Effect of delay on the emergent stability patterns in generalized Lotka–Volterra ecological dynamics

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Understanding the conditions of feasibility and stability in ecological systems is a major challenge in theoretical ecology. The seminal work of May in 1972 and recent developments based on the theory of random matrices have shown the existence of emergent universal patterns of both stability and feasibility in ecological dynamics. However, only a few studies have investigated the role of delay coupled with population dynamics in the emergence of feasible and stable states. In this work, we study the effects of delay on generalized Lotka–Volterra population dynamics of several interacting species in closed ecological environments. First, we investigate the relation between feasibility and stability of the modelled ecological community in the absence of delay and find a simple analytical relation when intra-species interactions are dominant. We then show how, by increasing the time delay, there is a transition in the stability phases of the population dynamics: from an equilibrium state to a stable non-point attractor phase. We calculate analytically the critical delay of that transition and show that it is in excellent agreement with numerical simulations. Finally, following a similar approach to characterizing stability in empirical studies, we investigate the coefficient of variation, which

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quantifies the magnitude of population fluctuations. We show that in the oscillatory regime induced by the delay, the variability at community level decreases for increasing diversity.

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1. Introduction

A fascinating aspect of biological and ecological systems is the emergence of ubiquitous patterns that do not depend on the specific details of the system [1–7]. In this context, one of the main problems of theoretical ecology is the search for key mechanisms leading to the emergence and maintenance of biodiversity. The conditions for many species to coexist in spite of changing environment or perturbations are tightly connected to the problem of understanding when and how ecological systems are feasible (i.e. all solutions are positive at large times) and asymptotically stable (i.e. the real parts of all the eigenvalues of the Jacobian are negative).

The stability of ecosystems is mainly determined by some driving features, including diversity (number of species), the type of ecological interactions (antagonistic, competitive or mutualistic) among species, their strength and network structure, and sensitivity to environmental perturbation. Diversity is probably one of the easiest components that can be measured empirically [8,9] and, along with the density of the species interactions in the community (known as connectance), it has been considered a standard indicator of ecosystem complexity.

Before the 1970s, ecologists such as Elton [10], Odum [11], MacArthur [12] and many others believed that diversity enhances the stability of ecosystems. However, later theoretical studies suggested exactly the opposite, and more works often confirmed a disagreement between empirical and theoretical studies on the relationship between diversity and stability [13]. This is known as the stability–complexity debate and it has been initiated by the seminal work of May in 1972 [1]. In that work, May investigated the linear stability of a null ecological ecosystem with random interactions, and found an analytical result based on random matrix theory, indicating that the more complex the ecosystem is, the less stable it is. Many other works, including recent developments on generalizations of May’s work [14–16], confirmed the original result of May. Since then, the complexity-stability paradox has been tackled through two main approaches: some works argued that the stationary condition of ecological systems cannot be described by equilibrium points [9,17], hence suggesting a change of perspective on stability. This led to replacing asymptotic stability measures with alternative variables of interest (e.g. the coefficient of variation of the ecosystem population abundance). Several other studies, instead, focused on investigating the role of ecological function [18] and structure of food webs [19,20]. A few studies analysed the role of nonlinearity of the ecological dynamics on ecosystem stability [21,22] or on the possible effect of delay [23]. To our knowledge, the impacts of nonlinearity and delay on the stability of ecological systems remain elusive.

To tackle this problem, first we consider a classic interacting ecological model called the generalized Lotka–Volterra (GLV) system. The term ‘generalized’ refers to a model that contains an arbitrary mixture of ecological interactions, such as prey–predator (PP), mutualistic (MU), competitive (CO) or other types of interactions. Following previous work, we model the interaction network through a random matrix (RM) approach and assume no-pattern structure in the ecosystem, as in May’s seminal work.

We will then add a temporal delay into the dynamics of species’ populations. The resulting delayed GLV equations with a small number of species (low diversity) have analytically been studied mostly for the case of prey–predator systems [23–27]. These studies have investigated various implementations of the delay in the temporal dynamics of the prey–predator. Almost all variants indicate the emergence of a Hopf bifurcation from an equilibrium state to periodic solutions. Also, similar works have investigated other characteristics of the delayed
prey–predator systems such as boundedness of solutions, persistence, local and global stability of equilibria, and the existence of oscillatory solutions [28–34].

Delayed interactions are intrinsic to a variety of systems and are realistic and ubiquitous features which ought to be incorporated in many population-dynamics models. Consider for example a closed ecological environment like a small lake which contains phytoplankton (P), zooplankton (Z), fish (F) and some inorganic nutrients (N) as a limiting resource [23]. After these organisms (P,Z,F) die, the decomposers recycle the dead organic carcass to inorganic nutrients (N) after a certain delay time \( \tau \). Therefore, the increase of \( N(t) \) does not merely depend on the population \( P(t) \) at time \( t \), but also on the population of individuals (P,Z,F) that died in the past, i.e. \( P(t-\tau), Z(t-\tau) \) and \( F(t-\tau) \). In addition, there have been developed a lot of mechanisms that may induce delay interactions in the ecosystems such as: maturation period [35] (see also fig. 3 of [36]), a gestation period [37], feeding times and hunger coefficients in predator-prey interactions [38], replenishment or regeneration time for resources (e.g. of vegetation for grazing herbivores [24,39]). One can easily imagine other causes of delays in population dynamics on various time scales: those caused by food storage of predators or gatherers, reaction times, threshold levels, etc. [40]. Finally, the presence of time delay may also depend on the spatial scale of observation: mean-field equations (i.e. without explicit space) of spatially extended systems may include distributed time delays [7], depending on the spatial scale that is implicit.

The main objective of this work is to characterize the emergence of instability in delayed GLV ecosystems and in connection with the complexity-stability debate. We first start by turning off the delay and characterize analytically the stability in non-delayed GLV. In this case, we have found an analytical connection between feasibility, stability and diversity in the coexistence state, where the system is feasible and stable. When we turn on the delay, we find that it has a detrimental effect on the stability of the ecological dynamics. To be more precise, by gradually increasing the delay, we first observe a decrease in stability (or resilience) of the system (measured by the absolute value of the leading eigenvalue of the community matrix). At a certain critical delay, the system experiences a Hopf bifurcation from an equilibrium state to an oscillatory one (with non-point attractors, including regular and irregular cyclic behaviours). We investigate such transition as a function of different delays and ecosystems complexity. We find that the critical delay of the bifurcation decreases by increasing the diversity, consistently with May’s results. By increasing the delay, the oscillatory regime persists until we observe numerical instabilities in the trajectories of the populations. Finally, following [9,17], we show that in the oscillatory regime induced by the delay, we can introduce a stability index defined as the inverse of coefficient of variability (CV) of the total population in the community. We find that in this case the stability index increases for increasing ecosystem diversity [41]. This result is in agreement with similar conclusions, albeit obtained with different mechanisms, which have been obtained in theoretical [9,42] and experimental studies [43–54].

