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The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns

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1 **Abstract**

2 Empirical knowledge of diversity-stability relationships is mostly based on the analysis of
3 temporal variability. Variability, however, often depends on external factors that act as dis-
4 turbances, which makes comparisons across systems difficult to interpret. Here we show how
5 variability can reveal inherent stability properties of ecological communities. This requires
6 abandoning one-dimensional representations, in which a single variability measurement is
7 taken as a proxy for how stable a system is, and instead consider the whole set of variabil-
8 ity values generated by all possible stochastic perturbations. Furthermore, in species-rich
9 systems, a generic pattern emerges from community assembly, relating variability to the
10 abundance of perturbed species. The contrasting contributions of different species abun-
11 dance classes to variability, driven by different types of perturbations, can lead to opposite
12 diversity-stability patterns. We conclude that a multidimensional perspective on variability
13 helps reveal the dynamical richness of ecological systems and the underlying meaning of their
14 stability patterns.

15 Introduction

16 Ecological stability is a notoriously elusive and multifaceted concept (Pimm, 1984; Donohue
17 *et al.*, 2016). At the same time, understanding its drivers and relationship with biodiversity
18 is a fundamental, pressing, yet enduring challenge for ecology (Elton, 1946; MacArthur, 1955;
19 May, 1973a; McCann, 2000). The temporal variability of populations or ecosystem functions,
20 where lower variability is interpreted as higher stability, is an attractive facet of ecological
21 stability, for several reasons. First, variability is empirically accessible using simple time-series
22 statistics (Tilman *et al.*, 1996). Second, variability – or its inverse, invariability – is a flexible
23 notion that can be applied across levels of biological organization (Haegeman *et al.*, 2016) and
24 spatial scales (Wang & Loreau, 2014; Wang *et al.*, 2017). Third, variability can be indicative
25 of the risk that an ecological system might go extinct, collapse or experience a regime shift
26 (Scheffer *et al.*, 2009). During the last decade, the relationship between biodiversity and eco-
27 logical stability has thus been extensively studied empirically using invariability as a measure
28 of stability (Tilman *et al.*, 2006; Jiang & Pu, 2009; Hector *et al.*, 2010; Campbell *et al.*, 2011;
29 Gross *et al.*, 2014; Pennekamp *et al.*, 2018).

30 In a literal sense, stability is the property of what tends to remain unchanged (Pimm,
31 1991). Variability denotes the tendency of a variable to change in time, so that its inverse fits
32 this intuitive definition. However, variability is not necessarily an inherent property of the
33 system that is observed (e.g., a community of interacting species), as it typically also depends
34 on external factors that act as perturbations. Thus, the variability of a community is not a
35 property of that community *alone*. It may be caused by a particular perturbation regime so
36 that a different regime could lead to a different value of variability. Stronger perturbations
37 will generate larger fluctuations, and the way a perturbation's intensity is distributed and
38 correlated across species is also critical. In other words, a variability measurement reflects

39 the response of a system to the specific environmental context in which it is embedded.

40 Despite this complexity, quantifying the fluctuations of an ecosystem property (e.g., pri-
41 mary production) can be of foremost practical interest as it provides a measure of predictabil-
42 ity in a given environmental context (Griffin *et al.*, 2009). However, to generalize results
43 beyond the specific context in which variability is measured, use variability to compare the
44 stability of different systems, establish links between different stability notions, or reconcile
45 the conflicting diversity-stability patterns and predictions reported in the empirical and the-
46 oretical literature (Ives & Carpenter, 2007), one needs to know how variability measurements
47 can reflect a system's inherent dynamical features.

48 Here, we adopt an approach in which stability is viewed as the inherent ability of a
49 dynamical system to endure perturbations (Fig. 1A). For simplicity we will restrict to systems
50 near equilibrium, by opposition to, e.g., limit cycles or chaotic attractors. We propose that
51 a measure of stability should reflect, not a particular perturbation (as in Fig. 1B), but a
52 system's propensity to withstand *a whole class* of perturbations. We therefore consider a vast
53 perturbation set, and study the corresponding range of community responses (Fig. 1C). Even
54 from a theoretical perspective, considering all possible perturbations that an ecosystem can
55 face is a daunting task. We will thus restrict our attention to communities near equilibrium,
56 perturbed by stochastic perturbations, and derive analytical formulas for two complementary
57 features of the set of their variability values: its average and maximum, corresponding to
58 the mean- and worst-case perturbation scenarios, respectively. Our work follows traditional
59 approaches of theoretical ecology (May, 1973a; Ives *et al.*, 2003), extending the analysis to
60 encompass a large perturbation set.

61 After having developed a general theory of variability that can be applied to any system
62 near equilibrium, we turn our attention to species-rich communities assembled from nonlinear
63 dynamics. We show that a generic variability-abundance pattern emerges from the complex

64 interactions between species during assembly. We argue that this pattern, in conjunction with
65 the type of perturbations considered (environmental, demographic, or caused by stochastic
66 immigration), determines the specific species abundance class that governs the variability
67 distribution. In particular, we establish a fundamental link between rare species, worst-case
68 variability, and asymptotic resilience – the long-term rate of return to equilibrium following a
69 pulse perturbation. We finally illustrate that the contrasting contributions of various species
70 abundance classes can be responsible for opposite diversity-invariability patterns.

71 **Material and Methods**

72 **Perturbed communities**

73 Let $N_i(t)$ represent the abundance (or biomass) of species i at time t , and $x_i(t) = N_i(t) - N_i$
74 its displacement from an equilibrium value N_i , with i running over S coexisting species that
75 form an ecological community. We model variability as a response to stochastic forcing. We
76 focus on stationary fluctuations caused by weak perturbations with zero mean, governed by
77 the following dynamical system, written from the perspective of species i as

$$\frac{d}{dt} \underbrace{x_i(t)}_{\text{fluctuations}} = \sum_{j=1}^S \underbrace{A_{ij}x_j(t)}_{\text{interactions}} + \underbrace{\sigma_i \sqrt{N_i}^\alpha \xi_i(t)}_{\text{perturbation}}. \quad (1)$$

78 The coefficients A_{ij} represent the effect that a small change of abundance of species j has
79 on the abundance of species i . Organized in the *community matrix* $A = (A_{ij})$, they encode
80 the linearization of the nonlinear system of which (N_i) is an equilibrium. In the perturbation
81 term, $\xi_i(t)$ denotes a standard white-noise source (Arnold, 1974; Van Kampen, 1997). In
82 discrete time $\xi_i(t)$ would be a normally distributed random variable with zero mean and unit

83 variance, drawn independently at each time step (Appendix 1).

84 Such models were studied by Ives *et al.* (2003) to analyze ecological time series. In their
85 approach, stability properties are inferred from the system’s response to specific perturbations.
86 Here we build on a similar formalism, but explicitly explore a vast set of possible perturbations.
87 Although environmental fluctuations often follow temporal patterns (Vasseur & Yodzis, 2004;
88 Ruokolainen *et al.*, 2009; Fowler & Ruokolainen, 2013) we will not consider autocorrelated
89 perturbations. What we will explicitly consider, however, are temporal correlations between
90 $\xi_i(t)$ and $\xi_j(t)$, a situation in which individuals of species i and j are similar in their perception
91 of a given perturbation, a property known to have potentially strong, and unintuitive effects
92 on species dynamics (Ripa & Ives, 2003).

93 For the fluctuations of species abundance in eq. (1) to be stationary, the equilibrium state
94 (N_i) must be stable. More technically, the eigenvalues of the community matrix A must have
95 negative real part (May, 1973a; Gurney & Nisbet, 1998). The maximal real part determines
96 the slowest long-term rate of return to equilibrium following a pulse perturbation. This rate
97 is a commonly used stability measure in theoretical studies; we call it *asymptotic resilience*
98 and denote it by \mathcal{R}_∞ (Arnoldi *et al.*, 2016). To illustrate the connections between stability
99 concepts, we will compare asymptotic resilience to measures of variability.

100 **Perturbation type**

101 The perturbation term in eq. (1) represents the direct effect that a perturbation has on the
102 abundance of species i . It consists of two terms: some power α of $\sqrt{N_i}$, and a species-specific
103 term $\sigma_i \xi_i(t)$. The latter is a function of the perturbation itself, and of traits of species i that
104 determine how individuals of that species perceive the perturbation. The former defines a
105 statistical relationship between a perturbation’s direct effects and the mean abundance of

106 perturbed species. It allows us to consider ecologically distinct sources of variability (Fig. 2).

107 When individuals of a given species respond in synchrony to a perturbation, the direct
108 effect of the perturbation will be proportional to the abundance of the perturbed species, thus
109 a value of α close to 2 (Lande *et al.*, 2003). We call this type of perturbation *environmental*
110 as fluctuations of environmental variables typically affect all individuals of a given species,
111 leading, e.g. to changes in the population growth rate (May, 1973b).

112 If individuals respond incoherently, e.g., some negatively and some positively, the direct
113 effect of the perturbation will scale sublinearly with species abundance. For instance, demo-
114 graphic stochasticity can be seen as a perturbation resulting from the inherent stochasticity
115 of birth and death events, which are typically assumed independent between individuals. In
116 this case $\alpha = 1$, and we thus call such type *demographic* (Lande *et al.*, 2003).

117 We can also consider purely exogenous perturbations, such as the random removal or ad-
118 dition of individuals. In this case $\alpha = 0$. We call such perturbations *immigration-type* but
119 stress that actual immigration events do not necessarily satisfy this condition (e.g., they can
120 be density-dependent). Furthermore, because we focus on zero-mean perturbations, pertur-
121 bations of this type contain as much *emigration* than immigration. The reasoning behind
122 this nomenclature is that, in an open system, fluctuations of an otherwise constant influx of
123 individuals would correspond to an immigration-type perturbation.

124 More generally, eq. (1) with $\alpha \in [0, 2]$ describes a continuum of perturbation types. Al-
125 though not unrelated, the statistical relationship that defines perturbation type is not equiv-
126 alent to Taylor's law (Taylor, 1961). The latter is an empirically observed power-law re-
127 lationship between the variance and mean of population fluctuations. In contrast to the
128 perturbation type α , the exponent of Taylor's law depends on community dynamics, e.g., on
129 species interactions (Kilpatrick & Ives, 2003). We will come back to this point below and in
130 the Discussion.

131 **Perturbation intensity**

132 For a given community, a stronger perturbation will lead to stronger fluctuations. A dispro-
 133 portionate increase in their amplitude as perturbation intensity changes would reveal nonlin-
 134 earity in the dynamics (Zelnik *et al.*, 2019). In a linear setting, however, there is only a linear
 135 dependency on perturbation intensity. This trivial dependency can be removed by controlling
 136 for perturbation intensity. We now illustrate how to do so, for a given definition of variability.

