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

Supporting Information

Jean-François Arnoldi, Michel Loreau, and Bart Haegeman

The Supporting Information is organized as follows: Appendix S1 through S4 provides a self-contained presentation of the mathematical foundations of our variability theory. Appendix S5 through S8 provide details concerning specific applications considered in the main text: two-species communities in Appendix S5, complex Lotka-Volterra communities in appendices S6 and S7, and the link between abundance statistics and variability in Appendix S8. A list of the most important notation used in the Appendices is given in Table S1.

Table S1: Notation used throughout the Appendices

symbol	meaning	equation
σ_{in}^2	per species variance of applied perturbation	(S12)
σ_{out}^2	per species variance of system response to perturbation	(S14, S22)
C_u	covariance matrix of individual pulses in multi-pulse perturbation	(S3)
f	frequency at which pulses occur in multi-pulse perturbation	
E	perturbation direction, proportional to fC_u	(S15)
C_x	covariance matrix of species responses to perturbation	(S5, S9)
$\mathcal{L}$	solution of Lyapunov equation, used to compute stationary C_x	(S7, S8)
$\mathcal{V}_\alpha$	variability for perturbation type α; when index α is omitted, immigration-type perturbations are assumed ($\alpha = 0$)	(S23)
$\mathcal{V}^{\text{worst}}$	mean-case variability, i.e., variability averaged over perturbation directions	(S18, S24)
$\mathcal{V}^{\text{mean}}$	worst-case variability, i.e., variability maximized over perturbation directions	(S19, S25)
$\mathcal{V}^{\text{spec } i}$	variability for the perturbation that affects only species i	
$\mathcal{I}$	invariability, i.e., variability-based stability measure	(S16)

S1 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,

$$\frac{d\boldsymbol{x}}{dt} = A\boldsymbol{x} + \boldsymbol{\xi}(t), \tag{S1}$$

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

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 $\boldsymbol{u}_k = (u_{k,i})$. The multi-pulse perturbation can then be written as

$$\boldsymbol{\xi}(t) = \sum_k \delta(t - t_k)\, \boldsymbol{u}_k. \tag{S2}$$

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

We model both the pulse times t_k and the pulse directions $\boldsymbol{u}_k$ 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 $\boldsymbol{u}_k$ 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 $\boldsymbol{u}_k$ 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,

$$C_u = \mathbb{E}_u\, \boldsymbol{u}_k \boldsymbol{u}_k^\top \qquad \text{and} \qquad \mathbb{E}_u\, \boldsymbol{u}_k \boldsymbol{u}_\ell^\top = 0. \tag{S3}$$

We use this information to compute the statistics of species displacements $\boldsymbol{x}(t)$. Because the system response to a single pulse perturbation at time t_k in direction $\boldsymbol{u}_k$ is equal to $e^{(t-t_k)A}\boldsymbol{u}_k$, the system response to the sequence (S2) of pulse perturbations is equal to

$$\boldsymbol{x}(t) = \sum_{k|t_k<t} e^{(t-t_k)A}\, \boldsymbol{u}_k. \tag{S4}$$

Taking the mean over the perturbation directions, we obtain

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

showing that the species displacements fluctuate around the unperturbed equilibrium.

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

$$C_x = \mathbb{E}_{f,u}\, \boldsymbol{x}(t)\boldsymbol{x}(t)^\top. \tag{S5}$$

We substitute the response to the multi-pulse perturbation, eq. (S4),

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

where we have used eq. (S3). 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

$$
\begin{aligned}
C_x &= \int_{-\infty}^{t} e^{(t-s)A}\, C_u\, e^{(t-s)A^\top} f\, ds \\
&= \int_{0}^{\infty} e^{sA}\, C_u\, e^{sA^\top} f\, ds \\
&= \int_{0}^{\infty} e^{sA}\left(f C_u\right) e^{sA^\top} ds.
\end{aligned}
\tag{S6}
$$

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 $\|\boldsymbol{u}\|$). More precisely, we have to take the coupled limit $f \to \infty$ and $C_u \to 0$ while keeping $f C_u$ constant. Because eq. (S6) 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,

$$AC_x + C_x A^\top + E = 0, \tag{S7}$$

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. (S6) satisfies eq. (S7),

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

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

$$
\mathcal{L}(A, E) = \int_0^\infty e^{sA} E e^{sA^\top} ds. \tag{S8}
$$

Hence, we can write

$$
C_x = \mathcal{L}(A, f C_u), . \tag{S9}
$$

From a numerical viewpoint, the covariance matrix C_x can be easily obtained by solving the Lyapunov equation (S7), which can be written as a system of S^2 linear equations, rather than by computing the integral in (S8). Note also that the solution of the Lyapunov equation is linear in the perturbation covariance matrix,

$$
\mathcal{L}(A, c_1 E_1 + c_2 E_2) = c_1 \mathcal{L}(A, E_1) + c_2 \mathcal{L}(A, E_2). \tag{S10}
$$