The paper is organized as follows. First, we present the theoretical framework GLV in the absence and the presence of the delay. Next, we investigate the feasibility and stability of the GLV ecosystem in the absence of delay. Afterward, we start to study the GLV in the presence of the delay. In the following, we give some hints about the empirical perspective of stability in delayed GLV. The final section summarizes our main results.

2. Theoretical framework

We consider a pool of \( S \) interacting species with abundances \( x = \{x_1, x_2, \ldots, x_S\} \). Each species is characterized by an intrinsic growth rate, \( r_i \), and by the interactions with other species that we here consider to affect its abundance after a time delay \( \tau \). Therefore, the equations governing the dynamics of \( x_i \) read as

\[
\dot{x}_i(t) = x_i(t)\left(r_i + \sum_j b_{ij} x_j(t-\tau)\right),
\]
which are known as delayed GLV equations. The matrix elements $b_{ij}$ measure the strength of the impact of species $j$ on species $i$, which occurs after a (discrete) time delay $\tau$, while $r_i$ are the intrinsic growth rates.

Real ecosystems with a large number of species include a mixture of all types of ecological interactions, such as predator-prey, competitive and mutualistic, and with a variable interaction strength. Typically, such interactions are very difficult to infer from empirical data, and therefore, following the same spirit of the seminal work by May, we draw at random both the intrinsic growth rate $r_i$—from a uniform distribution—and the non-diagonal components of the matrix $B$—from a normal distribution. Furthermore, the species are connected with probability $C \in [0, 1]$, where $C$ is the so-called connectance. The mean and standard deviation of the intrinsic growth rates are denoted by $\mu_r$ and $\sigma_r$, while those for the strength of the interactions are denoted by $\mu_B$ and $\sigma_B$. In this model, the intra-species competition, represented by the diagonal elements of the interaction matrix, are constant, i.e. $b_{ii} = -dB$. In this work, we are interested in understanding the effect of the delay on the feasible (i.e. non-negative) and stable equilibria of the ecosystem as a function of the complexity $(S \cdot C)$, all other ecological parameters (e.g. growth rates, interaction strengths) being fixed.

Characterizing the stability and feasibility of a GLV system (equation (2.1)) or similar ecological systems even in the absence of delay (i.e. $\tau = 0$) is a non-trivial task. When considering asymptotically equilibrium regimes, several types of stability have been suggested [13]. Moreover, there has been a lot of effort in establishing some sufficient conditions which grant stability of community dynamics without delay [55–61]. These sufficient conditions are mostly either established by linear stability analysis (such as D-Stability), or proper Lyapunov functions (or even stronger conditions) [61].

When turning on the delay (i.e. $\tau > 0$), we focus on the local systems stability. Let $y$ be a small perturbation away from equilibrium state $x^\star$, then the linearized equation for $y(t) = x(t) - x^\star$ reads

$$\dot{y}_i = \sum_j \tilde{B}_{ij}y_j(t - \tau), \quad (2.2)$$

where $\tilde{B}$ is the community matrix of the system due to the delayed interactions. Plugging the ansatz solution $u_i(t) = ve^{\lambda_i t}$ for the eigenmodes into equation (2.2), where $\lambda_i$ are the eigenvalues of the system and $v$ is a constant vector in $\mathbb{R}^S$, the $i$-th eigenvalue of the system satisfies the equation

$$\lambda_i = \tilde{b}_i e^{-\tau \lambda_i}, \quad (2.3)$$

where $\tilde{b}_i$ are the eigenvalues of $\tilde{B}$. This relation can be equivalently expressed by means of the Lambert function [62] $W(\cdot)$ as

$$\lambda_i = \frac{W(\tilde{b}_i \tau)}{\tau}. \quad (2.4)$$

Of course, when $\tau$ goes to 0, $\lambda_i \to \tilde{b}_i$, because $W(x) \simeq x$ for small $x$. Finally, note that in general the eigenvalues are complex numbers, hence we will write $\lambda_i = \xi_j + i\nu_j$ and $\tilde{b}_i = \alpha_j + i\beta_j$.

3. Results

(a) The feasibility and stability of the GLV ecosystem in the absence of delay

As a starting point for the study of nonlinear effects on large systems dynamics, let us begin by presenting some results on the feasibility and stability of the classical GLV model without delay [63]. In particular, we present a criterion to quantify the probability for the steady-state vector $x^\star$ to be feasible, i.e. to have all positive components. Actually, a correlation between feasibility and stability does exist, at least when the intra-species interactions are dominant with respect to the inter-species ones.
Let us consider equation (2.1) with $\tau = 0$, that is,
\[ \dot{x}_i(t) = x_i(t)g_i[x(t)] = f_i[x(t)], \]  
(3.1)

where
\[ g_j[x(t)] = r_i + \sum_{j=1}^{S} b_{ij} x_j(t). \]  
(3.2)

This system admits up to $2^S$ different equilibria, since the equilibrium condition $f[x^*] = 0$ is satisfied by setting either $x_i^*$ or $g_i[x^*]$ to zero for each species. Thus, in principle one should study the feasibility and the stability of every equilibrium point, which becomes hard as the number of species grows exponentially. As we are interested in ecological models for the evolution of species’ abundances or densities, we focus on the non-zero equilibrium given by the condition $g[x^*] = 0$, that is, on $x^* = -B^{-1}r$. It is worth noticing that, on the basis of simple combinatorial considerations, this equilibrium, i.e. the coexistence of all the $S$ species, is much less likely than the coexistence of a smaller number of species [64]. In addition, the study of such equilibrium is meaningful only if it is feasible. Indeed, when some components of $x^*$ are negative, the system will never reach such a state: starting with a positive initial condition $x(0)$, the abundance of each population $x_i$ can either increase or decrease, but it will never become negative, owing to the $x_i(t)$ factor in equation (3.1). Furthermore, we cannot claim anything about which other equilibrium the system will eventually reach, nor the final number of surviving species. In other words, if we compute $x^* = -B^{-1}r$ and some components are negative, this implies neither that those represent species which will become extinct, nor that the number of surviving species corresponds to the number of positive components of $x^*$, as explained through a simple example in appendix B.

