
215 mean-variance scaling (i.e. green points, $n = 1,610$, above the diagonal line, Figure 3d) for $z < 2$,
216 whereas communities with $z > 2$ had larger PE when accounting for mean-variance scaling (i.e.
217 pink points, $n = 80$, below the diagonal line, Figure 3d).

218 Our model of RAC turnover provides new insight into explaining the wide variation
219 observed in in our empirical dataset (Figures 4d, 5), addressing **G3**. The simulation from RAC
220 turnover model, as depicted in Figure 4d, shows communities exhibiting high annual turnover
221 among all species had z values within the expected range (black solid points ~ 1.5 showed the
222 mean of 1,000 estimates, Case III). Moreover, we find that communities with high turnover for
223 any particular group (rare: Case I, dominant: Case II) show a much wider range of z . For
224 above-average year-to-year correlation ($r > 0.5$), communities where rare species change their
225 ranks more frequently are more likely to have z less than 1 (Case I, follow blue dotted lines in
226 Figure 4d after the crossing at $r = 0.5$). Whereas, communities in which dominant species changed
227 their ranks more frequently are more likely to have z greater than 2 (Case II, follow red dotted
228 lines in Figure 4d beyond $r = 0.5$). The patterns are opposite below $r = 0.5$, where Case I and Case
229 II have a higher probability to have $z > 2$, and $z < 1$, respectively. Our repeated simulation for

230 different combinations of richness (R), and time series length (N) gives similar general finding,
231 and is robust to the choice of both R and N .

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

248 In our compilation of community timeseries, the species richness varies from 15 to 89
249 (median=40 species, Figure 5a), the length of timeseries sampled varies from 20 to 57 years
250 (median=22 years), the correlations between years are typically >0.5 (Figure 5b), and the
251 synchrony among species (as measured by the variance ratio) is typically <0.75 (Figure 5c). The
252 Variance Ratio (VR) has a range of (0, 1). VR values close to 0 implies less synchrony and

253 values of 1 indicate perfect synchrony. Though most data lies in the bottom-left box of Figure 5c
254 with low synchrony ($VR < 0.5$, $1 < z < 2$), there are also some communities with $z > 2$ but low
255 synchrony (in the top-left box).

256

257 **Discussion**

258 Overall, our data compilation, analysis, and simulation model allows us to explore how
259 heterogeneity in z can affect inferences about stability-diversity relationships and the portfolio
260 effect (PE) (Figure 3), and provides a novel explanation for the wide distribution of temporal
261 Taylor's slope (z) observed in ecological communities (Figure 4). Previous work has established
262 that strong positive relationships between richness and stability are only expected when $z < 2$
263 (Figure 3b), and that variability in z among communities can mask how we estimate the
264 contribution of PE to community stability (Figure 3c-d). Although the majority of empirical
265 observations of communities find z between 1 and 2 (Figure 3a), large values of z are common
266 enough to affect inferences about the causes of stability variation. For example, measuring the
267 PE without considering the mean-variance scaling relationship can lead to substantial
268 overestimates of stability when $z < 2$, and increasingly large underestimates when $z > 2$ (Figure 2b).
269 As the statistical averaging effect is likely a fundamental mechanism of stability (Zhao et al.
270 2022), it is essential to make accurate assessments in order to support conservation and
271 management efforts.

272 Several previous mechanisms have been proposed to explain variability in z , and have
273 speculated about causal drivers of community stability. Interspecific competition and
274 environmental variability, for example, can explain some variation in z that can impact stability
275 (Kilpatrick and Ives 2003; Cobain, Brede, and Trueman 2019). For example, negative

276 interactions among species (e.g. competition) is a commonly proposed mechanism for explaining
277 why abundant species are less variable than expected given their mean abundance, leading to
278 communities with $z < 2$ (Kilpatrick and Ives 2003). Here, our proposed mechanism can explain z
279 values both less than and greater than 2 (Figure 4). This implies there can be multiple reasons for
280 the observed range of z values in natural communities, and also multiple explanations, beyond
281 simply competition, for why communities can both have low synchrony and have z -values less
282 than and greater than two (Figure 5c).