S2 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 $\|\boldsymbol{u_k}\|^2$ induced by pulses $\boldsymbol{u_k}$. The accumulated squared displacement in time interval $[t, t+T]$ is

$$\sum_{t_k \in [t,t+T]} \|\boldsymbol{u_k}\|^2.$$

Taking the average over pulse times and pulse directions,

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

where we have partitioned the time axis in small intervals of length Δs (see derivation of eq. (S6)). Then,

$$\mathbb{E}_{f,u} \sum_{t_k \in [t,t+T]} \|\boldsymbol{u_k}\|^2 = \operatorname{Tr}\big(C_u\big) fT.$$

The result is proportional to the length T of the considered time interval. The average accumulated squared displacement per unit of time is

$$\frac{1}{T} \, \mathbb{E}_{f,u} \sum_{t_k \in [t,t+T]} \|\boldsymbol{u_k}\|^2 = \operatorname{Tr}\big(f C_u\big). \tag{S11}$$

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. (S11) quantifies the intensity of the perturbation applied to the entire ecosystem. This measure is not directly appropriate to normalize the pertubation 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

$$\sigma_{\mathrm{in}}^2 = \frac{f}{S} \operatorname{Tr} C_u. \tag{S12}$$

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

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

where vector $\boldsymbol{v} = \nabla\varphi$ is the gradient of the function φ evaluated at the equilibrium $\boldsymbol{N}$. 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

$$
\begin{aligned}
\mathrm{Var}_t\left(\varphi(\boldsymbol{n}(t))\right) &= \mathbb{E}_t\left(\left(\boldsymbol{v}^\top \boldsymbol{x}(t)\right)^2\right) \\
&= \mathbb{E}_t\left(\boldsymbol{v}^\top \boldsymbol{x}(t)\boldsymbol{x}(t)^\top \boldsymbol{v}\right) \\
&= \boldsymbol{v}^\top \mathbb{E}_t\left(\boldsymbol{x}(t)\boldsymbol{x}(t)^\top\right)\boldsymbol{v} \\
&= \boldsymbol{v}^\top C_x\, \boldsymbol{v}. \tag{S13}
\end{aligned}
$$

We use this variance to quantify the intensity of the system response. Rather than choosing

a particular vector $\boldsymbol{v}$, we consider the average over all observation directions. Specifically, we restrict attention to unit vectors $\boldsymbol{v}$ and average over the uniform distribution of such vectors. Denoting this average by $\mathbb{E}_v$, we get

$$\mathbb{E}_v \operatorname{Var}_t\big(\varphi(\boldsymbol{n}(t))\big) = \mathbb{E}_v\left(\boldsymbol{v}^\top C_x \boldsymbol{v}\right) = \operatorname{Tr} \mathbb{E}_v\, \boldsymbol{v}\boldsymbol{v}^\top C_x.$$

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

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

Therefore, we propose to quantify the response intensity as

$$\sigma_{\text{out}}^2 = \frac{1}{S}\operatorname{Tr} C_x. \tag{S14}$$

Variability and invariability The response intensity σ_{out}^2 is linear in the perturbation intensity σ_{in}^2. More precisely, when increasing all species-specific pulse intensities by a factor c, the pulse covariance matrix C_u, the perturbation intensity σ_{in}^2, the response covariance matrix C_x (due to the linearity of the Lyapunov equation, see eqs. (S9–S10)) and the response intensity σ_{out}^2 all also increase by a factor c.

Therefore, we define variability $\mathcal{V}$ as the ratio of the response intensity σ_{out}^2 and the perturbation intensity σ_{in}^2,

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

Substituting eq. (S9) for C_x, we get

$$\mathcal{V} = \frac{\operatorname{Tr}\mathcal{L}(A, fC_u)}{f\operatorname{Tr} C_u} = \operatorname{Tr}\mathcal{L}\big(A, \frac{C_u}{\operatorname{Tr} C_u}\big),$$

where we have used the linearity property (S10). 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

$$\mathcal{V}(E) = \operatorname{Tr} \mathcal{L}(A, E), \tag{S15}$$

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

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

$$\mathcal{I}(E) = \frac{1}{2\,\mathcal{V}(E)}. \tag{S16}$$

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 (S7) 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.