Hence, it is important to determine what conditions guarantee the feasibility of $x^*$ and therefore we are allowed to interpret them as actual equilibrium populations. Although recent works have investigated some conditions necessary for the feasible coexistence [65], a general condition is still lacking. Herein, we compute the feasibility probability when $B$ is a diagonally dominant matrix, namely, when $dB \gg \sigma_B$. Under this hypothesis, if we define $M$ as the off-diagonal part of $B$, i.e., $B = dB I + M$, then we can expand the inverse of the interaction matrix as
\[ B^{-1} = -\frac{1}{dB} \left( I + \frac{M}{dB} \right) + \epsilon, \]  
(3.3)

where $\epsilon$ is the truncation error matrix of the expansion, whose norm scales as $\|\epsilon\| \sim \frac{\sqrt{3CS^2\sigma_B^2}}{dB|dB - \sigma_B5\sqrt{C}|}$ (see appendix B). Hence, when $\|\epsilon\| \ll 1$, at the first order the steady states read
\[ x_i^* = \frac{r_i}{dB} + \sum_{j=1}^{S} \frac{M_{ij}r_j}{dB^2} + \text{higher order terms}. \]  
(3.4)

Since $r$ is a random variable and $M$ is a random matrix, $x^*$ is a random vector and it is therefore possible to compute approximately the feasibility probability as a function of the system parameters. For instance, if the growth rates are constant and positive, $r_i = r > 0$, and $M$ is a zero-diagonal, normal random matrix with zero mean, standard deviation $\sigma = \sigma_B$ and connectance $C$, then in the large size limit after some calculations (see appendix B) we have
\[ P_{\text{feas}}(dB, \sigma_B, S, c) = \left\{ \frac{1}{2} \text{erfc} \left[ -\frac{dB}{\sqrt{2C(S-1)\sigma_B}} \right] \right\}^S, \]  
(3.5)

where $\text{erfc}(\cdot)$ is the complementary error function [66]. Remarkably, the feasibility probability decreases exponentially with the system size (at leading order in $S$, $P_{\text{feas}} \simeq 2^{-S}$, as shown in [64]).
The second property that characterizes the equilibria is their (local) stability. This property can be studied by means of the spectrum of the Jacobian evaluated at a given fixed point $x^*$, that is,

$$J_{ij}(x^*) \equiv \left. \frac{\partial f_j}{\partial x_j} \right|_{x^*} = \delta_{ij} g_i(x^*) + x_i^* \left. \frac{\partial g_i}{\partial x_j} \right|_{x^*} = \delta_{ij} g_i(x^*) + x_i^* b_{ij}. \quad (3.6)$$

It is worth mentioning that the Jacobian relative to the trivial equilibrium $x^* = 0$ is $J_{ij}(0) = \delta_{ij} r_i$, and thus its stability depends only on the (sign) of the growth rates. Instead, if we focus on the non-zero equilibrium $x^* = -B^{-1}r$ and we assume that it is feasible, the Jacobian at $x^*$ simply reads $J_{ij} = x_i^* b_{ij}$. Although a general form for determining the eigenspectrum of $J$ is not known, it is possible to exploit perturbative expansion techniques for estimating the eigenvalues of the interaction matrix when $B$ is diagonally-dominant, i.e. when $d_B \gg \sigma_B$ (see appendix B). In this case, a good approximation for the eigenvalues $\lambda_i$ reads

$$\lambda_i = -d_B x_i^* \left[ 1 - \frac{1}{d_B} \sum_{j \neq i} A_{ij} A_{ji} \frac{x_j^*}{x_j^* - x_i^*} \right] + \text{higher order terms.} \quad (3.7)$$

Thus, when $d_B \gg \sigma_B$ there is a simple relation at leading order between the eigenvalues and the steady states, and in this case stability and feasibility are tightly linked, as depicted in figure 1. Of course, this is not true for general matrices that are not diagonally dominant. Finally, note that in the subsequent sections we stick to this condition.

**b) Delay as a bifurcation parameter: Hopf bifurcation from the asymptotically stable regime to the oscillatory regime**

In this section, we investigate the non-trivial solutions of the delayed GLV model with a large number of species. To this purpose, we consider $\tau \neq 0$ in order to study the pure effect of the delayed interaction. First, we calibrate the non-delayed system on the coexistence-of-species state, where the solution of the system is feasible and stable. This state is easily obtained by considering $B \in \text{DiS}$, i.e. by requiring the existence of a positive definite diagonal matrix $D$ such that $DB + B^T D$ is negative definite (see appendix A), and $r \in \mathbb{R}^+_0$ [64] although also equation (3.7) could be exploited. Being in the coexistence region, we introduce the delay parameter and we study the solutions of the system in the extended parameter space $(r, B, \tau)$. 

**Figure 1.** (a) Comparison between the theoretical prediction (solid line, equation (3.5)) and numerical simulations (red squares) for the feasibility probability as a function of the system size $S$. Each red square represents the fraction of feasible $x^*$ obtained over 1000 realizations. We have considered $d_B = 1$, $C = 0.1$ and $\sigma_B = 1$. (b) Numerical analysis of the relationship between the stability (given by the maximum real part eigenvalue $\max(\text{Re}[\lambda])$ of the matrix $B$ in equation (3.2)) and the population of the rarest species (min$(x^*)$, where $x^* = -B^{-1}r$) for different values of $\sigma_B$. Each square represents an average over 100 realizations of the matrix $B$. The linear correlation (black line) is the first order of equation (3.7). Such correlation holds only when $\sigma_B < d_B$ (upper panels). In all panels, $d_B = 10$, $C = 0.1$, $r = 1$ and $S$ spans the interval from 10 to 200. (Online version in colour.)
By definition, a Hopf bifurcation occurs when two complex conjugate eigenvalues of the community matrix, with non-zero imaginary part, simultaneously cross the imaginary axis into the right half-plane [67]. Now, we investigate this condition in the community (Jacobian) matrix of the linearized delayed GLV, and compare the results with the corresponding nonlinear delayed GLV.

The community matrix of equation (2.1) with \( \tau = 0 \) for a feasible equilibrium state is obtained from \( J = \text{diag}(-B^{-1}r)B \). The eigenvalues of the community matrix (in the absence of delay) are plotted in the complex plane in (a) of figures 2–4. Being in the coexistence region \((r > 0, B \in \text{DiS})\), the real parts of the eigenvalues are in the left half-plane (i.e. Re \( \lambda < 0 \)). As expected, the trajectories of the system, obtained from the numerical integration of equations (2.1), are asymptotically stable as shown by the dashed lines in (c) of figure 2.

Now, we turn on the delay by gradually increasing \( \tau \). The eigenvalues of the community matrix in the presence of delay are obtained from equation (2.4), and are plotted in (b) of figures 2–4. Before a certain \( \tau_c \), the real part of the leading eigenvalue is still in the left half-plane (Re \( \lambda < 0 \)), and the trajectories are still asymptotically stable, as shown by the solid lines in figure 2c. In this regime, the resilience of the system (as measured by the absolute value of the leading eigenvalue of the community matrix) decreases by increasing the delay. As \( \tau \) passes through the \( \tau_c \), the two conjugate leading eigenvalues cross the vertical line given by Re \( \lambda = 0 \), thus confirming a Hopf bifurcation. This is evident by comparing (b) of figures 2 and 3. This is confirmed by the trajectories of the dynamics which present persistent periodic oscillations as shown by the solid lines in figure 3c.
Figure 3. Characterization of an oscillatory phase for equation (2.1). (a) Eigenspectrum of the community matrix $J = \text{diag}(-B^{-1}r)B$ for the non-delayed GLV system. (b) Eigenspectrum of the delayed GLV system for $\tau = 18$ (see equation (2.4)). While in (a), the real part of the leading eigenvalue is negative, it is instead positive in (b). Thus, as depicted by the results of the numerical integration of equation (2.1) in (c), the system without delay is asymptotically stable (dashed line), whereas it displays an oscillatory motion in the presence of delay (solid line). Note, in all panels, $B$ is a random matrix. (Online version in colour.)