283 Our simulations demonstrate how high turnover among all species' ranks (reordering all
284 species) can yield communities with z -values in the range of [1, 2], whereas group-specific
285 turnover, namely rank-inconsistency only for the dominant species or rare species throughout the
286 years, can yield communities with z values outside the range of [1, 2]. Few previous studies have
287 connected species abundance distribution with Taylor's law (Ma 2015; Cohen 2020), but doing
288 so can reveal how changes in rank abundance distribution (Figure 5) can impact our assessment
289 of community stability (Figure 3). Our results show that monitoring the RACs for rare vs.
290 dominant groups of species can help explain the broad range of z observed in nature. There is a
291 long history of tracking RACs to understand community dynamics in response to global change
292 drivers (Collins et al. 2008; Avolio et al. 2015; Jones, Ripplinger, and Collins 2017; Avolio et al.
293 2019). Our work suggests we need a better understanding of the reasons for temporal variation in
294 RACs and z . For a specific richness, RAC can change due to both species reordering and
295 changes in evenness without reordering ((Collins et al. 2008; Avolio et al. 2015; Jones, Ripplinger,
296 and Collins 2017; Avolio et al. 2019)). A previous study (Wohlgemuth, Solan, and Godbold
297 2016) highlighted the role of species reordering rather than evenness in maintaining ecosystem
298 functioning. Our study also highlights that changes in species reordering, rather than evenness, is

309 most likely to affect z and hence how we make inferences from observed community dynamics
300 (Figures 1, 2, and 5).

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

319 In conclusion, we have shown that considering Taylor's law can improve our
320 understanding of community variability, stability, portfolio effects, and species abundance
321 distribution over time. There are several important insights from our study. First, identifying the

322 causes of mean-variance scaling of population abundances is important for the longstanding
323 challenge of understanding relationships between diversity and stability of communities
324 (McCann 2000). Importantly, greater species richness does not necessarily ensure more temporal
325 stability if abundant species are more variable than expected, such that communities have $z > 2$
326 (Figure 3b). Second, identifying the importance of portfolio effects as a stabilizing mechanism of
327 communities can be both over- or underestimated if the mean-variance scaling relationship is not
328 carefully considered (Zhao et al. 2022). Third, we establish a novel and general biological
329 mechanism that can help explain observed wide variation in z (i.e., < 1 or > 2) seen in natural
330 communities. We confirm our hypothesis with simulated (i.e., from the *RAC-turnover model*;
331 Figure 4) and empirical data (i.e., from 1,694 long-term natural communities; Figure 5) that
332 temporal turnover in RACs via species-reordering is an important factor determining the value of
333 z . This finding is consistent with earlier studies that showed global change drivers can reshape
334 RACs via species reordering (Avolio et al. 2015, 2022), and could be crucial for better
335 understanding the mechanism behind the community response to global change drivers.

336

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529 **Figure Captions**

530

531 **Figure 1**

532 The concept of temporal Taylor's law: in ecological communities population abundance has a
533 variance to mean scaling relationship. Temporal variance can fluctuate with an exponent (z) to
534 the temporal mean - in log scale, the relationship would be a fitted straight line of slope z .
535 Taylor's slope (z) can be below <2 (panel a), or >2 (panel c), with $z=2$ often considered as a
536 limiting case (panel b). a-c show three representative species among a total of 70 species in the
537 community (thinner lines) and total community abundance timeseries on the top (thicker lines).
538 Species are very weakly related in each of these simulated communities (synchrony or variance
539 ratio < 0.025). Due to the fluctuation scaling relationship, the variance of total community
540 abundance is often lower (symbol X) than the predicted value on the dotted line for a given
541 community mean, d. Higher value of z results in a larger difference, and lowers community
542 stability (i.e., the inverse of variability in total community abundance timeseries), e.

543

544 **Figure 2**

545 Temporal Taylor's law slope, z , affects stability (a) and portfolio effect (b) for three different
546 levels of richness: $R=30, 50, \text{ and } 70$. The diversity-stability relationship has a steeper positive
547 slope for lower z , but a weaker positive slope at higher z (inset, a). Within the feasible set of $[1,$
548 $2]$ portfolio effect (PE) computed based on average-CV (i.e., without mean-variance scaling,
549 solid lines, b) gives an overestimate of accurate measure of PE (i.e. considering mean-variance
550 scaling, dashed lines, b). For $z>2$, PE without mean-variance scaling underestimates the true
551 effort. At $z=2$, both measures are exactly the same.