S3 Worst-case and mean-case variability

Worst-case variability is defined as

$$\mathcal{V}^{\text{worst}} = \max_E \mathcal{V}(E) = \max_E \text{Tr}\,\mathcal{L}(A, E) \tag{S17}$$

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. (S10), 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 S5 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 $\widehat{A}^{-1}$ that maps E to $\mathcal{L}(A, E)$. Concretely, defining $\widehat{A} = A \otimes \mathbb{1} + \mathbb{1} \otimes A$,

$$\mathcal{V}^{\text{worst}} = ||\widehat{A}^{-1}||, \tag{S18}$$

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 (S10), 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 S5), if, averaged over the distribution of perturbation directions, perturbation intensities are evenly distributed across species, and perturbation directions are uniformly distributed across all possible directions, 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,

$$\mathcal{V}^{\text{mean}} = \text{Tr}\,\mathcal{L}(A, \tfrac{1}{S}\mathbb{1}). \tag{S19}$$

S4 Perturbation types and variability

The perturbation type affects how the perturbation intensity is distributed across species. Therefore, it also affects our measure of variability, as defined in Appendix S2. Here we describe how the variability definition has to be modified.

We defined variability measure (S15) 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

$$\xi_i^{\text{tot}}(t) = N_i^{\frac{\alpha}{2}} \, \xi_i^{\text{intr}}(t), \tag{S20}$$

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. (S20) can be written in vector notation as

$$\boldsymbol{\xi}^{\text{tot}}(t) = D^{\frac{\alpha}{2}} \boldsymbol{\xi}^{\text{intr}}(t), \tag{S21}$$

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 $\boldsymbol{u}_k$, then, by eq. (S21), those of the total perturbation are $D^{\frac{\alpha}{2}} \boldsymbol{u}_k$. Then, to quantify the perturbation intensity, we use the covariance matrix of the pulses in the intrinsic perturbation. The derivation leading to eq. (S12) 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. (S14), so that we get

$$\sigma_{\text{out}}^2 = \frac{1}{S} \operatorname{Tr} \mathcal{L}\big(A, f D^{\frac{\alpha}{2}} C_u D^{\frac{\alpha}{2}}\big). \tag{S22}$$

The variability measure for a type-α perturbation becomes

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

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

$$\mathcal{V}_\alpha(E) = \operatorname{Tr} \mathcal{L}\big(A, D^{\frac{\alpha}{2}} E D^{\frac{\alpha}{2}}\big). \tag{S23}$$

Applying the same arguments as in Appendix S3, we find that worst-case variability,

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

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

$$\mathcal{V}_\alpha^{\text{worst}} = ||\widehat{A}^{-1} \circ \mathcal{D}_\alpha||, \tag{S24}$$

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

$$\mathcal{V}_\alpha^{\text{mean}} = \operatorname{Tr} \mathcal{L}\big(A, \tfrac{1}{S} D^\alpha\big), \tag{S25}$$

is attained by the uniform, uncorrelated perturbation.

S5   Perturbation directions in two dimensions

Variability spectra are built on the notion of perturbation directions. They are characterized by a covariance matrix E with $\mathrm{Tr}\,E = 1$. 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

$$E = \begin{pmatrix} 1-x & y \\ y & x \end{pmatrix}. \tag{S26}$$

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 (S26) has always $\mathrm{Tr}\,E = 1$.

It follows from eq. (S26) 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.

S6 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

$$\frac{dN_i(t)}{dt} = \frac{r_i N_i(t)}{K_i}\left(K_i - N_i - \sum_{\substack{j=1 \\ j \neq i}}^{S_{\text{pool}}} B_{ij} N_j(t)\right), \tag{S27}$$

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.

S7 Genericity in strongly interacting communities

We give some elements as to why the behaviour 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 $\mathcal{V}_\alpha^{\mathrm{spec}\ i}$ 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 $\mathcal{V}_\alpha^{\mathrm{spec}\ i}$ for different perturbation types α are directly linked. From definition (S23) we get that

$$\mathcal{V}_\alpha^{\mathrm{spec}\ i} = N_i^\alpha\ \mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i}. \tag{S28}$$

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

Next, consider again the Lotka-Volterra dynamics (S27) 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

$$\frac{dx_i}{dt} = \frac{r_i N_i}{K_i}\left(-x_i - \sum_{j \neq i} B_{ij} x_j\right) = \frac{1}{\tau_i}\left(-x_i - \sum_{j \neq i} B_{ij} x_j\right), \tag{S29}$$

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 $\mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i}$: 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 $\mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i}$ in Fig. S1 (inset panels). For the six communities of Fig. 5, we fit the power-law relationship

$$\mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i} \propto \tau_i^\nu, \tag{S30}$$

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. S1 (main panels) shows this relationship for the six communities of Fig. 5. Fitting the power law

$$\tau_i \propto N_i^{\gamma}, \tag{S31}$$

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. S1, 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. S1, 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

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

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

if r_i and K_i are independent, and if they satisfy a trade-off (Fig. S1, right-hand panels).