Remarkably, $\tau_c$ can be calculated analytically by means of linear stability analysis. Indeed, if we linearize the system around the feasible equilibrium $x^* = -B^{-1}r$, the system eigenvalues $\lambda_i$ satisfy equation (2.3). From this equation, it is possible to calculate the critical delay directly from the eigenspectrum of the community matrix (see appendix C) as

$$\tau_c = \min_{b \in \text{eig}(\tilde{B})} \left| \frac{1}{|\tilde{b}|} \arctan \left( \frac{\text{Re}(\tilde{b})}{\text{Im}(\tilde{b})} \right) \right|,$$

and the corresponding critical oscillation frequency as $\nu_c = |\arg \min_{b \in \text{eig}(\tilde{B})} (1/|\tilde{b}|) \arctan |(\text{Re}(\tilde{b})/\text{Im}(\tilde{b}))||$.

By increasing $\tau$ above $\tau_c$, the amplitude of the trajectories increases, as can be seen by comparing the blue trajectories in figures 2c–4c. When $\tau$ is much larger than $\tau_c$ the amplitude of the oscillations becomes so large that it gives rise to numerical instabilities, namely, the trajectories of the populations numerically diverge. We were not able to fix such numerical divergences either by improving the accuracy of the Euler method or by employing more accurate methods like linear multistep methods (https://pypi.org/project/ddeint/)(figure 4c). This occurred at some threshold $\tau_C > \tau_c$.

We plot in figure 5, the critical time delay for the bifurcation, $\tau_c$, and the critical time delay for the computational instabilities, $\tau_C$, as a function of diversity, $S$. The curves of $\tau_c$ and $\tau_C$ are monotonously decreasing. This identifies two regimes: all the trajectories associated with the region below the dotted line are asymptotically stable; the trajectories associated with the region
between the dotted and the solid lines indicate the region of the oscillatory regime (non-point attractors) which depends on $r$ and $B$. The dynamics above the solid line are computationally unstable.

In conclusion, by means of numerical simulations and analytical calculations, we have confirmed the existence of a Hopf bifurcation at $\tau_c$ for a delayed GLV with a large number of species. This bifurcation is also observed for the case of the stable but partially feasible equilibrium state (violation of the coexistence condition).

(c) A more empirical perspective of stability

Local stability is an instructive theoretical concept, but very difficult to measure in real ecological scenarios. First of all the underlying assumption is that the ecosystem in its unperturbed state is considered at the equilibrium. However, a real ecosystem is continuously changing, exchanging fluxes of energy with the environment and among species. In other words, a real ecological community is either at stationarity or an out of equilibrium system. For these reasons, many field ecologists do not use the mathematical definition of stability, rather they apply the concept of variability (e.g. the variance of population densities over time, or the coefficient of variation (CV) of the populations) as an indicator of the ecosystem stability [9,17], i.e. the less the variability the more stable the ecological community.

In this regard, some field experiments on plant biodiversity [43–47] have shown that the diversity within an ecosystem tends to be correlated positively with the community-level stability
(measured as the inverse of the CV in community biomass) while it is only weakly correlated with CV for year to year variation in biomass of individual species (e.g. see figs (6) and (9) in [45]). Also, some other studies on controlled microcosm experiments [48–54] have suggested that individual species population-level variation is relatively unaffected by diversity, whereas community-level variations tend to decrease with increased diversity.

We thus want to investigate whether this relation holds also in our GLV dynamics. In this respect, we highlight that the delay may elicit oscillatory dynamics, as such it may represent, after a transient, a source of variability at both species and community level. In our context, we consider the variations of the populations at the single species and community level, and we define, respectively

$$\text{CV}_s = \sum_{i=1}^{S} \sqrt{\frac{\left(\sum_{t=T}^{T_f}(x_i(t) - \bar{x}_i)^2\right)}{S\bar{x}_i}}$$

and

$$\text{CV}_c = \sqrt{\frac{\left(\sum_{t=T}^{T_f}(N(t) - \bar{N})^2\right)}{N}}$$

where $T$ is the time step when stationarity is reached, $T_f$ is the length of the simulated time series (here $T = 0.1T_f$),

$$\bar{x}_i = \frac{\sum_{t=T}^{T_f} x_i(t)}{T_f - T}$$

$$N(t) = \sum_{i} x_i(t)$$

and

$$\bar{N} = \frac{\sum_{t=T}^{T_f} N(t)}{T_f - T}$$

Figure 5. Stability phase diagram for the system defined by equation (2.1). In this figure, Phase I corresponds to the asymptotically stable phase, Phase II to the oscillatory regime, whereas the computational instabilities are detected above the solid line. The phase separation line $\tau_c$ between the stable and the oscillatory regime is obtained both by means of simulations (black stars, see equation (2.1)) and analytically (dotted line, see equation (3.8)). The solid line represents instead $\tau_C$, which is defined as the maximum $\tau$ below which the system does not experience any computational instability (up to the accuracy of the Euler and linear multistep methods). In the calculations, we have considered the intrinsic growth rates $r_i$ to be uniformly distributed in $\mathcal{U}(0.05,0.1)$ and the interaction $B$ to be a random matrix, with constant diagonal $d_B = 10$ and off-diagonal elements normally distributed with zero mean and $\sigma_B = 0.1$. The initial conditions $x_i(0)$ are drawn from an uniform distribution $\mathcal{U}(0.01,0.05)$. (Online version in colour.)
The coefficient of variation is a dimensionless parameter which is appropriate for comparing the variability at different scales of population sizes, ranging from trajectories of single species’ population to total population. We note that in the equilibrium regime ($\tau < \tau_c$) $\text{CV}_s = \text{CV}_c = 0$. In the oscillatory regime of delayed GLV, instead, we can plot the $\text{CV}_s$ and $\text{CV}_c$ as a function of the diversity, respectively. As evident from figure 6a,b, $\text{CV}_c$ decreases by increasing the diversity, while the $\text{CV}_s$ increases by increasing the diversity. In other words, in this regime, we find the emergence of a positive diversity-stability relationship as measured by the community level variability, in agreement with experimental observations [41]. On average, the CV at community level decreases with increasing diversity, likely because the average of the total population increases faster than its fluctuations. This effect, however, is not present at the single species, where population variability increases on average as a function of the number of species. Similar empirical results have been shown in [45]. As a possible alternative explanation, the negative covariance effect among the trajectories of populations [41] has been suggested as a mechanism behind the decreasing behaviour of the variability as a function of diversity at the community level (figure 6b).