137 Fluctuations induced by white-noise forcing are normally distributed, thus fully charac-
 138 terized by their variance and covariance. We thus construct a measure of variability based on
 139 the variance of species time-series. To compare variability of communities of different species
 140 richness we consider the average variance:

$$\sigma_{\text{out}}^2 = \frac{1}{S} \sum_i \text{Var}(N_i(t)). \quad (2)$$

141 We now remove the trivial effect of perturbation intensity from eq. (2), starting from the
 142 one-dimensional system $dx/dt = -\lambda x + \sigma\xi(t)$. Its stationary variance is $\sigma_{\text{out}}^2 = \frac{\sigma^2}{2\lambda}$. Here we
 143 see the combined effect of perturbation σ^2 and dynamics λ , leading us to define σ^2 as measure
 144 of perturbation intensity. For species-rich communities, we define perturbation intensity as
 145 the average intensity per species, that is, using the species-specific intensities σ_i^2 :

$$\sigma_{\text{in}}^2 = \frac{1}{S} \sum_i \sigma_i^2. \quad (3)$$

146 When increasing all species-specific perturbation intensities by a factor c , both σ_{in}^2 and σ_{out}^2
 147 increase by the same factor. To remove this linear dependence, we define variability as

$$\mathcal{V} = \frac{\sigma_{\text{out}}^2}{\sigma_{\text{in}}^2}, \quad (4)$$

148 i.e., as the average species variance relative to perturbation intensity (see Ives *et al.*, 2003 for
149 a similar definition). Generalizing previous work (Arnoldi *et al.*, 2016; Arnoldi & Haegeman,
150 2016) to all perturbation types, we construct *invariability* as

$$\mathcal{I} = \frac{1}{2\mathcal{V}}. \quad (5)$$

151 The factor 1/2 allows \mathcal{I} to coincide, for simple systems, with asymptotic resilience (Arnoldi
152 *et al.*, 2016). In particular, for the one-dimensional example considered above for which
153 $\mathcal{R}_\infty = \lambda$, we do have $\mathcal{V} = 1/2\lambda$ and thus $\mathcal{I} = \lambda = \mathcal{R}_\infty$.

154 **Perturbation direction**

155 At fixed intensity, perturbations can still differ in how their intensity is distributed and tem-
156 porally correlated across species. Species with similar physiological traits will be affected in
157 similar ways by, say, temperature fluctuations, whereas individuals from dissimilar species
158 may react in unrelated, or even opposite, ways (Ripa & Ives, 2003). We thus study the effect
159 of the covariance structure of the perturbation terms, i.e., the effect of the *direction* of pertur-
160 bations. Spanning the set of all perturbation directions defines a whole range of community
161 responses. Assuming some probability distribution leads to a probability distribution over
162 the set of responses, i.e., a variability distribution (see Fig. 2). Finally, spanning the set of
163 perturbation types reveals a continuous *family* of variability distributions. In Fig. 2 we show
164 three archetypal elements of this family, corresponding to $\alpha = 0$ (blue distribution), $\alpha = 1$
165 (green distribution) and $\alpha = 2$ (red distribution).

166 For each distribution we consider two complementary statistics: mean- and worst-case
167 responses. In Appendices 3 and 4 we prove that the worst-case response is always achieved by
168 a perfectly coherent perturbation, i.e., a perturbation whose direct effects on species are not

169 independent, but on the contrary, perfectly correlated in time. We derive explicit formulas
 170 to compute the worst-case variability from the community matrix and species equilibrium
 171 abundances, see eqs. (C2, D5). The mean-case scenario, on the other hand, is defined with
 172 respect to a prior over the set of perturbation directions. For the least informative prior,
 173 we prove in Appendices 3 and 4 that a perturbation affecting all species independently but
 174 with equal intensity, realizes the mean-case response. This provides a way to compute this
 175 response from the community matrix and the species abundances, given in eqs. (C3, D6).

176 **Results**

177 **Variability patterns for two-species community**

178 We illustrate our variability framework on the following elementary example, in the form of
 179 a 2×2 community matrix

$$A = \begin{pmatrix} -1 & 0.1 \\ -4 & -1 \end{pmatrix}. \quad (6)$$

180 This matrix defines a linear dynamical system that could represent a predator-prey commu-
 181 nity, with the first species benefiting from the second at the latter's expense. Its asymptotic
 182 resilience is $\mathcal{R}_\infty = 1$. Let us suppose that the prey, N_2 (second row/column of A) is 7.5
 183 times more abundant than its predator, N_1 (first row/column of A) and consider stochastic
 184 perturbations of this community, as formalized in eq. (1).

185 In Fig. 3 we represent the set of perturbation directions as a disc, in which every point is
 186 a unique perturbation direction (see Appendix 5 for details). The effect of a perturbation on
 187 a community is represented as a color; darker tones imply larger responses, with the baseline
 188 color (blue, green or red) recalling the perturbation type ($\alpha = 0, 1, 2$, respectively). Points

189 at the boundary of the disc correspond to coherent perturbations, which have the potential
190 to generate the largest (but also the smallest) variability. This is why the color maps of
191 Fig. 3 take their extreme values at the boundary. We see that variability strongly depends on
192 the perturbation direction, and that this dependence is strongly affected by the perturbation
193 type. For immigration-type perturbations (in blue) variability is largest when perturbing the
194 predator species most strongly (the least abundant species in this example). For demographic-
195 type perturbations (in green) perturbations that equally affect the two species but in opposite
196 ways achieve the largest variability. For environmental-type perturbations (in red) variability
197 is largest when perturbing the prey species (the most abundant species in this example). For
198 all types we see that positive correlations between the components of the perturbation (i.e.,
199 moving upwards on the disc) reduce variability (see Ripa & Ives, 2003 for related results).

200 Thus, in general, a given community cannot be associated to a single value of variability.
201 Depending on the type of perturbations causing variability, different species can have com-
202 pletely different contributions. This stands in sharp contrast with asymptotic resilience \mathcal{R}_∞ ,
203 which associates a single stability value to the community. Although we know from previous
204 work (Arnoldi *et al.*, 2016) that the smallest invariability value in response to immigration-
205 type perturbations will always be smaller than \mathcal{R}_∞ , in general (i.e., any perturbation type
206 and/or any perturbation direction) there is, a priori, no reason to expect a relationship be-
207 tween invariability and asymptotic resilience.

208 **Variability patterns in complex communities**

209 The dimensionality of variability will be larger in communities comprised of many species,
210 as their sheer number, S , increases the dimension of the perturbation set quadratically. Yet,
211 when species interact, a generic structure can emerge from ecological assembly, revealing a

212 simple relationship between variability and the abundance of perturbed species. To show this,
213 we study randomly assembled communities. We start from a large random pool of species and
214 let the system settle to an equilibrium following Lotka-Volterra dynamics. During assembly
215 species would go extinct, but no limit cycles, chaotic behavior or multi-stability were observed.
216 A complete description of the nonlinear model is given in Appendix 6 and Matlab simulation
217 code is available as supplementary material.

218 In Fig. 4 we show the variability patterns for a single randomly assembled community,
219 but the results hold more generally (see below). The species pool consists of $S_{\text{pool}} = 50$
220 species, with species interaction strengths one order of magnitude weaker than species self-
221 regulation. 40 species coexist in the community. In this species-rich context, the perturbation
222 set cannot be represented exhaustively. We therefore plot the variability induced by species-
223 specific perturbations (of various types) against the abundance of perturbed species. That is,
224 we focus on the effect of a specific subset of perturbations, those affecting a single species.
225 Linear combinations of these perturbations will span all scenarios in which species are affected
226 independently, but exclude scenarios in which they are perturbed in systematically correlated
227 or anti-correlated way.

228 The leftmost panel shows a negative unit slope on log scales: when caused by immigration-
229 type perturbations, variability is inversely proportional to the abundance of perturbed species.
230 Randomly adding and removing individuals from common species generates less variability
231 than when the species is rare. In fact, the worst-case scenario corresponds to perturbing the
232 rarest species. Worst-case invariability is close to asymptotic resilience, which corroborates
233 previous findings showing that the long-term rate of return to equilibrium is often associated
234 to rare species (Haegeman *et al.*, 2016; Arnoldi *et al.*, 2018). On the other hand, the middle
235 panel of Fig. 4 shows that, in response to demographic-type perturbations, variability is inde-
236 pendent of perturbed species' abundance. Finally, the rightmost panel shows a positive unit

237 slope on log scales: when caused by environmental-type perturbations, variability is propor-
238 tional to the abundance of perturbed species. The worst case is thus attained by perturbing
239 the most abundant one. Despite being more stable than rare ones (they buffer exogenous per-
240 turbations more efficiently, see left-hand panel), common species are more strongly affected
241 by environmental perturbations, and can thus generate the most variability.

242 Those patterns are not coincidental, but emerge from species interactions, as we illustrate
243 in Fig. 5. In their absence, other patterns can be envisioned. Without interactions, the
244 response to a species-specific perturbation involves the perturbed species only. The variability-
245 abundance relationship is then $\mathcal{V} = N^\alpha/2r$, with $N = K$. If r and K are statistically
246 independent in the community (top-left panel in Fig. 5), this yields a different scaling than the
247 one seen in Fig. 4. In the case of an r - K trade-off (i.e., species with larger carrying capacities
248 have slower growth rate), abundant species would be the least stable species (bottom-left panel
249 in Fig. 5, in blue) which is the opposite of what the leftmost panel of Fig. 4 shows. However, as
250 interaction strength increases (from left to right in Fig. 5; the ratios of inter- to intraspecific
251 interaction strength are 0, 0.02 and 0.1 approximately), we see emerging the relationship
252 between abundance and variability of Fig. 4, regardless of the choice made for species growth
253 rates and carrying capacities. We explain in Appendix 7 why this reflects a generic, limit-case
254 behavior of complex communities. It occurs when species abundances, due to substantial
255 indirect effects during assembly, become only faintly determined by their carrying capacities.
256 This example demonstrates that this limit can be reached even for relatively weak interactions
257 (in Fig. 4 and in the right-hand panels of Fig. 5, the interspecific interaction strengths are
258 ten times smaller than the intraspecific ones).

259 Although we considered a specific section of the perturbation set, the response to single-
260 species perturbations of immigration and environmental types can still span the whole variabil-
261 ity distribution, from worst-case (rarest and most abundant species perturbed, respectively)

262 to mean- and best-case scenarios (most abundant and rarest species perturbed, respectively).
263 For demographic-type perturbation the situation is more subtle as the response is indepen-
264 dent of species abundance, and, in general, extreme scenarios will be associated to temporally
265 correlated perturbations affecting multiple species.

266 The variability-abundance patterns shown in Figs. 4 and 5 should not be confused with
267 Taylor’s law (Taylor, 1961), a power-law relationship between a species’ variance and its mean
268 abundance. In fact, the variability-abundance pattern is *dual* to Taylor’s law, it represents
269 the community response to single-species perturbations instead of that of individual species
270 to a community-wide perturbation.

271 **Diversity-invariability relationships**

272 To illustrate implications of the generic variability-abundance pattern, we revisit the diversity-
273 stability relationship, with stability quantified as invariability \mathcal{I} . We assembled communities
274 of increasing species richness S , each associated with an invariability distribution generated
275 from random perturbations, predictions for mean- and worst-case scenarios, and a value of
276 asymptotic resilience \mathcal{R}_∞ .

277 The leftmost panel of Fig. 6 shows a negative relationship between immigration-type
278 invariability and species richness. Asymptotic resilience and worst-case invariability mostly
279 coincide, with a decreasing rate roughly twice as large as that of the mean case. The middle
280 panel suggests a different story. Mean-case demographic-type invariability stays more or
281 less constant whereas the worst case diminishes with species richness, although much more
282 slowly than \mathcal{R}_∞ . The relationship between diversity and stability is thus ambiguous. In the
283 rightmost panel we see an increase in all realized environmental-type invariability values with
284 species richness, showcasing a positive diversity-stability relationship.

285 The diversity stability relationships can be explained by the generic variability-abundance
286 patterns of Figs. 4 and 5 (see Appendix 8). In the case of immigration-type perturbations,
287 species contributions to variability are proportional to the inverse of their abundance (first
288 panel of Fig. 4). The worst-case scenario follows the abundance of the rarest species, which
289 rapidly declines with species richness. As detailed in Appendix 8, mean-case invariability
290 scales as the average species abundance, which also typically decreases with S .

291 The responses to demographic perturbations, on the other hand, are not determined by
292 any specific species abundance class (second panel of Fig. 4), so that no simple expectations
293 based on typical trends of abundance distributions can be deduced.

294 We recover a simpler behavior when looking at the response to environmental-type per-
295 turbation: abundant species now drive variability (rightmost panel of Fig. 4). As explained
296 in Appendix 8, mean-case invariability now scales as the *inverse* of an average species abun-
297 dance. The latter typically declines with S explaining the observed increase of mean-case
298 invariability.