552

553 **Figure 3**

554 Empirical observations verify the concepts of Figure 2. The majority of the communities had
555 temporal Taylor's law slope (z) <2 ($n=1,610$), and 5% of communities had $z>2$ ($n=84$) (panel a).
556 Stability, the inverse of variability in total community abundance ($=1/CV$), was lower for
557 communities with $z>2$ and the stability-diversity relationship had a weaker positive slope
558 compared to communities that had $z<2$ (panel b). Distributions of portfolio effects computed
559 with and without mean-variance relationship are depicted in panel c. Panel d shows for
560 communities having $z>2$, the portfolio effect due to mean-variance scaling was higher (pink
561 points below the dotted 1:1 line) than the portfolio effect if mean-variance scaling had not been
562 considered. On the other hand, for communities with $z<2$, the pattern was opposite (green points
563 above the dotted 1:1 line, panel d), i.e., a higher estimate for portfolio effect happened without
564 considering mean-variance scaling.

565

566 **Figure 4**

567 Mechanism explaining variation in temporal Taylor's law slope (z) for ecological communities
568 when species show a positive year-to-year correlation ($r>0$) in the *RAC-turnover model* (see
569 *Materials & Methods*). In a community where some dominant species are always dominant
570 throughout the years (so consistent in high rank-abundances) but rare species show a more
571 annual turnover, z could be <1 or >2 depending on the value of r (Case I: a, the blue line in d). In
572 an opposite scenario, in a community where some rare species are always rare throughout the
573 years (so consistent in low rank-abundances) but dominant species show a more annual turnover,
574 z could also be <1 or >2 depending on the value of r (Case II: b, the red line in d). When in a

575 community all species would fluctuate in their annual rank abundance, $1 < z < 2$ would happen,
576 irrespective of r values (Case III: c, the black line in d). Simulation with surrogate communities
577 (40 species were simulated for 22 years to match the median values of sampled richness and
578 years from empirical communities) shows dependence in either rank (lower or upper) can make
579 $z < 1$ or $z > 2$, whereas turnover for all species always results in $1 < z < 2$; for details see *Materials &*
580 *Methods*. The bars in panel d are due to two standard deviations for the estimates from 1,000
581 surrogate communities, and plotted around the mean (solid points).

582

583 **Figure 5**

584 Empirical observations show results consistent with the mechanism from Figure 4. A total of
585 1,694 communities have richness in between [15, 88] (panel a), an on-average correlation
586 between years $r > 0.5$ (panel b), and interspecific synchrony (variance ratio) < 0.75 (panel c).
587 Range of r indicates z can be greater than 2 if ranks of rare species were consistent throughout
588 years as shown for the red line in Figure 4d. Empirical communities also show $z > 2$ is possible as
589 consistency or dependence increases in the lower ranks (Pearson correlation, R , from the linear
590 regression is significantly positive, shown in panel d).