Finally, putting together eqs. (S28, S30, S31), we get

$$\mathcal{V}_\alpha^{\text{spec } i} \propto N_i^\alpha \, \tau_i^\nu \propto N_i^{\alpha+\gamma\nu} \approx N_i^{\alpha+\gamma}, \tag{S32}$$

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

$$\mathcal{V}_\alpha^{\text{spec } i} \propto N_i^{\alpha-1}. \tag{S33}$$

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.
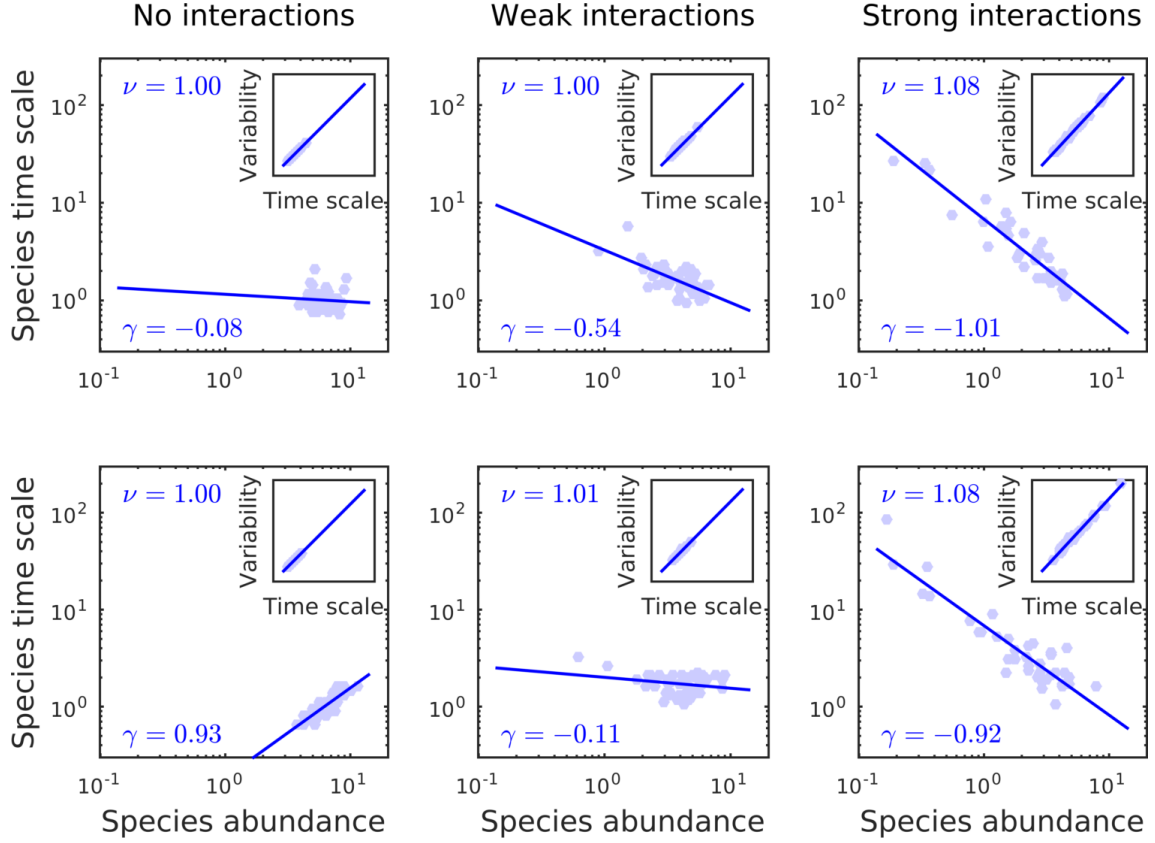
Figure S1: Clarifying the relationship between abundance of perturbed species and community variability. In Appendix S7 we introduce the auxiliary variable τ_i, the characteristic time scale of species i, to explain the relationship between variability $\mathcal{V}^{\text{spec } i}_{\alpha=0}$ and abundance 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 $\mathcal{V}^{\text{spec } i}_{\alpha=0}$ 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 $\mathcal{V}^{\text{spec } i}_{\alpha=0}$ vs τ_i) are reported in the panels.