299 There is an analogy to be made between stability and diversity. As has been said about
300 diversity metrics (e.g., species richness, Simpson index or Shannon entropy), different invari-
301 ability measures “*differ in their propensity to include or to exclude the relatively rarer species*”
302 (Hill, 1973). In this sense, different invariability measures can probe different dynamical as-
303 pects of a same community, with potentially opposite dependencies on a given ecological
304 parameter of interest.

305 Discussion

306 Because it is empirically accessible using simple time-series statistics, temporal variability
307 is an attractive facet of ecological stability. But there are many ways to define variability

308 in models and empirical data, a proliferation of definitions reminiscent of the proliferation of
309 definitions of stability itself (Grimm & Wissel, 1997). Variability measurements often depend,
310 not only on the system of interest, but also on external factors that act as disturbances, which
311 makes it difficult to relate variability to other stability concepts. These caveats constitute
312 important obstacles toward a synthetic understanding of ecological stability, and its potential
313 drivers (Ives & Carpenter, 2007).

314 We proposed to consider variability as a way to probe and measure an ecosystem's response
315 to perturbations, thus revealing inherent dynamical properties of the perturbed system. We
316 did not seek for an optimal, single measure of variability but, on the contrary, we accounted
317 for a vast set of perturbations, leading to a whole distribution of responses. We focused on
318 the worst- and mean-case values of this distribution as functions of species abundance, their
319 interactions, and the *type* of perturbations that generates variability.

320 A perturbation type characterizes a statistical relationship between its direct effect on a
321 population and the latter's abundance. We distinguished between environmental perturba-
322 tions, whose direct effects on populations scales proportionally to their abundance; demo-
323 graphic perturbations, whose direct effect on populations scales sublinearly to their abun-
324 dance; and purely exogenous perturbations, representing random addition and removal of
325 individual, independent of the size of the perturbed population (immigration-type). Con-
326 trolling for perturbation type and intensity, we considered all the ways this intensity can be
327 distributed and correlated across species.

328 After having described a general (linear) theory for variability, which emphasizes its highly
329 multidimensional nature, we turned our attention towards species-rich communities assem-
330 bled by random (nonlinear) Lotka-Volterra dynamics. Because of the sheer number of species
331 contained in such communities ($S \approx 40$ in our examples), we could have expected the dimen-
332 sionality of perturbations and responses to be so large that variability distributions would be

333 too complex and broad to be clearly described. However, the process of assembly allowed for
334 a simple behavior to emerge: a generic relationship between variability and the abundance
335 of individually perturbed species. In essence, this pattern predicts that the species' ability
336 to buffer exogenous perturbations is proportional to their abundance. In conjunction to this
337 simple pattern, the type of perturbation will then determine the individual contributions of
338 species to the variability distribution, so that both common and rare species can determine
339 variability. This is reminiscent of diversity measures (Hill, 1973), some of which (e.g., species
340 richness) are sensitive to the presence of rare species, while others are mostly indicative of
341 the distribution of abundant species (e.g., Simpson diversity index).

342 These connections with different diversity metrics can explain contrasting trends in invari-
343 ability as a function of species richness. Since immigration-type perturbations mostly affect
344 rare species, they lead to a negative diversity-invariability relationship, reflecting a growing
345 number and rarity of rare species. On the other hand, in response to demographic pertur-
346 bations, species contributions to variability can be independent of their abundance. In this
347 case, variability is not expected to follow trends in diversity, so that diversity-invariability
348 patterns can be less predictable and harder to interpret. Finally, although common species
349 buffer exogenous perturbations efficiently, they are also the most affected by environmental-
350 type perturbations. This can lead to a proportional relationship between average abundance
351 and mean-case invariability, and hence to a positive diversity-invariability relationship.

352 **Implications for empirical patterns**

353 We showed that species abundances greatly affect variability distributions. This new in-
354 sight has broad consequences. For example, it has been reported that ecosystem-level and
355 population-level stability tend to increase and decrease, respectively, with increasing diversity

356 (Jiang & Pu, 2009; Campbell *et al.*, 2011). Ecosystem-level stability is often quantified based
357 on the variability of total biomass, which gives, by construction, a predominant weight to
358 abundant species. On the other hand, averages of single-species variabilities have been used
359 to measure population-level stability (Tilman, 1996). These averages are strongly affected,
360 and can even be fully determined, by rare, highly variable species (Haegeman *et al.*, 2016).
361 Thus, here as well as in our theoretical results (Fig. 6), stability metrics governed by common,
362 or rare, species tend to generate respectively positive and negative diversity-stability relation-
363 ships. It would be interesting to test whether this observation holds more generally, e.g., if it
364 can explain the contrasting relationships recently reported by Pennekamp *et al.* (2018).

365 The type of perturbations affects which species abundance class contributes most to vari-
366 ability. In turn, the physical size of the system considered affects which perturbation type
367 dominates. This is well known in population dynamics (Engen *et al.*, 2008), but it also trans-
368 poses to the community level. At small spatial scales, implying small populations, we may
369 expect variability to be driven by demographic stochasticity. At larger scales, implying larger
370 populations, demographic stochasticity will be negligible compared with environmental per-
371 turbations. Just as changing the perturbation type transforms the respective roles of common
372 and rare species, patterns of variability at different scales should reflect different aspects of
373 a community (Chalcraft, 2013), associated to different species abundance classes (abundant
374 species at large spatial scales, rare/rarer species at small spatial scales).

375 Empirically determining the perturbation type is a non-trivial task. To develop suitable
376 methods, it might be helpful to first understand the link between the variability-abundance
377 patterns (see Figs. 4 and 5) and Taylor's law (Taylor, 1961). The latter is an empirically ac-
378 cessible pattern, relating the mean and variance of population sizes. We studied the behavior
379 of the community response to an individual species perturbation, while Taylor's law focuses
380 on the individual species response to a perturbation of the whole community. This duality

381 also suggests that Taylor’s law is, at the community level, strongly affected by species inter-
382 actions. This is known (Kilpatrick & Ives, 2003), yet our approach could shed new light on
383 the information regarding species interactions and other dynamical traits, actually contained
384 in community-level Taylor’s laws.

385 **On the dimensionality of stability**

386 We noted a connection between variability and asymptotic resilience, the most popular no-
387 tion in theoretical studies (Donohue *et al.*, 2016). We showed that asymptotic resilience is
388 comparable to the largest variability in response to an immigration-type perturbation, which
389 is often a perturbation of the rarest species (first panel of Fig. 4). While asymptotic resilience
390 is sometimes considered as a measure representative of collective recovery dynamics, we pre-
391 viously explained why that this is seldom the case (Arnoldi *et al.*, 2018). The asymptotic rate
392 of return to equilibrium generally reflects properties of rare “satellite” species, pushed at the
393 edge of local extinction by abundant “core” species. On the other hand, short-time return
394 rates can exhibit qualitatively different properties related to more abundant species.

395 The multiple dimensions of variability are related to the multiple dimensions of return
396 times. Variability is an integral measure of the transient regime following pulse perturbations,
397 i.e., a superposition of responses to various pulses, some of which have just occurred and are
398 thus hardly absorbed, while others occurred long ago and are largely resorbed. If abundant
399 species are faster than rare ones (the case in complex communities, see Appendix 7), if they are
400 also more strongly perturbed (e.g., by environmental perturbations), the bulk of the transient
401 regime will be short: variability in response to environmental perturbations is associated
402 with a short-term recovery. By contrast, if all species are, on average, equally displaced by
403 perturbations (e.g., by immigration-type perturbations), rare species initially contribute to

404 the overall community displacement as much as do abundant ones. Since their recovery is
405 typically very slow, the transient regime will be long: variability in response to immigration-
406 type perturbations is associated with a long-term recovery.

407 Ecologists have long acknowledged the multi-faceted nature of ecological stability (Pimm,
408 1984; Grimm & Wissel, 1997; Ives & Carpenter, 2007; Donohue *et al.*, 2016), but here we show
409 that a single facet (variability) is in itself inherently multidimensional, thus suggesting that
410 links across facets can be subtle. Short-term return rates may be linked with environmen-
411 tal variability, but environmental variability may have nothing to do with immigration-type
412 variability, the latter possibly related with long-term return rates and driven by rare species.
413 Because measures can be determined by different species abundance classes, we should not
414 expect a general and simple connection to hold between facets of ecological stability.

415 **Conclusion**

416 The multidimensional nature of variability can lead to conflicting predictions, but once this
417 multidimensionality is acknowledged, it can be used to extensively probe the dynamical prop-
418 erties of a community. In particular, in species-rich systems, we revealed a generic pattern
419 emerging from ecological assembly, relating species abundance to their variability contribu-
420 tion. This allowed connections to be drawn between variability and statistics of abundance
421 distributions. We argued that similar patterns should underlie ecosystem responses to other
422 families of perturbations (e.g., pulse perturbations). Therefore, we conclude that embracing
423 the whole set of a ecosystem responses can help provide a unifying view on ecological stability
424 and shed new light on the meaning of empirical and theoretical stability patterns.

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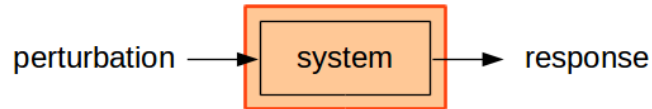
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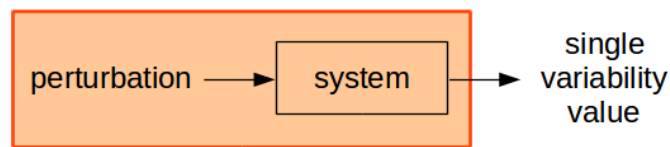
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A System-view on stability



B Variability dependent on system and perturbation



C Variability as an inherent system property

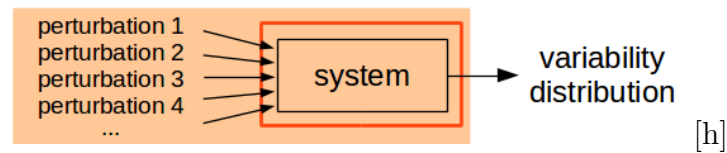


Figure 1: Variability vs stability. A: Stability quantifies the way a system responds to perturbations, seen as an inherent property of the system (indicated by the red framed box). B: By contrast, temporal variability is typically a feature of both the system studied and external factors that act as perturbations. C: For variability to be an inherent property of the system, one can consider a whole set of perturbations, thus integrating out the dependence on specific external factors.