Further elements of realism can be introduced in the model by using discrete delays which depend on the species identity. Thus we have studied the oscillatory regime of the delayed GLV (solid curves in figure 6) by considering a species-dependent delay as follows:

$$\dot{x}_i(t) = x_i(t)(r_i + \sum_j b_{ij}x_j(t - \tau_{ij}^q)),$$

(3.11)

where $\tau_{ij}^q$ have been drawn at random from a uniform distribution $\mathcal{U}[\tau_{\min}^q, \tau_{\max}^q]$, with mean value $<\tau^q> = (\tau_{\max}^q - \tau_{\min}^q)/2$ and variance $\sigma_{\tau^q}^2 = (\tau_{\max}^q - \tau_{\min}^q)^2/12$. The randomness in $\tau_{ij}^q$ is quenched, hence it does not vary over time. For this new model, equation (3.11), we calculated $\text{CV}_s$ and $\text{CV}_c$ as a function of diversity in the oscillatory regime and plotted the curves in figure 6 (dashed lines). In order to compare the results of the original and perturbed models, we choose the $<\tau^q>$ in equation (3.11) equal to $\tau$ in equation (2.1). As a result, we have observed that the curves associated with the species-dependent delay model (dashed lines) appear below the curves.
associated with the original model (solid lines). This means that the random $\tau_{ij}^q$ decrease the variability at the population as well as the community level. The dashed curves are a bit more fluctuating than the solid curves, although they are calculated by averaging over the same number of realizations. This is likely due to the random variability of the coefficients $\tau_{ij}^q$, whose variance was set to $\sigma_{\tau_{ij}^q}^2 = 3$.

By means of numerical simulations, we found out that the instability brought about by the species-dependent delays does not eliminate or modify the feasibility of the system considered in the first place. In other words, the discrete delays keep the trajectories of the populations moving around the equilibrium points which the system admits in the absence of delay (figure 3c). The results of this more realistic model show the robustness of the simpler one we have studied in the previous case. Also, it shows that the coefficient of variations are in general reduced when introducing species-dependent delays.

4. Discussion and conclusion

In spite of the relevant theoretical efforts to better understand the relationship between stability and diversity, the celebrated complexity-stability paradox is far from being settled. However, more and more studies highlight many ecological mechanisms that may allow for the emergence of stable ecological communities, where several species coexist. In this work, we have investigated the role of the nonlinearity induced by the delay in how species interactions affect species growth rates. We have thus incorporated the delay in a GLV model’s ecosystem and considered a null ecological ecosystem with random quenched interactions.

First, we have found an analytical connection between the feasibility, stability and diversity of the non-delayed GLV. Then, by gradually increasing the delay, we have numerically observed the emergence of a new dynamical regime. Actually, beyond the asymptotically stable regime where the species reach equilibrium points, we have found an oscillatory regime for delays larger than a critical value. We have also calculated analytically the critical delay which is in very good agreement with numerical simulations. In summary, our results confirm that delay is detrimental for local GLV stability.

Finally, by employing the variability of oscillations in the population dynamics induced by the delay, we have investigated the variability of species’ populations and community population as an alternative measure of stability, more suitable for comparisons with experimental data. Such variation is well defined in non-equilibrium regimes and can be defined as the coefficient of variation of the ecosystem population dynamics. Consistently with experimental results, we find that the variability of the community-level decreases by increasing ecosystem diversity, namely the number of species. This suggests different ways to consider the role of the delay in ecological dynamics.

In this paper, we have neither considered the effects of the environment on ecosystems, nor the randomness due to the intrinsic nature of the birth and death process in individuals. When adding environmental stochasticity to the ecosystem dynamics, extinction might be reversed into coexistence. However, the converse is also true, and stochasticity may lead to extinction [68,69]. The variety of outcomes due to stochasticity mirrors the vast range of stability measures that have been suggested in the literature [70], whose applicability is often limited to ecological systems with point equilibrium dynamics without any delay effect. Here, we have instead focused on empirically driven stability measures which are not restricted to equilibrium dynamics, but can be more widely applied to more general dynamics which also includes delay effects.

More recently, there has been an increasing awareness that ecological stability and its relation to diversity is complex and multifaceted, and different stability measures cannot be considered independent. For instance, stability components may co-vary and non-monotonic relations between diversity and ecosystem stability have been documented [54]. So far the effects of delay on the inter-relations among asymptotic stability, resilience, resistance, robustness, persistence and variability [17,71,72] have not been studied. Although this is challenging, it is however
important to understand how past interactions reverberate onto the empirical and theoretical aspects of persistence and extinction. The interconnections which we have alluded to will constitute the core of future work.

Data accessibility. The GitHub link which include some part of the repository of the codes that we used for reproducing the numerical results: https://github.com/MeghdadSaeedian/Delayed_GLV.

Authors’ contributions. M.S.: investigation, writing—original draft; E.P.: investigation, writing—review and editing; A.M.: conceptualization, writing—review and editing; S.S.: conceptualization, writing—review and editing; S.A.: conceptualization, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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Appendix A

Here, we provide some sufficient conditions for stability of equation (2.1), i.e. for the classical GLV model without delay.

(a) Linear stability analysis

Let \( H = \{1, 2, \ldots, S\} \) be the set of the species present in the system. If we consider a partially feasible equilibrium \( x^* \), i.e. an equilibrium that could have a positive number of extincted species, we can denote \( P \) and \( Q \) as two subsets of \( H \) such that \( i \in P \) if \( x^*_i > 0 \) and \( i \in Q \) if \( x^*_i = 0 \). Naturally, when \( H = P \) the equilibrium is feasible. Let us also define \( x_i = u_i + x^*_i \), where \( u \) is a small perturbation from the equilibrium state \( x^* \). Then, the linearized form of equation (2.1) at \( \tau = 0 \) reads

\[
\dot{u} = Mu, \tag{A1}
\]

where the rearranged community (Jacobian) matrix yields

\[
M = \left( \begin{array}{cc}
\frac{\partial g_i}{\partial x_j} & \frac{\partial g_i}{\partial x_k} \\
0 & \delta_{hk}g_k
\end{array} \right)_{x^*}, \tag{A2}
\]

where \( i, j \in P \) and \( h, k \in Q \) and \( \delta_{hk} \) is the Kronecker delta function, which is 1 if \( h = k \), and 0 otherwise. The function of \( g_i \) is presented in equation (3.2). The subscript of the round bracket means that all the partial derivatives are computed in \( x^* \). Let us also call the upper left block of \( M \) as

\[
K = x^*_i \left( \frac{\partial g_i}{\partial x_j} \right)_{x^*}. \tag{A3}
\]