S8 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 $\mathcal{V}_\alpha^{\mathrm{spec}\ i}$ the community variability induced by a type-α perturbation fully focused on species i. We start from the power-relationship (S33), linking this variability and the equilibrium abundance of species i. As argued in Appendix S7, 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

$$\mathcal{V}_{\alpha=0}^{\mathrm{worst}} \approx \max_i \mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i} \propto \frac{1}{\min_i N_i}. \tag{S34}$$

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

$$\mathcal{V}_{\alpha=0}^{\mathrm{mean}} = \frac{1}{S} \sum_i \mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i} \propto \frac{1}{S} \sum_i \frac{1}{N_i} = \langle N \rangle_{\mathrm{harm}}^{-1}, \tag{S35}$$

where $\langle N \rangle_{\mathrm{harm}}$ 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

$$\mathcal{V}_{\alpha=2}^{\mathrm{worst}} \approx \max_i \mathcal{V}_{\alpha=0}^{\mathrm{spec}\ i} \propto \max_i N_i, \tag{S36}$$

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

we get

$$\mathcal{V}_{\alpha=2}^{\text{mean}} \propto \frac{1}{S} \sum_i N_i = \langle N \rangle_{\text{arith}}, \tag{S37}$$

the arithmetic mean of species abundances. Mean abundance typically decreases with diversity, 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. S2.
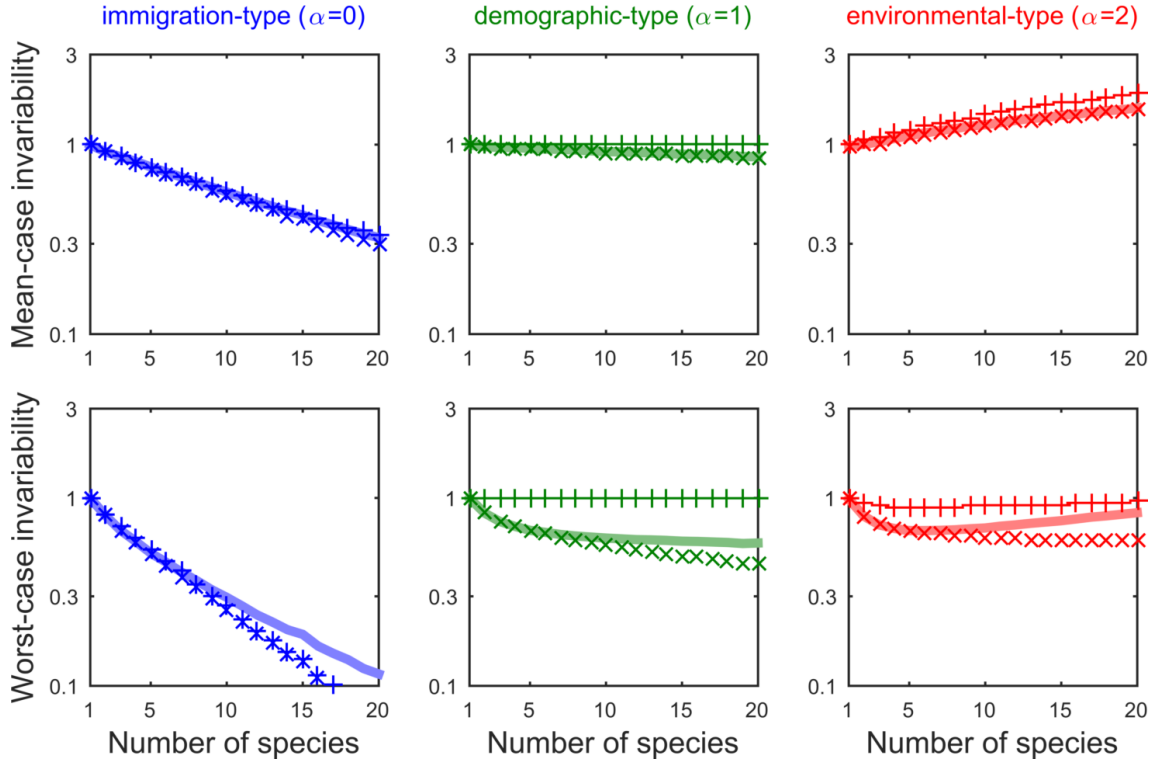
Figure S2: Invariability and species abundance. Top row: mean-case, bottom row: worst-case. ×-marks: analytical formula; +-marks: approximation in terms of abundance (see Appendix S8); thick line: simulation results. For immigration-type perturbations (first column, in blue), mean-case invariability scales as the harmonic mean abundance (see eq. (S35)), 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. (S37)) 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.