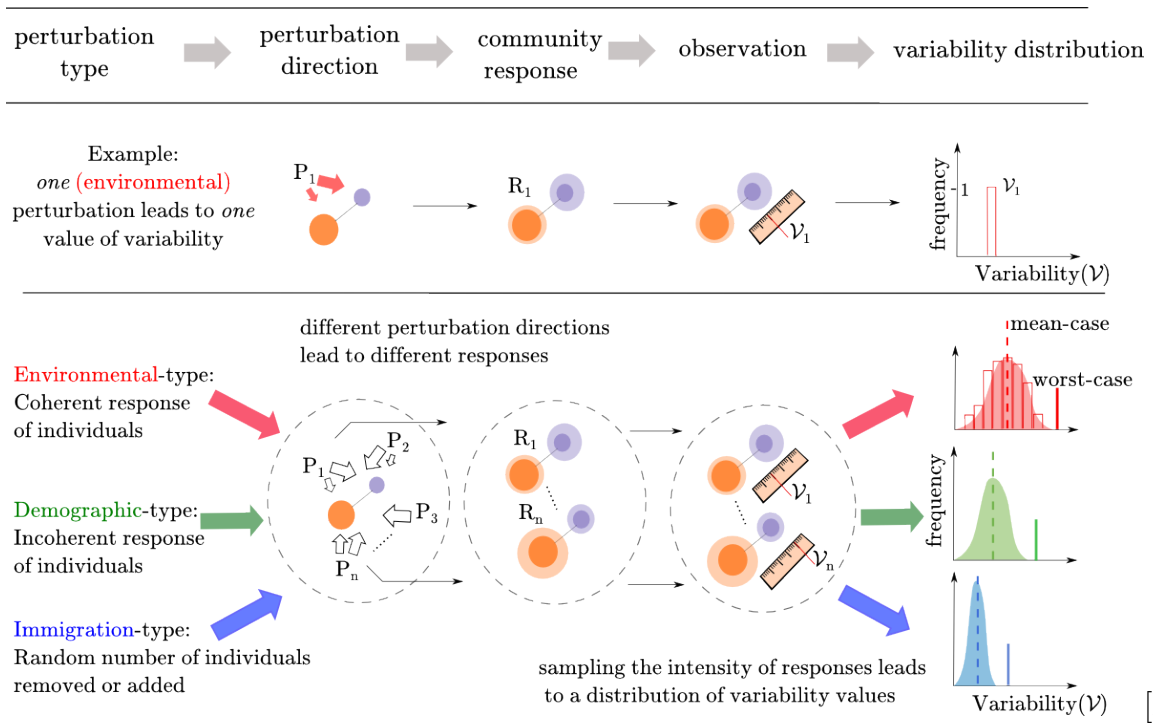


Figure 2: A theoretical framework for variability. Perturbations are characterized by their type, a statistical relationship between the direct effect of perturbations and the abundance of perturbed species. For a given type and fixed intensity, there remains a whole set of covariance structures of perturbations, i.e., various perturbation directions, that will be transformed by community dynamics into a whole set of community responses, i.e., various covariance structures of species stationary time series. A sampling of those responses leads to a variability distribution, one for each perturbation type. Spanning all perturbation types leads to a family of variability distributions (in blue, green and red in the rightmost column).

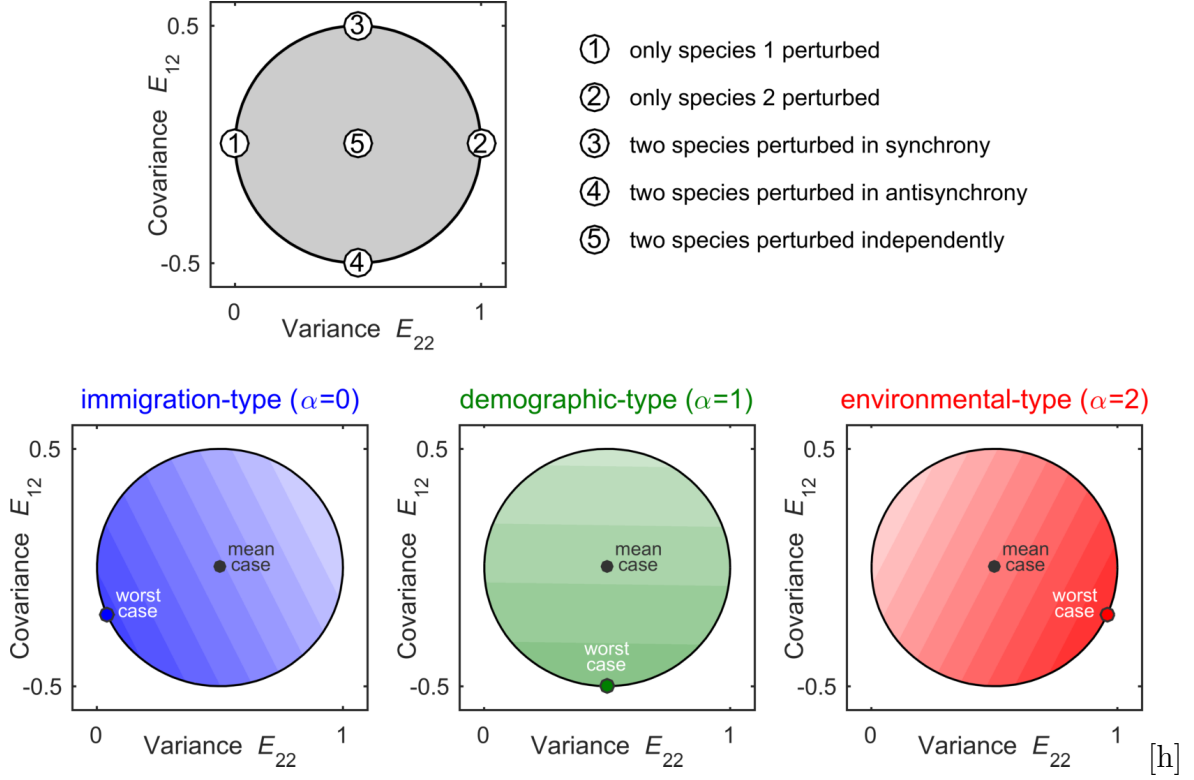


Figure 3: Variability patterns for a two-species community. Top panel: For a two-species community the set of all perturbation directions can be represented graphically as a disc (shaded in gray), with the variance of the perturbation term $\xi_2(t)$ on the x -axis and the covariance between $\xi_1(t)$ and $\xi_2(t)$ on the y -axis. Some special perturbation directions are indicated (numbers 1 to 5, see also Appendix 5). Bottom panels: We consider a predator-prey system; the community matrix A is given by eq. (6), and the prey (species 2) is 7.5 more abundant than its predator (species 1). The induced variability depends on the perturbation directions (darker colors indicate larger variability), and this dependence in turn depends on the perturbation type α . For immigration-type perturbations ($\alpha = 0$, in blue) variability is largest when perturbing species 1 most strongly. For demographic-type perturbations ($\alpha = 1$, in green) perturbations that affect the two species equally strongly but in opposite ways achieve the largest variability. For environmental-type perturbations ($\alpha = 2$, in red) variability is largest when perturbing species 2 most strongly. Notice that the worst case is always achieved by perturbations lying on the edge of the perturbation set. Such perturbations are perfectly correlated (see main text and Appendix 5).

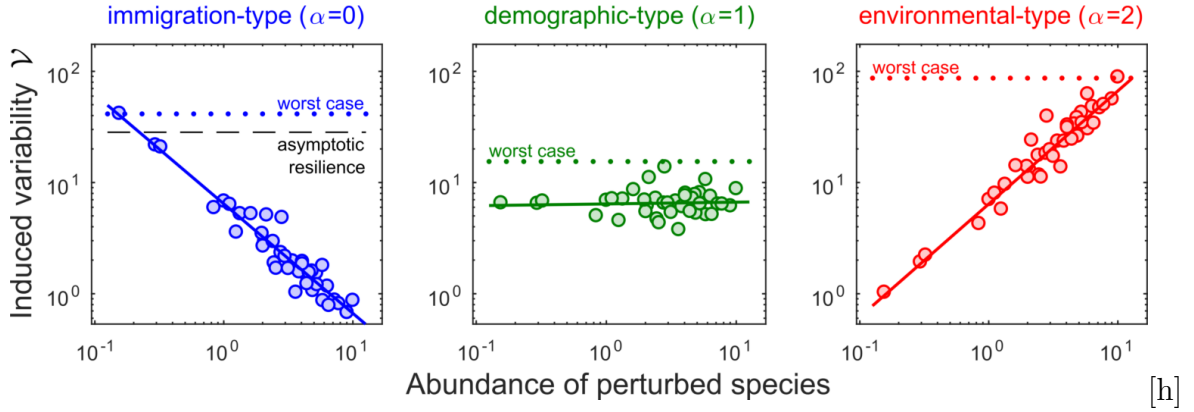


Figure 4: Variability-abundance pattern in a complex community. We consider a community of $S = 40$ species, and look at the variability induced by perturbing a single species, whose abundance is reported on the x -axis. Left: When caused by immigration-type perturbations ($\alpha = 0$), variability is inversely proportional to the abundance of the perturbed species (notice the log scales on both axis). The worst case is achieved by perturbing the rarest species, and is determined by asymptotic resilience (more precisely, it is close to $1/2\mathcal{R}_\infty$). Middle: For demographic-type perturbations ($\alpha = 1$), variability is independent of the abundance of the perturbed species. The worst case is not necessarily achieved by focusing the perturbation on one particular species. Right: For environmental-type perturbations ($\alpha = 2$), variability is directly proportional to the abundance of the perturbed species. The worst case is attained by perturbing the most abundant.

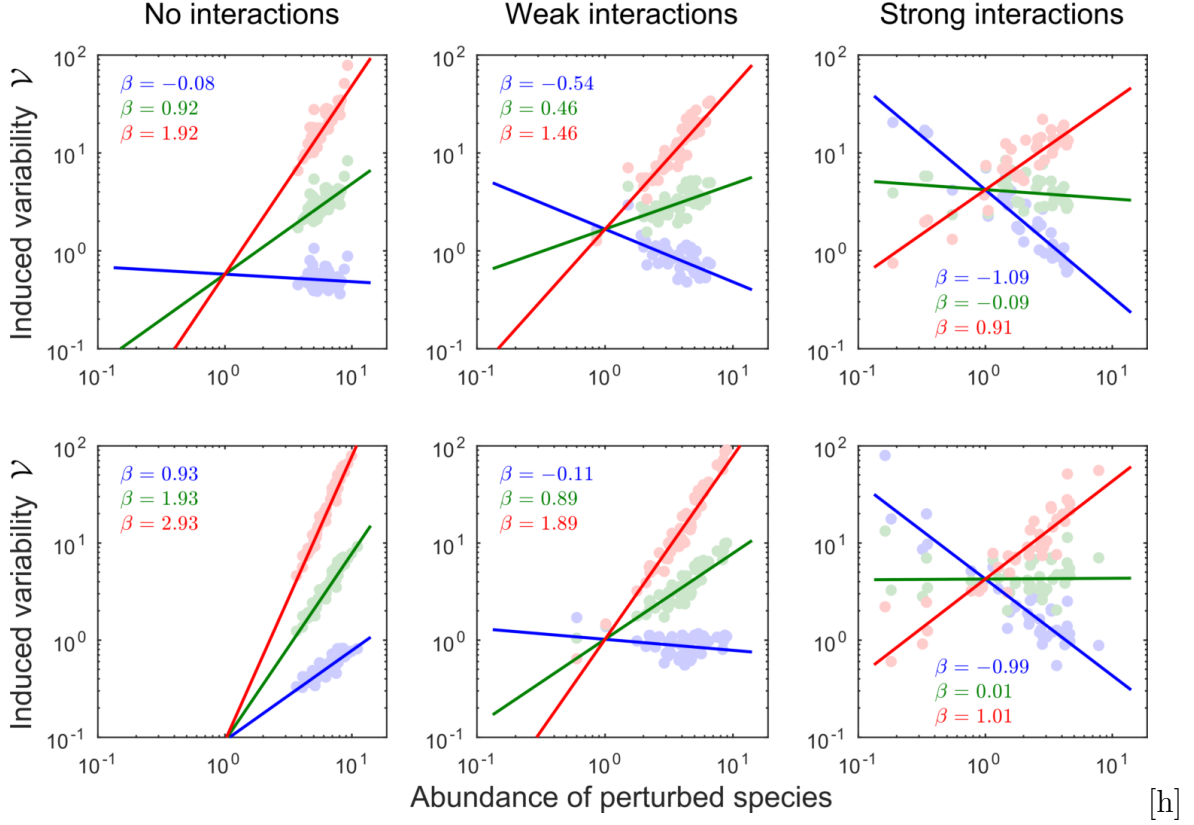


Figure 5: The emergence of the variability-abundance pattern (same procedure as in Fig. 4). Top row: intrinsic growth rates r and carrying capacities K are sampled independently. Bottom row: Species satisfy a r - K trade-off ($r \sim 1/K$). Colors correspond to the three perturbation types: $\alpha = 0$ (blue), $\alpha = 1$ (green) and $\alpha = 2$ (red). The value β reported in each panel corresponds to the exponent of the fitted relationship $V_i \propto N_i^\beta$ for each perturbation type. As interaction strength increases (left to right) we see emerging the relationship between abundance and variability described in Fig. 4, i.e., $\beta = \alpha - 1$. Thus when species interactions are sufficiently strong, variability always ends up being: (blue) inversely proportional, (green) independent and (red) directly proportional to the abundance of the perturbed species. Note that such relationships differ from Taylor's law: they represent an average community response to individual species perturbations, whereas Taylor's law deals with individual species responses to a perturbation of the whole community.