**Theorem A.1 ([57]).** The partially feasible equilibrium \( x^* \) of equation (2.1) is locally stable if all the eigenvalue of the \( K \) have negative real part and

\[
g_k(x^*) < 0, \quad \text{for all } k \in Q. \tag{A4}
\]

We denote here by \( LS \) the set of linear stable matrices. As apparent in figure 7, this condition is the superset of all the forthcoming sufficient conditions for the stability of equation (2.1). Note, this condition works for any general form of equation (3.1).
Figure 7. Schematic containment picture of stability conditions. The S stand for stability. The sufficient conditions, in order of inclusion, are Linear stability (LS), D-stability (DS), Total stability (TS) and Diagonal Lyapunov stability DiS. The necessary conditions are $P-$ matrix and $P^0$-matrix. The curves of sufficient (necessary) conditions are drawn by solid (dashed) lines. The outer (inner) dashed curves indicate a necessary condition for D-stability (total stability).

(b) D-stability: a guarantee for local stability

In the case of Lotka–Volterra model equation (2.1), if a feasible equilibrium state exists and $B$ is invertible, using equation (A 2), the community matrix reads

$$M = \text{diag}(x^*)B,$$

where

$$x^* = -B^{-1}r.$$  \hfill (A 6)

In this case, the stability of the community matrix $M$ is obtained from theorem A.1. Since $M$ is simply the multiplication of the interaction matrix $B$ times the positive diag($x^*$), which is in turn a function of (the inverse of) $B$ and the intrinsic growth rates $r$. This then raises the question about what conditions on $B$ grant the stability of $M$ for any positive diag($x^*$). This is the reason behind the D-stability condition.

**Definition A.2 ([73]).** A matrix $M \in \mathbb{R}^{S \times S}$ is said to be $D$-stable, if $DM$ is stable ($DM \in LS$), where $D$ is a diagonal matrix with positive diagonal elements $d_{ii} > 0$.

We denote here by DS the set of D-stable matrices. In the containment relation we can assert $DS \subset LS$. As noticed, characterizing the $D$-stability is not trivial. However, as a testable necessary condition for the definition of $D$-stability, we bring here theorem A.3 as

**Theorem A.3 ([61,74]).** Any $D$-stable matrix is a $-P^0$, or, in formal terms, $DS \subset -P^0$. Where

**Definition A.4 ([75]).** A matrix $M \in \mathbb{R}^{S \times S}$ is said to be $P^0$-matrix if all principal minors of $M$ are non-negative and if for each order $k = 1, \ldots, S$, at least one $k$ by $k$ principal minor is positive (By definition, the determinant of a principal submatrix is called the principal minor of $M$, where a principal submatrix of a square matrix $M$ is the matrix obtained by deleting any $k$ rows and the corresponding $k$ column).

**Definition A.5 ([58]).** A matrix $M \in \mathbb{R}^{S \times S}$ is said to be $P$-matrix if all principal minors of $M$ are positive.

To check the $D$-stability of the system of $S \leq 4$, there exist some testable conditions in [61,76].
(c) Total stability: a guarantee for species deletion stability

Disappearing (or deleting) the species that take place not because of the population dynamics can be considered as a relatively large perturbation on population dynamics [77]. If $M$ is interpreted as a community matrix, one can argue if there exist some conditions on the $M$ that do grant the stability of the community under the perturbation of species deletion. Here, after defining the concept of ‘species deletion stability’, we present a sufficient condition to grant this stability and then we present a necessary condition for this sufficient condition.

**Definition A.6 ([77]).** A system is said to be species deletion stable if, following the removal of a species from the system, all of the remaining species are retained at a new, locally stable equilibrium.

One sufficient condition to grant the ‘species deletion stability’ is the condition of ‘Total stability’

**Definition A.7 ([74]).** A matrix $M$ is said to be totally stable if every principal subset of $M$ (i.e. every sub-set whose determinant is a principal minor of $M$) is D-stable.

We denote here by $\text{TS}$ the set of total stable matrices. The definition A.7 implies that the total stability is a subset of $D$-stability, i.e. $\text{TS} \subset \text{DS} \subset \text{LS} \subset \text{S}$. One necessary condition to grant total stability is

**Theorem A.8 ([61]).** Any Total stable matrix is a $-P$, or, in formal terms, $\text{TS} \subset -P$.

If $M$ is interpreted as the interaction matrix, one very important consequence is that if $M \in -P$, for every $r \in \mathbb{R}^S$, there exist a unique non-negative equilibrium state for equation (2.1) [58,78]. However, the stability of that is not granted. In theorem A.10, the condition for stability of that will be presented.

(d) Lyapunov diagonal stability; a guarantee for global asymptotic stability

The existence of an unique domain (or basin) of attraction for an equilibrium state of equation (2.1) grants the global asymptotic stability of the trajectories of the populations. At this stage, we can look at the conditions on the interaction matrix $B$ that grant the global stability of the ecological community. To this purpose, we need to define the concept of Lyapunov diagonal stability. We denote here by $\text{DiS}$ the set of Lyapunov diagonal stable matrices.

**Definition A.9 ([79]).** When $M$ is an $n \times n$ real matrix, $M \in \text{DiS}$ implies that there exists an $n \times n$ positive definite diagonal matrix $D$ such that $DM + M^TD$ is negative definite.

**Theorem A.10 ([58]).** If $M \in \text{DiS}$, then the system defined by equation (2.1) has a non-negative and stable equilibrium point for every intrinsic growth rate $r \in \mathbb{R}^S$.

This important theorem is a direct consequence of Lyapunov functions [57,58] and linear complementary theory [78] that have been successfully applied to show the global stability of Lotka–Volterra systems.

There is a great deal of importance considering the existence of multiple domains of attractions for ecological systems [80]. Theorem A.10 gives a class of systems that do not have multiple domains of attractions. This class $\text{DiS}$ is defined only in terms of the interaction matrix $B$ and does not involve the intrinsic growth rate $r \in \mathbb{R}^S$.

Consequently, if the interaction matrix $B$ of a community being negative definite, every feasible equilibrium points are globally stable. Also, any principle matrix of a negative definite matrix is negative definite. Thus, any feasible point of a reduced system is globally stable. As a final statement here, the containment relation goes like $\text{DiS} \subset \text{TS} \subset \text{DS} \subset \text{LS} \subset \text{S}$. There are some other testable conditions that can be found in the beautiful and inspiring work of O. Logofet [61], such as Quasi-Dominant stability and Qualitative Stability [81].