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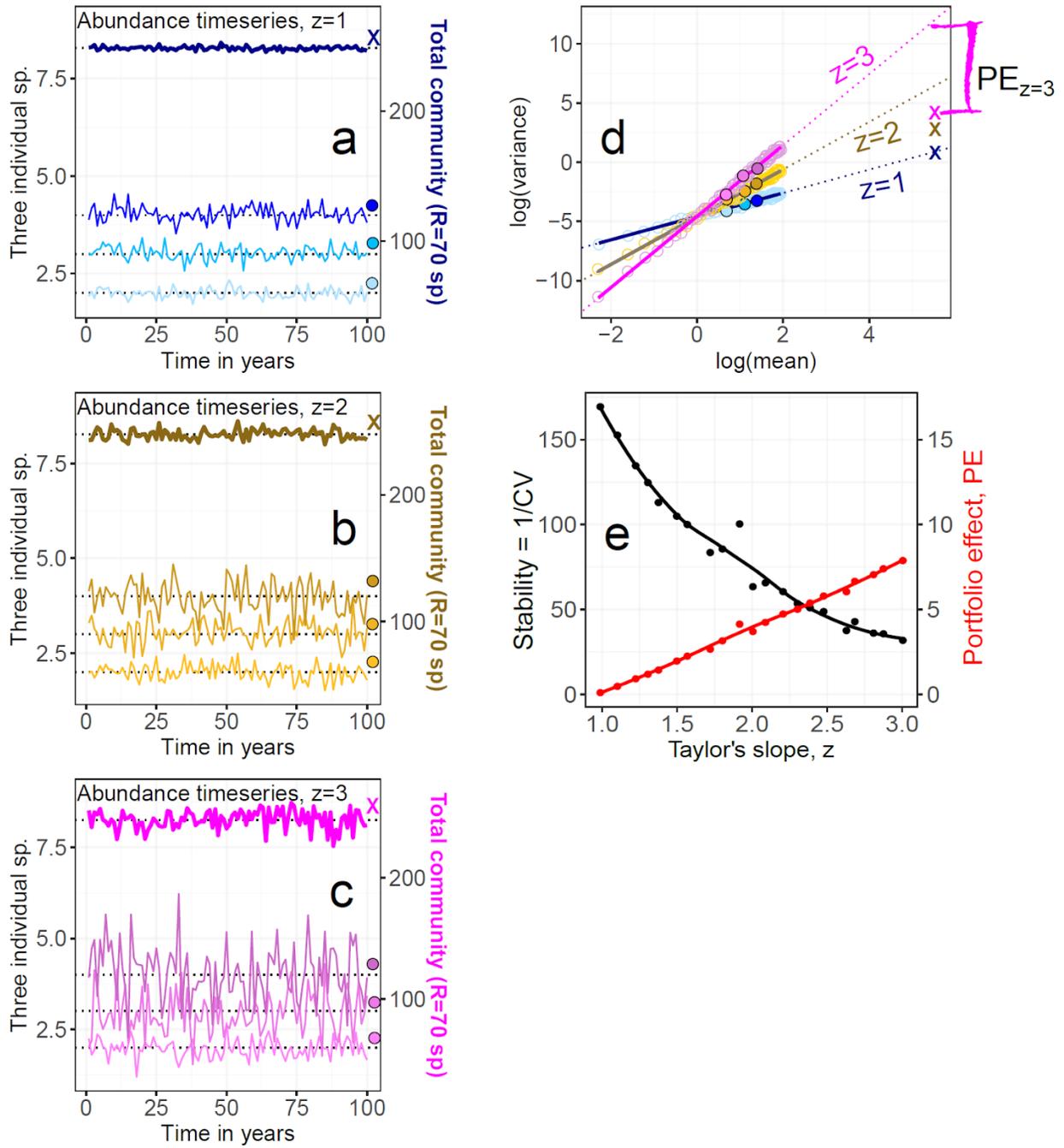
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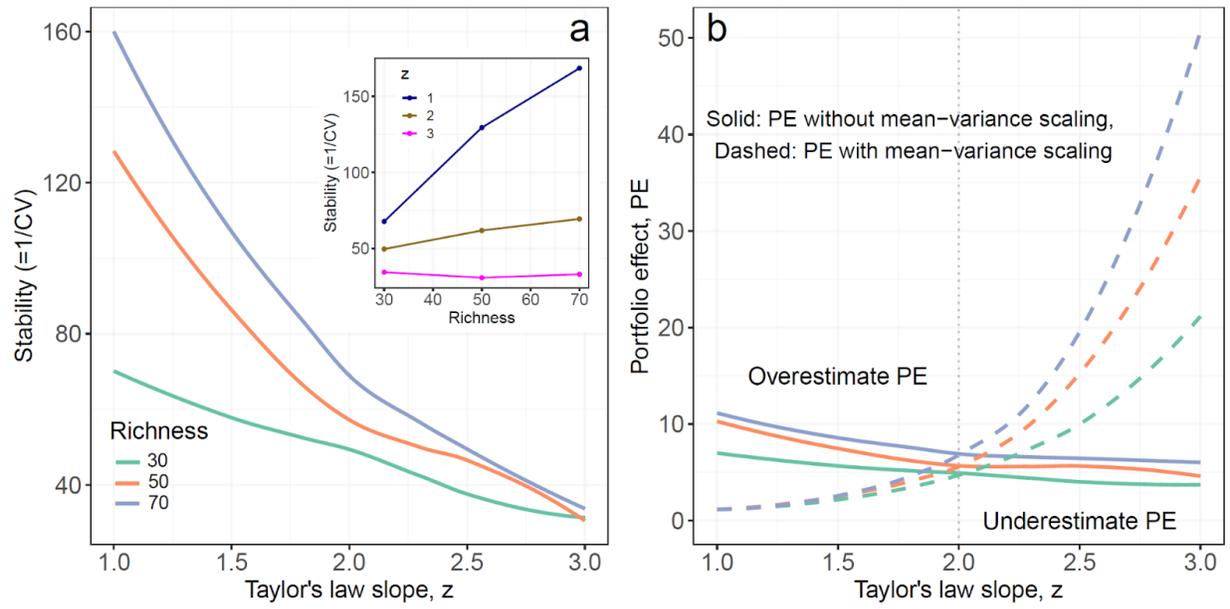
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