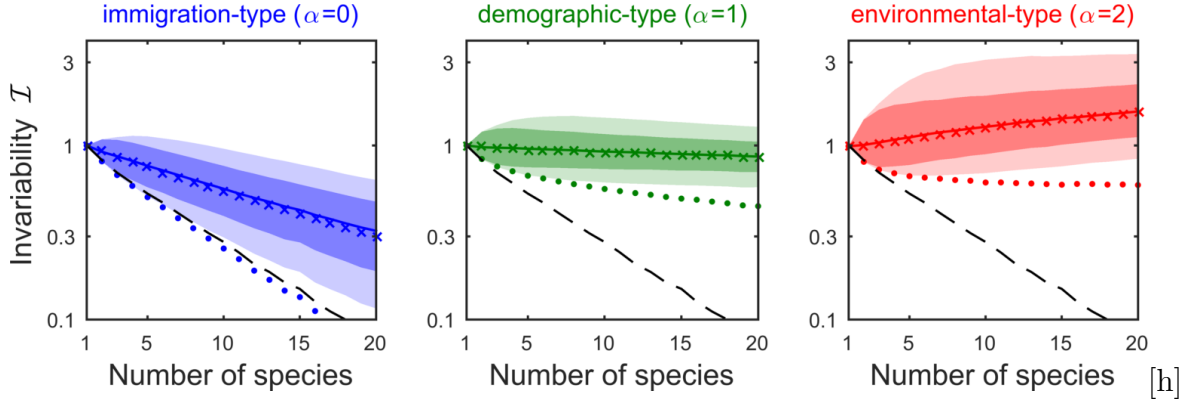


Figure 6: Different perturbation types yield contrasting diversity-stability relationships, with stability quantified as invariability \mathcal{I} . We generated random communities of increasing species richness S and computed their invariability distribution in response to 1000 random perturbations. Full line: median invariability, dark-shaded region: 5th to 95th percentile, light-shaded region: minimum to maximum realized values. The \times -marks correspond to the analytical approximation for the median, the dots to the analytical formula for the worst-case. Dashed line is asymptotic resilience \mathcal{R}_∞ . For immigration-type perturbations ($\alpha = 0$, blue) diversity begets instability, with \mathcal{R}_∞ following worst-case invariability. For demographic-type perturbations ($\alpha = 1$, green) the trend is ambiguous. For environmental-type perturbations ($\alpha = 2$, red) all realized values of invariability increase with S .

Appendices to "The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns"

Jean-François Arnoldi, Michel Loreau, and Bart Haegeman

The Appendices are organized as follows: Appendix A through D provides a self-contained presentation of the mathematical foundations of our variability theory. Appendix E through H provide details concerning specific applications considered in the main text: two-species communities in Appendix E, complex Lotka-Volterra communities in appendices F and G, and the link between abundance statistics and variability in Appendix H. A list of the most important notation used in the Appendices is given in Table A1.

1 Response to white-noise perturbation

We describe the response of a linear dynamical system, representing the dynamics of displacement of species around an equilibrium value, to a white-noise perturbation. Stochastic perturbations in continuous time are mathematically quite subtle (see, e.g., Turelli, 1977). However, in the setting of linear dynamical systems, the effect of a white-noise perturbation can be analyzed relatively easily. Because this analysis is not readily available in the ecology literature, we present here a short overview. We start from a formulation in vector notation,

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x} + \boldsymbol{\xi}(t), \tag{A1}$$

where $\mathbf{x} = (x_i)$ denotes the vector of species displacements, $\boldsymbol{\xi} = (\xi_i)$ the vector of species perturbations, and $A = (A_{ij})$ the community matrix.

Table A1: Notation used throughout the Appendices

symbol	meaning	equation
σ_{in}^2	per species variance of applied perturbation	(B2)
σ_{out}^2	per species variance of system response to perturbation	(B4, D3)
C_u	covariance matrix of individual pulses in multi-pulse perturbation	(A3)
f	frequency at which pulses occur in multi-pulse perturbation	
E	perturbation direction, proportional to fC_u	(B5)
C_x	covariance matrix of species responses to perturbation	(A5, A9)
\mathcal{L}	solution of Lyapunov equation, used to compute stationary C_x	(A7, A8)
\mathcal{V}_α	variability for perturbation type α ; when index α is omitted, immigration-type perturbations are assumed ($\alpha = 0$)	(D4)
$\mathcal{V}^{\text{worst}}$	mean-case variability, i.e., variability averaged over perturbation directions	(C2, D5)
$\mathcal{V}^{\text{mean}}$	worst-case variability, i.e., variability maximized over perturbation directions	(C3, D6)
$\mathcal{V}^{\text{spec } i}$	variability for the perturbation that affects only species i	
\mathcal{I}	invariability, i.e., variability-based stability measure	(B6)

Suppose that the perturbation $\boldsymbol{\xi}(t)$ consists in a sequence of pulses. We denote the times at which these pulses occur by t_k , and the corresponding pulse directions by $\mathbf{u}_k = (u_{k,i})$. The multi-pulse perturbation can then be written as

$$\boldsymbol{\xi}(t) = \sum_k \delta(t - t_k) \mathbf{u}_k. \quad (\text{A2})$$

where we have used the Dirac delta function $\delta(t)$.

We model both the pulse times t_k and the pulse directions \mathbf{u}_k as random variables. Specifically, we assume that the pulse times are distributed according to a Poisson point process with intensity f . This means that the probability that a pulse occurs in a small time interval of length Δs is equal to $f\Delta s$, and that this occurrence is independent of any other model randomness. We denote the average over the pulse times t_k by \mathbb{E}_f .

Furthermore, we assume that the pulse directions \mathbf{u}_k are independent (mutually independent, and independent of any other model randomness) and identically distributed. They have zero mean, and their second moments are given by the covariance matrix C_u . That is, denoting the average over the pulse directions \mathbf{u}_k by \mathbb{E}_u , we have $\mathbb{E}_u u_{k,i} = 0$, $\mathbb{E}_u u_{k,i}^2 = C_{u,ii}$, $\mathbb{E}_u u_{k,i} u_{k,j} = C_{u,ij}$, and $\mathbb{E}_u u_{k,i} u_{\ell,i} = \mathbb{E}_u u_{k,i} u_{\ell,j} = 0$ for $i \neq j$ and $k \neq \ell$. The latter equations can be written in vector notation,

$$C_u = \mathbb{E}_u \mathbf{u}_k \mathbf{u}_k^\top \quad \text{and} \quad \mathbb{E}_u \mathbf{u}_k \mathbf{u}_\ell^\top = 0. \quad (\text{A3})$$

We use this information to compute the statistics of species displacements $\mathbf{x}(t)$. Because the system response to a single pulse perturbation at time t_k in direction \mathbf{u}_k is equal to

$e^{(t-t_k)A}\mathbf{u}_k$, the system response to the sequence (A2) of pulse perturbations is equal to

$$\mathbf{x}(t) = \sum_{k|t_k < t} e^{(t-t_k)A} \mathbf{u}_k. \quad (\text{A4})$$

Taking the mean over the perturbation directions, we obtain

$$\mathbb{E}_u \mathbf{x}(t) = \sum_{k|t_k < t} e^{(t-t_k)A} \mathbb{E}_u \mathbf{u}_k = 0,$$

showing that the species displacements fluctuate around the unperturbed equilibrium.

Next, we compute the covariance matrix of the species displacements,

$$C_x = \mathbb{E}_{f,u} \mathbf{x}(t) \mathbf{x}(t)^\top. \quad (\text{A5})$$

We substitute the response to the multi-pulse perturbation, eq. (A4),

$$\begin{aligned} C_x &= \mathbb{E}_{f,u} \sum_{k|t_k < t} e^{(t-t_k)A} \mathbf{u}_k \sum_{\ell|t_\ell < t} \mathbf{u}_\ell^\top e^{(t-t_\ell)A^\top} \\ &= \mathbb{E}_f \sum_{k|t_k < t} \sum_{\ell|t_\ell < t} e^{(t-t_k)A} \mathbb{E}_u \mathbf{u}_k \mathbf{u}_\ell^\top e^{(t-t_\ell)A^\top} \\ &= \mathbb{E}_f \sum_{k|t_k < t} e^{(t-t_k)A} \mathbb{E}_u \mathbf{u}_k \mathbf{u}_k^\top e^{(t-t_k)A^\top} \\ &= \mathbb{E}_f \sum_{k|t_k < t} e^{(t-t_k)A} C_u e^{(t-t_k)A^\top}, \end{aligned}$$

where we have used eq. (A3). To take the average over the pulse times, we partition the time

axis in small intervals of length Δs . Writing $s_n = n\Delta s$ for any integer n , we get

$$C_x = \sum_{n|s_n < t} e^{(t-s_n)A} C_u e^{(t-s_n)A^\top} f \Delta s,$$

because the contribution of term n is equal to $e^{(t-s_n)A} C_u e^{(t-s_n)A^\top}$ with probability $f \Delta s$, and zero otherwise. Assuming that the time intervals Δs are infinitesimal, we find the integral

$$\begin{aligned} C_x &= \int_{-\infty}^t e^{(t-s)A} C_u e^{(t-s)A^\top} f ds \\ &= \int_0^\infty e^{sA} C_u e^{sA^\top} f ds \\ &= \int_0^\infty e^{sA} (f C_u) e^{sA^\top} ds. \end{aligned} \tag{A6}$$

Hence, we have obtained the stationary covariance matrix of the species displacements under a stochastic multi-pulse perturbation.

A white-noise perturbation corresponds to a special case of the stochastic multi-pulse perturbation, namely, to the case of extremely frequent pulses (large f) of extremely small size (small $\|\mathbf{u}\|$). More precisely, we have to take the coupled limit $f \rightarrow \infty$ and $C_u \rightarrow 0$ while keeping $f C_u$ constant. Because eq. (A6) depends on f and C_u through the product $f C_u$ only, the same expression is also valid for white-noise perturbations.

Alternatively, the stationary covariance matrix C_x can be obtained by solving the so-called Lyapunov equation,

$$AC + CA^\top + E = 0, \tag{A7}$$

where E is the covariance matrix characterizing the white noise, equal to $f C_u$ in our case.