To sum up this section, we plot the schematic containment picture of all aforementioned stability conditions in figure 7.
Appendix B

(a) Stability and feasibility for the generalized Lotka–Volterra without delay

As already stated in the main text, in some particular cases there exists a relation between feasibility and stability of the GLV model without delay. It is worth highlighting that quantifying the feasibility properties is a fundamental step in the study of such systems. Indeed, we remark that studying the non-trivial equilibrium $x^\ast = -B^{-1}r$ is meaningful only if it is feasible. On the other hand, when at least one component $x^\ast_i$ is negative, $x^\ast$ does not give any clue either to which species would become extinct, or to the number of surviving species. Let us clarify this concept by means of a simple but paradigmatic example with $S = 2$ species. For instance, let the system of ODEs be

$$
\begin{align*}
\dot{x}_1 &= x_1(1 - x_1 - 2x_2) \\
\dot{x}_2 &= x_2 \left(1 + \frac{3}{4}x_1 - x_2\right),
\end{align*}
$$

(B1)

whose equilibria are $(0, 0), (0, 1), (1, 0)$, and the unfeasible $x^\ast = \left(-\frac{4}{10}, \frac{7}{10}\right)$. Although one can naively think that the system would evolve towards $(0, 1)$ since $x^\ast_1 < 0$ and $x^\ast_2 > 0$, rather interestingly, $(1, 0)$ turns out to be the stable, attracting equilibrium. In the same way, it is not hard to construct a 3-species model where $x^\ast$ has two negative components, but the stable equilibrium can have two surviving species.

(b) Feasibility

Although a general characterization of the feasibility for the GLV model is difficult, it is relatively easy to quantify the feasibility probability when $B$ is a diagonal-dominant random matrix, i.e. when $dB \gg \sigma_B$. In this hypothesis, if we define $M$ as the off-diagonal part of $B$, i.e. as $B = -dB + M$, then we can expand the inverse of the interaction matrix as follows:

$$
B^{-1} = -\frac{1}{dB} \left( I + \frac{M}{dB} \right) + \epsilon,
$$

(B2)

where $\epsilon$ is the truncation error matrix. If we consider the Frobenius-inspired norm $\|\epsilon\| = \left[ \sum_{ij} E[\epsilon_{ij}^2]\right]^{1/2}$, we can numerically observe (figure 8) that it scales as

$$
\|\epsilon\| \sim \sqrt{3CS} \sigma_B^2 dB - \sigma_B S \sqrt{C}.
$$

(B3)

If $\|\epsilon\| \ll 1$, at the first order, the steady states reads

$$
x^\ast_i = \frac{r_i}{dB} + \sum_{j=1}^{S} \frac{M_{ij}r_j}{dB} + \text{higher order terms,}
$$

(B4)

while the feasibility condition naturally becomes

$$
r_i + \sum_{j=1}^{S} \frac{M_{ij}r_j}{dB} > 0 \quad \forall i = 1, \ldots, S.
$$

(B5)

We remark the importance of equation (B4): when $dB$ is large, if $B$ and $r$ are random variables as defined in the main text, the steady states populations are distributed around the mean value

$$
E[x^\ast_i] = \frac{E[r]}{dB},
$$

(B6)

with variance

$$
\text{Var}[x^\ast_i] = \frac{1}{dB} \left( \text{Var}[r] + \frac{C(S - 1)\sigma_B^2}{dB^2} (E[r]^2 + \text{Var}[r]) \right).
$$

(B7)
This result is general and does not depend on the particular choice of the distribution for $B$ and $r$. If we now additionally assume that the growth rates are all equal and in particular—since a rescaling of the modulus of $r$ does not affect the feasibility—that they are equal to 1, then the steady-state components are randomly distributed with mean and variance given by

$$\begin{align*}
E[x_i] &= \frac{1}{dB} \\
\text{Var}[x_i] &= \frac{C(S-1)\sigma^2}{d_B^4}.
\end{align*}$$

(B8)

This shows that the mean value of $x^*_i$ is always positive and depends only on $d_B$, the other parameters $S$, $C$ and $\sigma$ being involved only in the spreading around it. In particular, the larger the system size $S$ or the connectivity $C$ of the interactions, the more spread are the $x^*_i$, the more likely some components are negative. Indeed, as reported in the main text, a good estimator for the probability for the feasibility condition to hold is given by the quantity

$$\int_{-\infty}^{+\infty} N(x_i \mid E[x_i], \text{Var}[x_i]) \, dx_i = \frac{1}{2} \text{erfc} \left( -\frac{dB}{\sqrt{2C(S-1)\sigma}} \right).$$

(B9)

This can be seen also considering explicitly the feasibility condition, given by equation (B5), which in this case becomes

$$1 + \sum_{j=1}^{S} \frac{M_{ij}}{dB} > 0 \quad \forall \, i = 1, \ldots, S.$$  

(B10)

Defining the random variable $z_i$ as $z_i \equiv \sum_{j=1}^{S} M_{ij}$, we are interested in estimating its probability density function $p(z_i)$, so that the feasibility condition translates in computing the probability

$$\text{Prob}(z_i > -d_B) = \int_{-d_B}^{+\infty} p(z_i) \, dz_i.$$  

(B11)

This can be easily computed by mean of the law of total probability

$$p(z_i) = \sum_{N=0}^{S-1} p(z_i \mid N) \, p(N),$$

(B12)

where $p(N)$—the probability that the $i$-th row of $M$ has exactly $N$ non-zero distributed entries over the $S-1$ off-diagonal elements—is a binomial distribution, since the outcome in each entry of $M$
is a Bernoulli trial with probability $C$

$$p(N) = C^N (1 - C)^{S - 1 - N} \binom{S - 1}{N};$$  \hspace{1cm} (B 13)

while

$$p(z_i|N) = \begin{cases} \delta(z_i) & \text{if } N = 0 \\ \mathcal{N}(z_i | 0, N\sigma_B^2) & \text{if } N > 0, \end{cases}$$  \hspace{1cm} (B 14)

where the factor $N$ in the variance comes from the fact that $z_i$ is the sum of $N$ normally distributed terms with variance $\sigma^2$.

Therefore,

$$\text{Prob}(z_i > -d_B) = \int_{-d_B}^{\infty} p(N) p(z_i|N) \, dz_i$$

$$= (1 - C)^{S - 1} + \sum_{N=1}^{S-1} C^N (1 - C)^{S - 1 - N} \int_{-d_B}^{\infty} \mathcal{N}(z_i | 0, N\sigma_B^2) \, dz_i$$

$$= (1 - C)^{S - 1} + \sum_{N=1}^{S-1} C^N (1 - C)^{S - 1 - N} \left[ \int_{-d_B}^{\infty} \mathcal{N}(z_i | 0, N\sigma_B^2) \, dz_i \right]$$  \hspace{1cm} (B 15)

and since this condition should hold for each row $i$,

$$\text{Prob(feasibility}|S, d, c, \sigma_B) = [\text{Prob}(z_i > -d_B)]^S.$$  \hspace{1cm} (B 16)

The main advantage of this equation is its closed-form fashion. On the other hand, it becomes computationally hard to be computed for large $S$. Furthermore, the dependence of the feasibility probability on the model parameters is not immediately clear within this formulation. For this purpose, two approximations can be performed, thanks to the Central Limit Theorem.