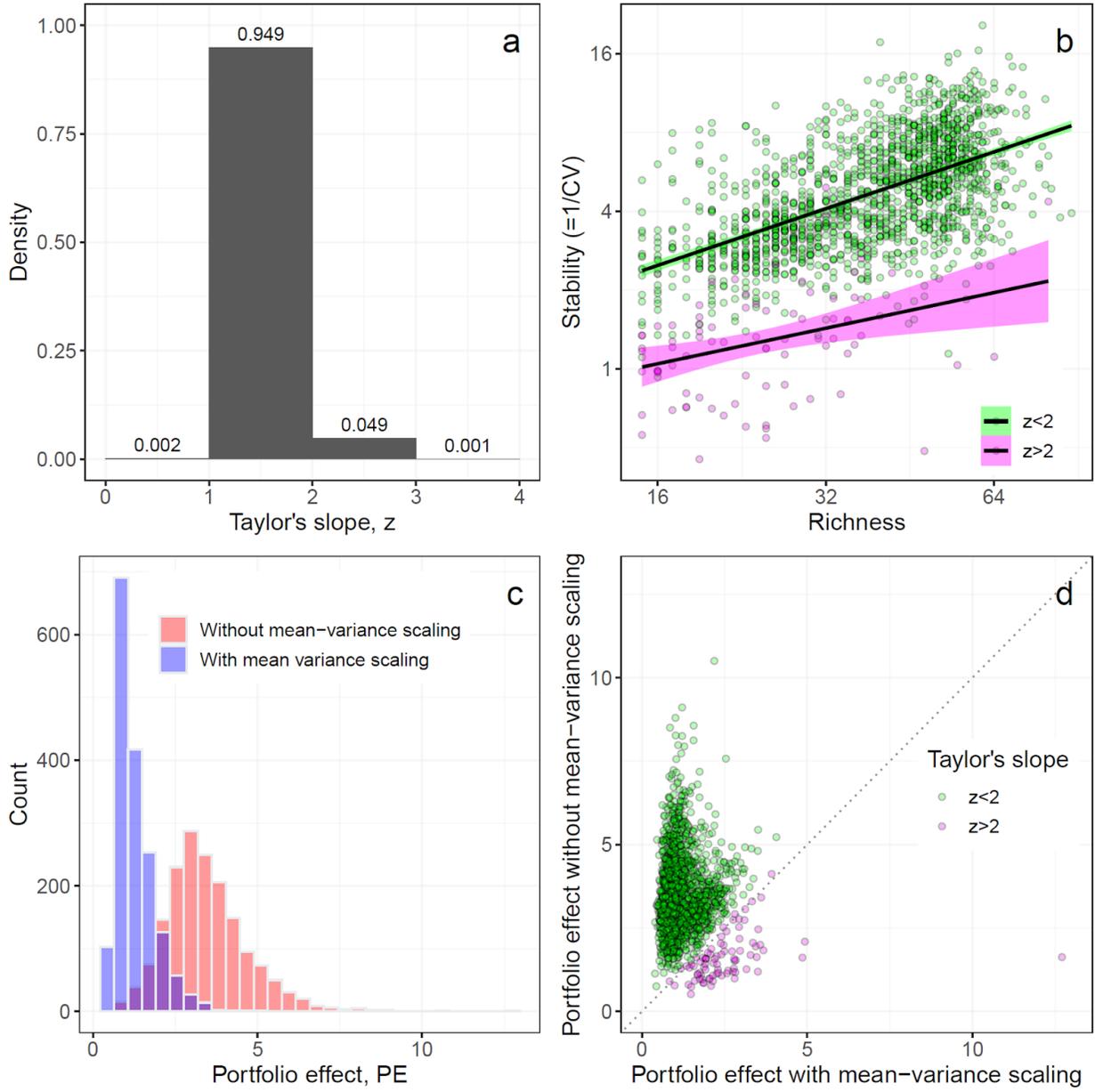
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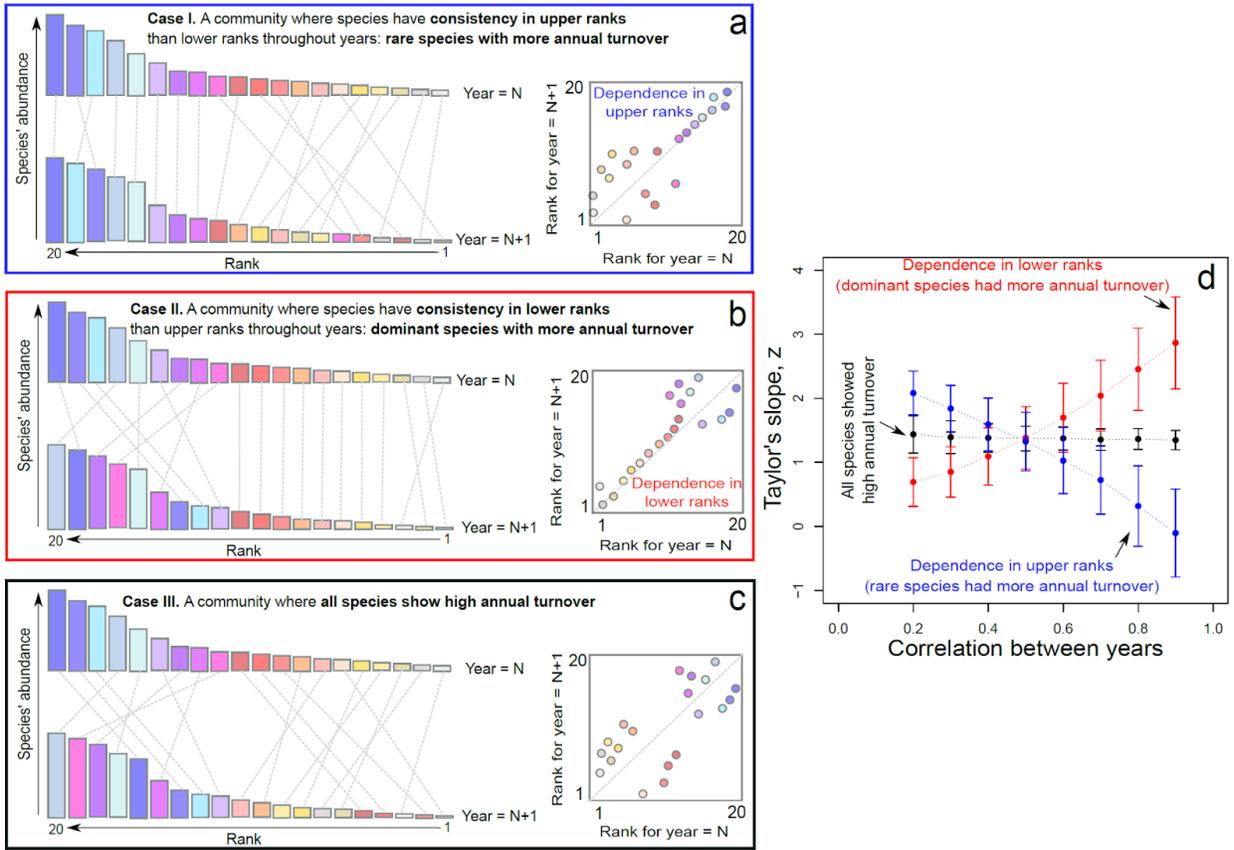
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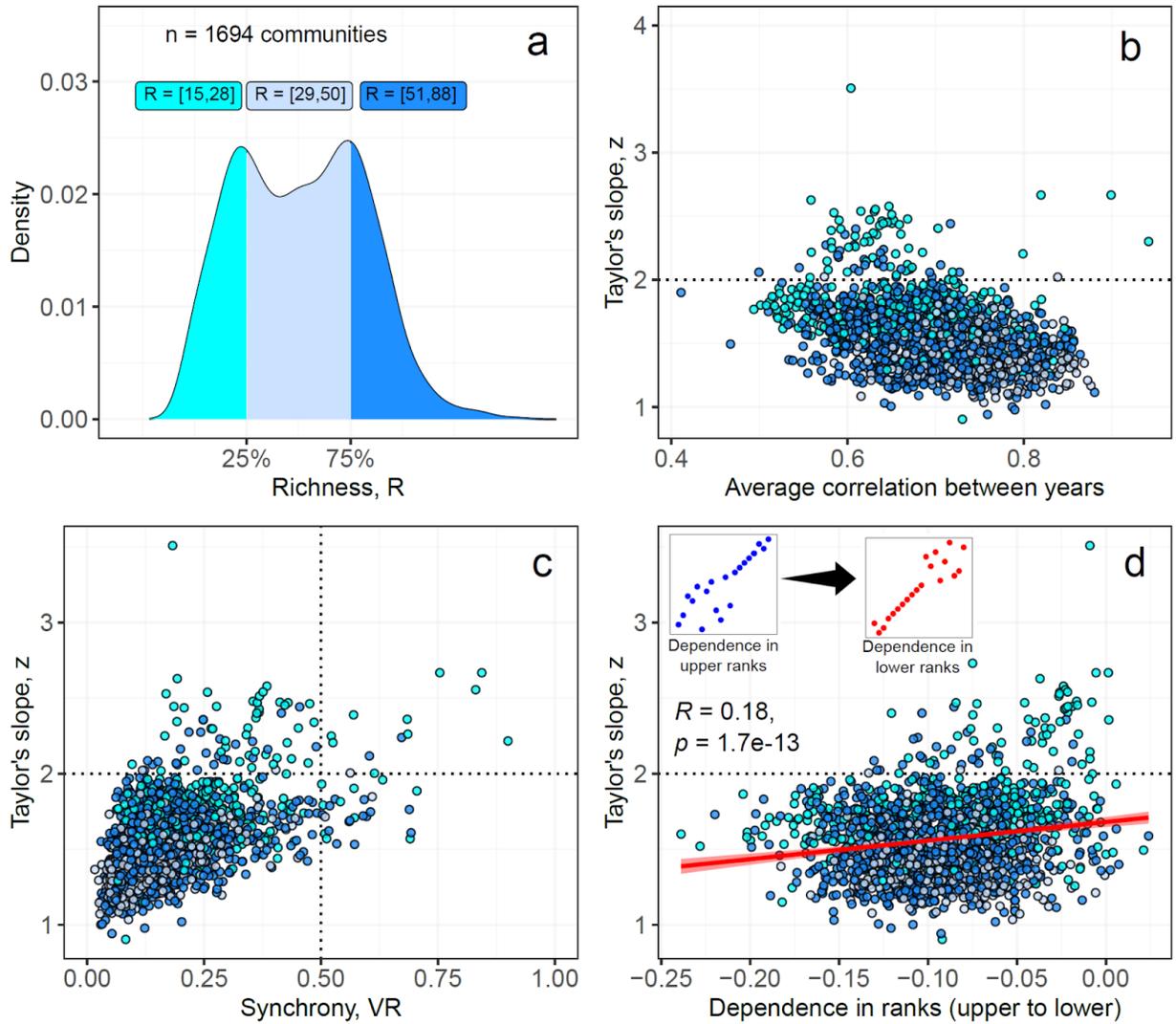
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Figure 5

**23 Box 1: Quantifying portfolio effect, PE, for a community considering with or without
24 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, Cooper, and Dulvy 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 :

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

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, Cooper, and Dulvy 2013)).

25

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