Indeed, it can be verified that eq. (A6) satisfies eq. (A7),

$$\begin{aligned}
AC_x + C_x A^\top &= \int_0^\infty \left(A e^{sA} f C_u e^{sA^\top} ds + e^{sA} f C_u e^{sA^\top} A^\top \right) ds \\
&= \int_0^\infty \frac{d}{ds} \left(e^{sA} f C_u e^{sA^\top} \right) ds \\
&= e^{sA} f C_u e^{sA^\top} \Big|_{s \rightarrow \infty} - e^{sA} f C_u e^{sA^\top} \Big|_{s=0} \\
&= -f C_u.
\end{aligned}$$

For a stable matrix A this is the unique solution of the Lyapunov equation, for which we introduce the short-hand notation $\mathcal{L}(A, E)$,

$$\mathcal{L}(A, E) = \int_0^\infty e^{sA} E e^{sA^\top} ds. \tag{A8}$$

Hence, we can write

$$C_x = \mathcal{L}(A, f C_u),. \tag{A9}$$

From a numerical viewpoint, the covariance matrix C_x can be easily obtained by solving the Lyapunov eq. (A7), which can be written as a system of S^2 linear equations, rather than by computing the integral in (A8). Note also that solution of Lyapunov equation is linear in the perturbation covariance matrix,

$$\mathcal{L}(A, c_1 E_1 + c_2 E_2) = c_1 \mathcal{L}(A, E_1) + c_2 \mathcal{L}(A, E_2). \tag{A10}$$

2 Construction of variability measure

We explain the construction of the variability measure \mathcal{V} , see eq. (4) in the main text. The construction is based on the comparison of the intensity of the system response relative to the intensity of the applied perturbation. It should be stressed that, while we take special care of quantifying these intensities in a reasonable way, alternative choices are possible.

Perturbation intensity A reasonable measure of the perturbation intensity should increase with the number of pulses and the intensity of each pulse separately. In particular, we expect it to be proportional to the pulse frequency f and to some function of the pulse covariance matrix C_u .

We propose to look at the squared displacements $\|\mathbf{u}_k\|^2$ induced by pulses \mathbf{u}_k . The accumulated squared displacement in time interval $[t, t + T]$ is

$$\sum_{t_k \in [t, t+T]} \|\mathbf{u}_k\|^2.$$

Taking the average over pulse times and pulse directions,

$$\mathbb{E}_{f,u} \sum_{t_k \in [t, t+T]} \|\mathbf{u}_k\|^2 = \sum_{n|t < s_n < t+T} \mathbb{E}_u \|\mathbf{u}\|^2 f \Delta s,$$

where we have partitioned the time axis in small intervals of length Δs (see derivation of eq. (A6)). Then,

$$\mathbb{E}_{f,u} \sum_{t_k \in [t, t+T]} \|\mathbf{u}_k\|^2 = \text{Tr}(C_u) f T.$$

The result is proportional to the length T of the considered time interval. The average

accumulated squared displacement per unit of time is

$$\frac{1}{T} \mathbb{E}_{f,u} \sum_{t_k \in [t, t+T]} \|\mathbf{u}_k\|^2 = \text{Tr}(fC_u). \quad (\text{B1})$$

As expected, this quantity is proportional to the pulse frequency f and increases with the pulse covariance matrix C_u . Note also that f and C_u appear as a product, so that the expression is compatible with the white-noise limit.

Eq. (B1) quantifies the intensity of the perturbation applied to the entire ecosystem. This measure is not directly appropriate to normalize the perturbation intensity across systems. Indeed, when keeping the total perturbation intensity constant, the perturbation applied to a given species would be weaker in a community with a larger number of species. To eliminate this artefact, we normalize the perturbation intensity on a per species basis. Thus, we propose to quantify the perturbation intensity as

$$\sigma_{\text{in}}^2 = \frac{f}{S} \text{Tr} C_u. \quad (\text{B2})$$

Response intensity We measure the intensity of the system response in terms of the covariance matrix C_x . This matrix encodes the statistical properties of the abundance (or biomass) fluctuations in stationary state. For example, species abundance $x_i(t)$ fluctuates around its equilibrium value N_i with variance $C_{x,ii}$. More generally, we can describe the fluctuations of any function φ of species abundance. The dynamics near equilibrium are

$$\varphi(\mathbf{n}(t)) = \varphi(\mathbf{N}) + \mathbf{v}^\top \mathbf{x}(t),$$

where vector $\mathbf{v} = \nabla \varphi$ is the gradient of the function φ evaluated at the equilibrium \mathbf{N} . This vector gives the direction in which the system fluctuations are observed. Then, denoting the

temporal mean and variance by \mathbb{E}_t and Var_t , we have

$$\begin{aligned}
\text{Var}_t(\varphi(\mathbf{n}(t))) &= \mathbb{E}_t\left(\left(\mathbf{v}^\top \mathbf{x}(t)\right)^2\right) \\
&= \mathbb{E}_t\left(\mathbf{v}^\top \mathbf{x}(t) \mathbf{x}(t)^\top \mathbf{v}\right) \\
&= \mathbf{v}^\top \mathbb{E}_t(\mathbf{x}(t) \mathbf{x}(t)^\top) \mathbf{v} \\
&= \mathbf{v}^\top C_x \mathbf{v}.
\end{aligned} \tag{B3}$$

We use this variance to quantify the intensity of the system response. Rather than choosing a particular vector \mathbf{v} , we consider the average over all observation directions. Specifically, we restrict attention to unit vectors \mathbf{v} and average over the uniform distribution of such vectors. Denoting this average by \mathbb{E}_v , we get

$$\mathbb{E}_v \text{Var}_t(\varphi(\mathbf{n}(t))) = \mathbb{E}_v(\mathbf{v}^\top C_x \mathbf{v}) = \text{Tr} \mathbb{E}_v \mathbf{v} \mathbf{v}^\top C_x.$$

It follows from species symmetry that the average $\mathbb{E}_v \mathbf{v} \mathbf{v}^\top$ is proportional to the unit matrix. Moreover, because $\text{Tr} \mathbf{v} \mathbf{v}^\top = 1$ for all vectors \mathbf{v} , the constant of proportionality is equal to $\frac{1}{S}$. Hence,

$$\mathbb{E}_v \text{Var}_t(\varphi(\mathbf{n}(t))) = \frac{1}{S} \text{Tr} C_x.$$

Therefore, we propose to quantify the response intensity as

$$\sigma_{\text{out}}^2 = \frac{1}{S} \text{Tr} C_x. \tag{B4}$$

Variability and invariability We define variability \mathcal{V} as the ratio of the response intensity σ_{out}^2 and the perturbation intensity σ_{in}^2 ,

$$\mathcal{V} = \frac{\sigma_{\text{out}}^2}{\sigma_{\text{in}}^2} = \frac{\frac{1}{S} \text{Tr } C_x}{\frac{f}{S} \text{Tr } C_u} = \frac{\text{Tr } C_x}{f \text{Tr } C_u}.$$

Substituting eq. (A9) for C_x , we get

$$\mathcal{V} = \frac{\text{Tr } \mathcal{L}(A, fC_u)}{f \text{Tr } C_u} = \text{Tr } \mathcal{L}\left(A, \frac{C_u}{\text{Tr } C_u}\right),$$

where we have used the linearity property (A10). We see that only the normalized perturbation covariance matrix matters in this expression. That is, the variability measure focuses on the directional effect of the perturbation. We make this dependence explicit in the notation, and write

$$\mathcal{V}(E) = \text{Tr } \mathcal{L}(A, E), \tag{B5}$$

where $E = \frac{C_u}{\text{Tr } C_u}$ is the perturbation direction, i.e., a covariance matrix with unit trace.

Variability is inversely related to stability: the more variable an ecosystem, the less stable it is. For purpose of comparison, we construct a stability measure based on variability $\mathcal{V}(E)$, which we call invariability $\mathcal{I}(E)$,

$$\mathcal{I}(E) = \frac{1}{2\mathcal{V}(E)}. \tag{B6}$$

The factor 2 in this definition guarantees that we recover asymptotic resilience for the simplest dynamical systems. To see this, consider a system of S non-interacting species, in which all species have the same return rate λ . The community matrix is equal to $A = -\lambda\mathbb{1}$ where $\mathbb{1}$ denotes the identity matrix. From the Lyapunov equation (A7) we get the stationary covariance matrix $\mathcal{L}(A, E) = \frac{1}{2\lambda}E$. Therefore, $\mathcal{V}(E) = \frac{1}{2\lambda}$ and $\mathcal{I}(E) = \lambda$, which is equal to

the asymptotic resilience of this example system.

3 Worst-case and mean-case variability

Worst-case variability is defined as

$$\mathcal{V}^{\text{worst}} = \max_E \mathcal{V}(E) = \max_E \text{Tr} \mathcal{L}(A, E) \quad (\text{C1})$$

where the maximum is taken over perturbation directions, i.e., over covariance matrices E with $\text{Tr} E = 1$. The function $\text{Tr} \mathcal{L}(A, E)$ is linear in the perturbation direction E , see eq. (A10), and the set of perturbation directions is convex. Hence, the maximum is reached at an extreme point, that is, on the boundary of the set. The extreme points are the purely directional perturbations (see Appendix 5 for the argument in the two-species case), so that the maximum is reached at a purely directional perturbation. Arnoldi *et al.* (2016) showed that the worst-case variability can be easily computed, namely, as a specific norm of the operator \hat{A}^{-1} that maps E to $\mathcal{L}(A, E)$. Concretely, defining $\hat{A} = A \otimes \mathbb{1} + \mathbb{1} \otimes A$,

$$\mathcal{V}^{\text{worst}} = \|\hat{A}^{-1}\|, \quad (\text{C2})$$

where $\|\cdot\|$ stands for the spectral norm of $S^2 \times S^2$ matrices.

To define **mean-case variability** $\mathcal{V}^{\text{mean}}$, we assume a probability distribution over the perturbation directions, and compute the mean system response over this distribution. Due to the linearity property (A10), this mean response is equal to the response to the mean perturbation direction. Hence, we do not have to specify the full probability distribution over the perturbation directions; it suffices to determine the mean perturbation direction. As can be directly verified in the two-species case (Appendix 5), if, averaged over the distribution

of perturbation directions, perturbation intensities are evenly distributed across species, and positive and negative correlations between species perturbations cancel out, then the mean perturbation direction is adirectional. This corresponds to the center of the set of perturbation directions (in the two-species case the disc center represented in Fig. 3), and is proportional to the identity matrix, that is, $E = \frac{1}{S}\mathbb{1}$. Therefore,

$$\mathcal{V}^{\text{mean}} = \text{Tr } \mathcal{L}(A, \frac{1}{S}\mathbb{1}). \quad (\text{C3})$$

4 Perturbation types and variability

The perturbation type (environmental-, demographic- or immigration-type) affects how the perturbation intensity is distributed across species. Therefore, it also affects our measure of variability, as defined in Appendix 2. Here we describe how the variability definition has to be modified.

We defined variability measure (B5) as the intensity of the system response relative to the intensity of the applied perturbation. To quantify the perturbation intensity in the case of abundance-dependent perturbations, we distinguish the intrinsic effect of the perturbation on a species, which does not depend on the species' abundance, and the total effect of the perturbation on the species, which does depend on abundance. We propose to express the perturbation intensity in terms of the intrinsic perturbation, while it is the total perturbation that acts on the species dynamics.

Formally, for species i , we denote the intrinsic perturbation by $\xi_i^{\text{intr}}(t)$ and the total perturbation by $\xi_i^{\text{tot}}(t)$. Then, for a type- α perturbation, we have

$$\xi_i^{\text{tot}}(t) = N_i^{\frac{\alpha}{2}} \xi_i^{\text{intr}}(t), \quad (\text{D1})$$

where N_i is the abundance of species i . Thus, the intrinsic perturbation $\xi^{\text{intr}}(t)$ can be interpreted as the per capita perturbation strength. Eq. (D1) can be written in vector notation as

$$\boldsymbol{\xi}^{\text{tot}}(t) = D^{\frac{\alpha}{2}} \boldsymbol{\xi}^{\text{intr}}(t), \quad (\text{D2})$$

where D is the diagonal matrix whose entries are species equilibrium values ($D_{ii} = N_i$).