The first approximation—which holds in the limit of large $S$—is simply to approximate the binomial distribution inside equation (B 15) with a normal one, with mean $\mu_N = C(S - 1)$ and variance $\sigma_N^2 = (1 - C)C(S - 1)$.

The second one, instead, is valid in the limit of large number of non-zero entries of $M$, i.e. in the limit of large $cS$. In this limit, we can approximate the probability density function $p(z_i)$ with a normal distribution with mean $E[z] = 0$ and variance $E[z^2] = \sigma_B^2 C(S - 1)$. Indeed,

$$E[z] = \int_{-\infty}^{\infty} p(z) \, dz = \sum_{N=0}^{S-1} p(N) \int_{-\infty}^{\infty} p(z|N) \, dz = 0$$  \hspace{1cm} (B 17)

and

$$E[z^2] = \int_{-\infty}^{\infty} p(z) z^2 \, dz = p(0) \int_{-\infty}^{\infty} \delta(z) z^2 \, dz + \sum_{N=1}^{S-1} p(N) \int_{-\infty}^{\infty} \mathcal{N}(z | 0, N\sigma_B^2) \, dz$$

$$= 0 + \sum_{N=1}^{S-1} p(N) N\sigma_B^2 = C(S - 1) \sigma_B^2.$$  \hspace{1cm} (B 18)

Thus, we recover exactly the quantity shown in equation (B 9), that is,

$$\text{Prob}(z_i > -d_B) = \int_{-d}^{\infty} \mathcal{N}(z_i | 0, C(S - 1)\sigma_B^2) \, dz_i = \frac{1}{2} \text{erfc} \left[ -\frac{d_B}{\sqrt{2C(S - 1)\sigma_B}} \right],$$  \hspace{1cm} (B 19)

and since this condition should hold for each row $i$, again the feasibility probability can be obtained by raising this result to the power of $S$. 

(c) Stability

As already stated in the main text, the local stability of an equilibrium can be studied by mean of the eigenspectrum of Jacobian evaluated around it. To this purpose, let us consider the rather general system of equation

$$\dot{x}_i(t) = x_i(t)g_i[x(t)] = f_i[x(t)],$$

(B 20)

where \( g_i \) is in general a nonlinear function of the abundances \( x_j(t) \). If we focus on a non-trivial equilibrium \( x^* \), i.e. on an equilibrium satisfying the condition \( g[x^*] = 0 \), then its Jacobian (also known as interaction matrix) reads

$$J_{ij} = x^*_i \frac{\partial g_i}{\partial x_j} \bigg|_{x^*}. \tag{B 21}$$

For instance, for the classical GLV model, where \( g[x] = r + Bx \), the community matrix thus simply reads \( J_{ij} = x^*_i b_{ij} \). If we hypothesize that this matrix has a diagonal, dominant part, and an off-diagonal, subdominant part, i.e. supposing that \( \|\partial g_i/\partial x_i\|_\infty \gg \|\partial g_i/\partial x_j\|_\infty \text{ and } \forall j \neq i \), then we can decompose the interaction matrix as

$$J_{ij} = \delta_{ij} x^*_i \frac{\partial g_i}{\partial x_i} \bigg|_{x^*} + (1 - \delta_{ij}) x^*_i \frac{\partial g_i}{\partial x_j} \bigg|_{x^*} \equiv j^0_{ij} + V_{ij}, \tag{B 22}$$

where the eigenvalues of the diagonal matrix \( j^0 \) are obviously \( \lambda_i^0 = j^0_{ii} = x^*_i \partial g_i/\partial x_i \big|_{x^*} \) and its eigenvectors \( u^{(i)} \) have components \( u^{(i)} = \delta_{ij} \). If \( \lambda_i \) is the \( i \)-th eigenvalue of \( J \), we can thus exploit perturbative expansion techniques [4] for estimating the eigenvalues of the interaction matrix

$$\lambda_i = M_i^0 + u^{(i)} \cdot V u^{(i)} + \sum_{j \neq i} \left( \frac{u^{(i)} \cdot V u^{(i)}}{M_j^0 - M_j^0} \right) + \text{h.o.t.}$$

$$= x^*_i \frac{\partial g_i}{\partial x_i} \bigg|_{x^*} + \sum_{j \neq i} \frac{\partial g_i}{\partial x_j} \bigg|_{x^*} x^*_j x^*_i - x^*_j + \text{h.o.t.} \tag{B 23}$$

and the second term is of the second order. Therefore, for the GLV we recover equation (3.7) of the main text.

Appendix C

(a) Critical delay for a pure delayed generalized Lotka–Volterra

Let us consider a pure delayed GLV system

$$\dot{x}_i(t) = x_i(t) (r_i + \sum_j b_{ij} x_j(t - \tau)). \tag{C 1}$$

Thus, the non-trivial equilibrium is \( x^* = -B^{-1}r \) and the linearization around it reads \( \dot{u}(t) = \tilde{B} u(t - \tau) \), where \( u(t) \equiv x(t) - x^* \) and \( \tilde{B} = \text{diag}(x^*)B \) is the community matrix. Plugging the ansatz solution \( u_i(t) \propto e^{\lambda_i t} \) we get

$$\lambda_i = \tilde{b}_i e^{-\lambda_i \tau}, \tag{C 2}$$

where \( \lambda_i \) are the system eigenvalues and \( \tilde{b}_i \) are the eigenvalues of the community matrix. By taking the real and the imaginary part of equation (C 2), we obtain the system

$$\begin{cases} 
\xi = e^{-\tau \xi} (\alpha \cos \tau v + \beta \sin \tau v) \\
v = e^{-\tau \xi} (\beta \cos \tau v - \alpha \sin \tau v)
\end{cases} \tag{C 3}$$

and
where we have denoted $\xi = \text{Re}(\lambda)$, $\nu = \text{Im}(\lambda)$, $\alpha = \text{Re}(\tilde{b})$ and $\beta = \text{Im}(\tilde{b})$. At criticality, $\xi = 0$ and we obtain after some manipulations

$$\nu^2 = \alpha^2 + \beta^2$$

and

$$\tau_c(\alpha, \beta) = \frac{1}{|\nu|} \arctan \left| \frac{\alpha}{\beta} \right| \tag{C4}$$

Hence, the critical delay $\tau_c$ would simply be the minimum $\tau_c(\alpha, \beta)$ over the eigenspectrum of the community matrix.

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