Both the intrinsic and total perturbation are multi-pulse. If we denote the pulses of the intrinsic perturbation by \mathbf{u}_k , then, by eq. (D2), those of the total perturbation are $D^{\frac{\alpha}{2}} \mathbf{u}_k$. Then, to quantify the perturbation intensity, we use the covariance matrix of the pulses in the intrinsic perturbation. The derivation leading to eq. (B2) is still valid. However, to compute the covariance matrix of the species displacements, we use the covariance matrix of the pulses in the total perturbation. This corresponds to replacing C_u by $D^{\frac{\alpha}{2}} C_u D^{\frac{\alpha}{2}}$ in the derivation of eq. (B4), so that we get

$$\sigma_{\text{out}}^2 = \frac{1}{S} \text{Tr} \mathcal{L}(A, f D^{\frac{\alpha}{2}} C_u D^{\frac{\alpha}{2}}). \quad (\text{D3})$$

The variability measure for a type- α perturbation becomes

$$\mathcal{V}_\alpha = \frac{\sigma_{\text{out}}^2}{\sigma_{\text{in}}^2} = \text{Tr} \mathcal{L}\left(A, \frac{D^{\frac{\alpha}{2}} C_u D^{\frac{\alpha}{2}}}{\text{Tr} C_u}\right),$$

or, in terms of the (intrinsic) perturbation direction E ,

$$\mathcal{V}_\alpha(E) = \text{Tr} \mathcal{L}(A, D^{\frac{\alpha}{2}} E D^{\frac{\alpha}{2}}). \quad (\text{D4})$$

Applying the same arguments as in Appendix 3, we find that worst-case variability,

$$\mathcal{V}_\alpha^{\text{worst}} = \max_E \mathcal{V}_\alpha(E) = \max_E \text{Tr} \mathcal{L}(A, D^{\frac{\alpha}{2}} E D^{\frac{\alpha}{2}}),$$

is attained at a perfectly correlated perturbation. If we define the operator (an $S^2 \times S^2$ matrix)

$$\mathcal{D}_\alpha = D^{\frac{\alpha}{2}} \otimes D^{\frac{\alpha}{2}},$$

then the worst case-variability can be computed as

$$\mathcal{V}_\alpha^{\text{worst}} = \|\widehat{A}^{-1} \circ \mathcal{D}_\alpha\|, \quad (\text{D5})$$

where $\|\cdot\|$ is the spectral norm for $S^2 \times S^2$ matrices. On the other hand, the mean-case variability,

$$\mathcal{V}_\alpha^{\text{mean}} = \text{Tr} \mathcal{L}(A, \frac{1}{S} D^\alpha), \quad (\text{D6})$$

is attained by the uniform, uncorrelated perturbation.

5 Perturbation directions in two dimensions

Variability spectra are built on the notion of perturbation directions. They are characterized by a covariance matrix E with $\text{Tr} E = 1$. To gain some intuition, we study the set of perturbation directions in the case of two species.

Any perturbation direction E in two dimensions can be written as

$$E = \begin{pmatrix} 1-x & y \\ y & x \end{pmatrix}. \quad (\text{E1})$$

with $0 \leq x \leq 1$ and $y^2 \leq x(1-x)$. The first inequality guarantees that the elements on the diagonal are variances, i.e., positive numbers. The second inequality guarantees that the off-diagonal element is a proper covariance, in particular, that the correlation coefficient is

contained between -1 and 1 . Note that matrix (E1) has always $\text{Tr } E = 1$.

It follows from eq. (E1) that the set of perturbation directions in two dimensions is parameterized by two numbers x and y . Using these numbers as axes of a two-dimensional plot, we see that the set of perturbation directions corresponds to a disc with radius 0.5 and centered at $(0.5, 0)$ (see Fig. 3).

It is instructive to study the position of specific perturbation directions on the disc. The point $(0, 0)$ corresponds to a perturbation affecting only the first species, whereas point $(1, 0)$ is a perturbation only affecting the second species. More generally, any point on the boundary of the disc correspond to a multi-pulse perturbation for which the individual pulses have a fixed direction. For example, the point $(0.5, 0.5)$ is a perturbation for which each pulse has the same effect on species 1 and species 2, whereas the perturbation corresponding to point $(0.5, -0.5)$ consists of pulses that affect the two species equally strongly, but in an opposite way. Perturbations on the boundary are *perfectly correlated*.

The perturbations towards the center of the disc are composed of pulses with more variable directions. For example, a multi-pulse perturbation for which half of the pulses affect only the second species, and the other pulses affect the two species equally strongly corresponds to the point $\frac{1}{2}(0, 1) + \frac{1}{2}(0.5, 0.5) = (0.25, 0.75)$. The mixture of different pulse directions is the strongest at the center of the disc $(0.5, 0)$. Examples of ways to realize this perturbation are $\frac{1}{2}(0, 0) + \frac{1}{2}(1, 0)$, $\frac{1}{2}(0.5, 0.5) + \frac{1}{2}(0.5, -0.5)$ and $\frac{1}{4}(0, 0) + \frac{1}{4}(0.5, 0.5) + \frac{1}{4}(1, 0) + \frac{1}{4}(0.5, -0.5)$. In each of these example, the pulses have their intensities, averaged over time, evenly distributed across species, and affect them, again averaged over time, in an uncorrelated way. The perturbation corresponding to the point $(0.5, 0)$ is thus evenly distributed across species but uncorrelated in time.

6 Random Lotka-Volterra model

The communities used in Figs. 4, 5 and 6 are constructed from the Lotka-Volterra model with random parameters. We consider a pool of species governed by the dynamics

$$\frac{dN_i(t)}{dt} = \frac{r_i N_i(t)}{K_i} \left(K_i - N_i - \sum_{\substack{j=1 \\ j \neq i}}^{S_{\text{pool}}} B_{ij} N_j(t) \right), \quad (\text{F1})$$

and we let the dynamics settle to an equilibrium community of S remaining species. By drawing random values for the parameters – growth rates r_i , carrying capacities K_i , and competition coefficients B_{ij} – we generate communities of various diversity.

For the communities in Fig. 4, we set $S_{\text{pool}} = 50$, and chose the parameter values as follows,

r_i randomly drawn from $\mathcal{N}(1, 0.2)$, a normal distribution with mean 1 and standard deviation 0.2 (independent draws for different species)

K_i drawn from $\mathcal{N}(1, 0.2)$

B_{ij} half of the competition coefficients are set equal to 0; the other half are drawn from $\mathcal{N}(0.1, 0.1)$.

This procedure resulted in a community of $S = 40$ persistent species. Note that some of the competition coefficients can be negative, so that there can be positive interactions (e.g. facilitation).

For the communities in the top row of Fig. 5, we followed the same procedure, except that we changed the way of generating the competition coefficients B_{ij} . In the case without interactions, all B_{ij} were set zero; in the case with weak interactions, the non-zero coefficients B_{ij} were drawn from $\mathcal{N}(0.02, 0.02)$; and in the case with strong interactions, the non-zero B_{ij} were drawn from $\mathcal{N}(0.1, 0.1)$, as for the community of Fig. 4.

We applied a similar procedure to obtain the bottom row of Fig. 5, but for these communities the growth rates r_i and carrying capacities K_i were not drawn independently. Instead, we first drew auxiliary variables a_i from $\mathcal{N}(1, 0.2)$, b_i from $\mathcal{N}(1, 0.1)$ and c_i from $\mathcal{N}(1, 0.1)$, and then set $r_i = b_i a_i$ and $K_i = c_i / a_i$.

For the communities of Fig. 6, we varied the size of the species pool S_{pool} so that the realized species richness covered the range from 1 to 20. Specifically, we drew S_{pool} randomly from 1 to 100, and generated the parameter values as in Fig. 4. We repeated this procedure many times, until obtaining 1000 communities for each value of realized species richness S from 1 to 20. Then, for each realized community, and for each of the three perturbation types ($\alpha = 0$, $\alpha = 1$ and $\alpha = 2$), we generated 1000 random perturbations leading to a variability distribution of 1000 values. From the variability distributions we extracted median, 5th and 95th percentile, and minimum and maximum. For the realized communities we computed asymptotic resilience, worst-case variability and the prediction for the median. Finally, we computed the median of these statistics and predictions, all represented in Fig. 6.

7 Genericity in strongly interacting communities

We give some elements as to why the behavior reported in Figs. 4 and 5 in the main text can be expected to be a general trend in diverse communities of interacting species. Denote by $\mathcal{V}_\alpha^{\text{spec } i}$ the community variability induced by a type- α perturbation that is fully focused on a single species i . We are interested in the relationship between this variability and the equilibrium abundance N_i of the perturbed species i .

First, note that for single-species perturbations the variability metrics $\mathcal{V}_\alpha^{\text{spec } i}$ for different

perturbation types α are directly linked. From definition (D4) we get that

$$\mathcal{V}_\alpha^{\text{spec } i} = N_i^\alpha \mathcal{V}_{\alpha=0}^{\text{spec } i}. \quad (\text{G1})$$

Hence, it suffices to study the behavior of $\mathcal{V}_{\alpha=0}^{\text{spec } i}$.

Next, consider again the Lotka-Volterra dynamics (F1) from the perspective of a focal species i . If a stable equilibrium exists in which the focal species survives, small displacements from equilibrium $x_i = N_i(t) - N_i$ are met with the dynamics

$$\frac{dx_i}{dt} = \frac{r_i N_i}{K_i} \left(-x_i - \sum_{j \neq i} B_{ij} x_j \right) = \frac{1}{\tau_i} \left(-x_i - \sum_{j \neq i} B_{ij} x_j \right), \quad (\text{G2})$$

where $\tau_i = \frac{K_i}{r_i N_i}$ has units of time. We claim that τ_i sets a characteristic time scale of the focal species dynamics; it measures the typical time it takes for the species to recover from a perturbation that displaces it from its equilibrium. This species response time is directly related to the species' variability $\mathcal{V}_{\alpha=0}^{\text{spec } i}$: the slower the species, the larger the impact of a repeated perturbation acting on this species, and the larger the induced variability.

We illustrate the relationship between τ_i and $\mathcal{V}_{\alpha=0}^{\text{spec } i}$ in Fig. G1 (inset panels). For the six communities of Fig. 5, we fit the power-law relationship

$$\mathcal{V}_{\alpha=0}^{\text{spec } i} \propto \tau_i^\nu, \quad (\text{G3})$$

where the index i runs over the set of persistent species. The estimates of the exponent ν (using linear regression on the log-log plot) are all close to one. This result is obvious for the communities without interactions, for which $\mathcal{V}_{\alpha=0}^{\text{spec } i} = \frac{1}{2} \tau_i$ (left-hand panels). But the same result remains valid in the presence of interactions. We find that interactions do not substantially modify the time scale on which a species responds to perturbations affecting

only that species.

Therefore, to study the relationship between N_i and $\mathcal{V}_\alpha^{\text{spec } i}$, we can restrict to the simpler relationship between N_i and $\tau_i = \frac{K_i}{r_i N_i}$, which is determined by the correlations between growth rates r_i , carrying capacities K_i and equilibrium abundances N_i . Fig. G1 (main panels) shows this relationship for the six communities of Fig. 5. Fitting the power law

$$\tau_i \propto N_i^\gamma, \quad (\text{G4})$$

we find various estimates for the exponent γ . Without interactions, we have $N_i = K_i$, and hence, $\tau_i = \frac{1}{r_i}$. If growth rates and carrying capacities are drawn independently, abundance and response time are unrelated, leading to $\gamma \approx 0$ (Fig. G1, upper-left panel). Alternatively, if growth rates and carrying capacities satisfy some trade-off, higher abundance (larger K_i) is associated with longer response time (smaller r_i), leading to $\gamma > 0$ (Fig. G1, lower-left panel). When increasing the interactions, the link between N_i and K_i becomes weaker. Indeed, from the equilibrium condition for species i we have

$$\begin{aligned} N_i &= K_i + \sum_{j \neq i} B_{ij} N_j \\ &= K_i + \left(\sum_{j \neq i} B_{ij} K_j + \sum_{k \neq j \neq i} B_{ij} B_{jk} K_k \right. \\ &\quad \left. + \sum_{l \neq k \neq j \neq i} B_{ij} B_{jk} B_{kl} K_l + \dots \right), \end{aligned}$$

where in the second line we have used the equilibrium condition for the other species. For sufficiently strong interactions, the terms between brackets dominate the term K_i , so that N_i and K_i become unrelated. In this case, we have $\tau_i \propto \frac{1}{N_i}$, leading to $\gamma \approx -1$: more abundant species have faster dynamics and smaller response time. This limiting case is observed both

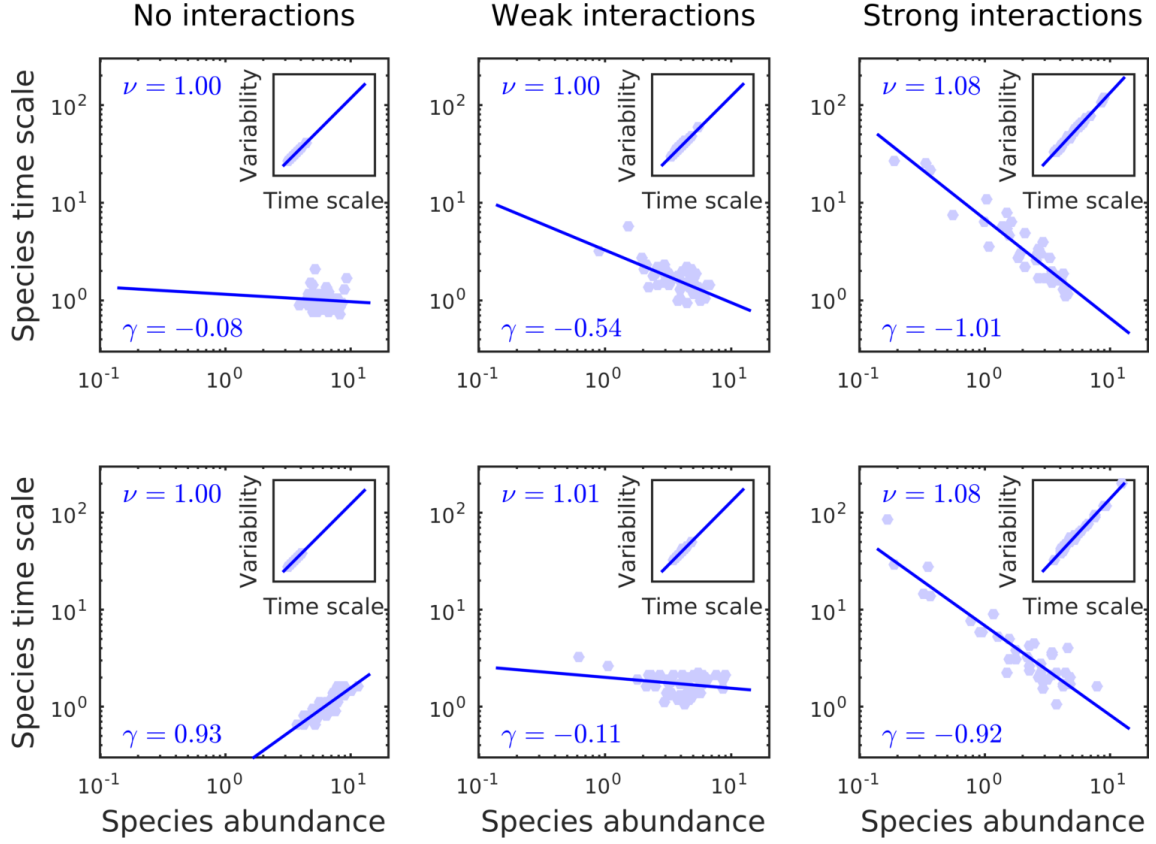


Figure G1: Clarifying the relationship between abundance of perturbed species and community variability. In Appendix 7 we introduce the auxiliary variable τ_i , the characteristic time scale of species i , to explain the relationship between variability $\mathcal{V}_{\alpha=0}^{\text{spec } i}$ and abundance N_i . For the six communities of Fig. 5 in the main text, we plot τ_i vs N_i in the main panels, and $\mathcal{V}_{\alpha=0}^{\text{spec } i}$ vs τ_i in the inset panels. We fit a power law to each of these relationships, using linear regression on the log-log plot. The estimated exponents γ (for the data τ_i vs N_i) and ν (for the data $\mathcal{V}_{\alpha=0}^{\text{spec } i}$ vs τ_i) are reported in the panels.

if r_i and K_i are independent, and if they satisfy a trade-off (Fig. G1, right-hand panels).

Finally, putting together eqs. (G1, G3, G4), we get

$$\mathcal{V}_\alpha^{\text{spec } i} \propto N_i^\alpha \tau_i^\nu \propto N_i^{\alpha+\gamma\nu} \approx N_i^{\alpha+\gamma}, \quad (\text{G5})$$

where in the last step we have used that $\nu \approx 1$. The relationship between abundance of perturbed species and community variability is strongly determined by the exponent γ , that is, by the relationship between abundance N_i and response time τ_i . In the case of weak interactions, the latter relationship depends on the assumed link between growth rate r_i and carrying capacity K_i , so that no unambiguous relationship is to be expected between abundance and variability. However, in the limit of strong interactions, we have $\gamma \approx -1$ and

$$\mathcal{V}_\alpha^{\text{spec } i} \propto N_i^{\alpha-1}. \quad (\text{G6})$$

Hence, for immigration-type perturbations ($\alpha = 0$) variability is inversely proportional to the abundance of the perturbed species. In contrast, for environmental perturbations ($\alpha = 2$), variability is directly proportional to the abundance of the perturbed species. These are the relationships depicted in Figs. 4 and 5 of the main text.

8 Variability and abundance statistics

From the observed relationship between abundance and variability (Figs. 4 and 5), patterns for worst- and mean-case variability can be deduced. This reveals a connection between stability and diversity metrics.

Denote by $\mathcal{V}_\alpha^{\text{spec } i}$ the community variability induced by a type- α perturbation fully focused on species i . We start from the power-relationship (G6), linking this variability and the

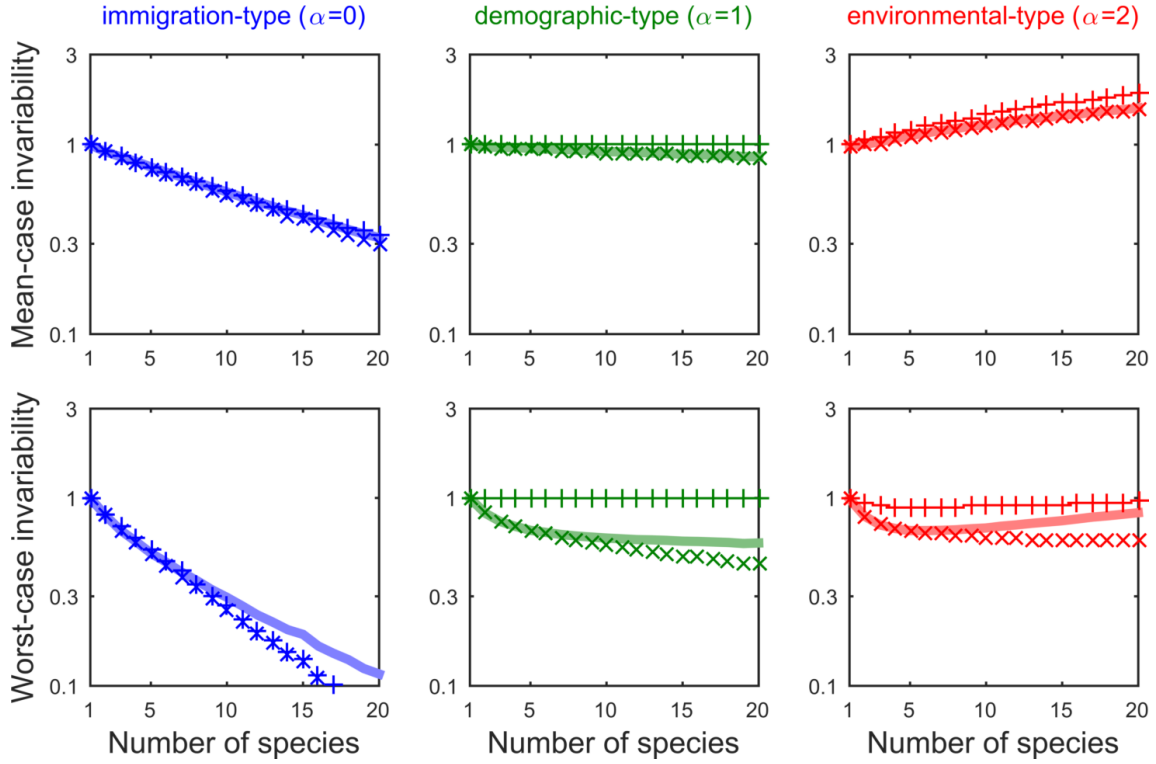


Figure H1: Invariability and species abundance. Top row: mean-case, bottom row: worst-case. \times -marks: analytical formula; $+$ -marks: approximation in terms of abundance (see Appendix 8); thick line: simulation results. For immigration-type perturbations (first column, in blue), mean-case invariability scales as the harmonic mean abundance (see eq. (H2)), which decreases with diversity. Worst-case invariability scales as the abundance of the rarest species. On the other hand, in response to environmental-type perturbations (third column, in red), mean-case variability scales as the arithmetic mean abundance (see eq. (H4)) so that invariability increases. Worst-case variability scales as the abundance of the most common species. In between (second column, in green), for demographic-type perturbations, neither worst- nor mean-case invariability is determined by statistics of species abundances.

equilibrium abundance of species i . As argued in Appendix 7, we expect this relationship to hold for sufficiently strong interactions.

For immigration-type perturbations ($\alpha = 0$), worst-case variability is approached by taking the maximum over species which gives

$$\mathcal{V}_{\alpha=0}^{\text{worst}} \approx \max_i \mathcal{V}_{\alpha=0}^{\text{spec } i} \propto \frac{1}{\min_i N_i}. \quad (\text{H1})$$

so that the worst case is governed by the rarest species. Because the abundance of the rarest species typically decreases with diversity, the corresponding diversity-stability relationship is decreasing. For mean-case variability, averaging over species individual contributions, we get

$$\mathcal{V}_{\alpha=0}^{\text{mean}} = \frac{1}{S} \sum_i \mathcal{V}_{\alpha=0}^{\text{spec } i} \propto \frac{1}{S} \sum_i \frac{1}{N_i} = \langle N \rangle_{\text{harm}}^{-1}, \quad (\text{H2})$$

where $\langle N \rangle_{\text{harm}}$ stands for the harmonic mean of species abundances. Mean abundance typically decreases with diversity, so that the corresponding diversity-stability relationship is decreasing.

When caused by environmental-type perturbations ($\alpha = 2$), worst-case variability is approached by taking the maximum over species, giving

$$\mathcal{V}_{\alpha=2}^{\text{worst}} \approx \max_i \mathcal{V}_{\alpha=0}^{\text{spec } i} \propto \max_i N_i, \quad (\text{H3})$$

so that the worst case is governed by the most abundant species. For mean-case variability we get

$$\mathcal{V}_{\alpha=2}^{\text{mean}} \propto \frac{1}{S} \sum_i N_i = \langle N \rangle_{\text{arith}}, \quad (\text{H4})$$

the arithmetic mean of species abundances. Mean abundance typically decreases with diver-

sity, so that the corresponding diversity-stability relationship is increasing.

Note that when caused by demographic-type perturbations ($\alpha = 1$) the species-by-species approach does not work: demographic variability probes a collective property of the community. The different relationships between abundance and variability are illustrated in Fig. H1.