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by

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We consider the effect of distributed delays in predator-prey models and ecological food webs. Whereas the occurrence of delays in population dynamics is usually regarded a destabilizing factor leading to the extinction of species, we here demonstrate complementarily that delay distributions yield larger stability regimes than single delays. Food webs with distributed delays closely resemble non-delayed systems in terms of ecological stability measures. Thus, we state that dependence of dynamics on multiple instances in the past is an important, but so far underestimated factor for stability in dynamical systems.

Interaction delays occur frequently in biological feedback systems, for example in sensorimotor control [1], dynamic diseases [2], neural networks [3], and population ecology [4, 5]. Here, they comprise effects like retarded reproduction due to hatching periods, duration of pregnancy and maturation, slow replacement of food supplies, and age structure [6]. It is usually assumed that delays in population dynamics have a destabilizing effect by driving the system over a stability boundary resulting in oscillatory or chaotic behavior [7–9], subsequently leading to the extinction of species.

Most ecological models neglect delays or employ single time lags [5, 10]. However, ecological systems have a "smoothed" behavior for which distributed delays are a better representation. Existing studies [6, 8, 11, 12] focused more on issues like the existence of steady states rather than on the stabilizing influence of distributions of lags. Motivated by theoretical work from other fields that state an influence of the distribution of delay times on the system dynamics [13], we here show that distributed delays increase the stability of general predator-prey systems including two-species systems, food chains, and food webs.

Two-species models. We first study two-species models to elucidate a mechanism of increased stability of dynamical systems for distributed delays. Consider Volterra's delay model with prey resource limitation [e. g., 6], described by the delay-differential equation

$$\frac{dN_1(t)}{dt} = r_1 N_1(t)\Big(1 - \frac{1}{K_1}N_1(t) - f_{21}N_2(t)\Big) \quad (1)$$

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\Big(-1 + f_{12}\mathcal{N}_\xi(N_1(t))\Big), \quad (2)$$

where $N_1 \geq 0$ and $N_2 \geq 0$ denote the densities of individuals in a population of prey and predator, respectively. r_1, r_2 are the corresponding reproduction rates satisfying $r_1 > r_2$. K_1 is the capacity of the prey population, that is, the population size for $t \to \infty$ if $N_2 \equiv 0$. The coefficient f_{21} quantifies the impact which an individual predator has on the reproduction rate of an individual prey. Conversely, f_{12} gives the impact which an individual prey has on the reproduction rate of a predator; we assume $f_{21} > f_{12}$ for biological reasons. The influence of the prey on the predator population is assumed to depend on past densities N_1 according to the convolution

$$\mathcal{N}_\xi(N_1(t)) = \int\limits_0^\infty N_1(t - t')\xi(t')dt' \quad (3)$$

with a delay kernel $\xi(t) \geq 0$ satisfying the normalization condition $\int_0^\infty \xi(t)dt = 1$. Normalization is assumed in order to obtain the same steady states as in the non-delayed case [11]. Without any delays, the system (1,2) shows globally asymptotically stable behavior, if the equilibrium exists [14].

The only steady state of the delay system with non-vanishing densities is given by $(N_1^0, N_2^0) = (\frac{1}{f_{12}}, \frac{1}{f_{21}}(1 - \frac{1}{K_1 f_{12}}))$ and is independent of the delay distribution $\xi(t)$. It exists for $K_1 f_{12} > 1$. After linearizing the dynamics about this fixed point and rescaling the time variable [15], an exponential *ansatz* for the linear system, $z_1(t) = \exp(\lambda t)$, $z_2(t) = k\exp(\lambda t)$ results in the characteristic equations

$$k = -\beta - \lambda \quad (4)$$

$$\lambda^2 + \beta\lambda + \alpha \int\limits_0^\infty e^{-\lambda t'}\xi(t')dt' = 0\,. \quad (5)$$

for eigenvalues $\lambda = \mu + i\omega$. The coefficients α, β are given by

$$\alpha = \frac{r_2}{r_1}\frac{f_{12}}{f_{21}^2}(f_{12} - \frac{1}{K_1})\,, \qquad \beta = \frac{1}{K_1 f_{21}}$$

and satisfy the conditions $\alpha \geq 0$, $\beta > 0$. We will henceforth assume $\alpha \neq 0$ because the case $\alpha = 0$ yields a trivial steady state.

The case of a single delay has received a lot of attention (e. g., [16]). Here, we first demonstrate the effect of distributed delays by comparing a single discrete delay at lag T, $\xi_1(t) = \delta(t - T)$, with two discrete delays with an average lag T but separated by a time interval 2τ, $\xi_2(t; \tau) = [\delta(t - (T - \tau)) + \delta(t - (T + \tau))]/2$ (see also [17] for the case of two discrete delays). In both cases, the lag T may serve as a bifurcation parameter. Typically, at some value T^*, a supercritical Hopf bifurcation occurs, i. e., for $T > T^*$, the fixed point becomes unstable and is replaced by a stable limit cycle. In our case of the single delay $\xi_1(t)$, a decomposition of (5) in real and imaginary parts and the condition $\mu = 0$ yield the bifurcation value

$$T_1^* = \frac{1}{\omega} \arccos \frac{\omega^2}{\alpha}, \qquad \omega = \sqrt{-\frac{\beta^2}{2} + \sqrt{\frac{\beta^4}{4} + \alpha^2}}.$$

For two discrete delays $\xi_2(t)$, one obtains a bifurcation value $T_2^*(\tau)$ depending on the parameter τ:

$$T_2^*(\tau) = \frac{1}{\omega} \arccos \frac{\omega^2}{\alpha \cos \omega \tau},$$
$$\omega = \sqrt{-\frac{\alpha^2 \tau^2 + \beta^2}{2} + \sqrt{\frac{(\alpha^2 \tau^2 + \beta^2)^2}{4} + \alpha^2}}.$$

In both cases, solutions exist for all $\alpha, \beta > 0$. We first note that $T_1^* = T_2^*(\tau = 0)$ as required. Furthermore, it is straightforward to show that $dT_2^*/d\tau > 0$ for all $\alpha, \beta, \tau > 0$: The bifurcation occurs at higher average delays as the two delta peaks in $\xi_2(t; \tau)$ are moved apart. Hence, the singular delay kernel $\xi_1(t)$ yields the smallest stability regime of the nontrivial steady state, replacing this single delay by two discrete delays already increases stability.

Next, we turn to gamma distributions which are frequently employed in models of population biology,

$$\xi(t) = \frac{(\frac{T}{v})^{\frac{T^2}{v}}}{\Gamma(\frac{T^2}{v})} t^{\frac{T^2}{v} - 1} e^{-\frac{T}{v} t} \tag{6}$$

where T and v denote the mean and the variance, respectively. For $v = 0$ the gamma distributions ξ degenerate to a δ-function: $\xi(t) = \delta(t - T)$. Equation (5) yields

$$\lambda^2 + \beta\lambda + \alpha (\frac{T}{v})^{\frac{T^2}{v}} \frac{1}{(\lambda + \frac{T}{v})^{\frac{T^2}{v}}} = 0 \tag{7}$$

which is obtained from the fact that the integral in (5) is a Laplace transform. The dynamics are first studied for the case of small variances. A Taylor expansion of (7) about $v = 0$ yields

$$\lambda^2 + \beta\lambda + \alpha e^{-\lambda T} \left(1 + \frac{\lambda^2}{2} v\right) = 0. \tag{8}$$

For fixed variance v, the average delay T^* for which the real part μ of the eigenvalue λ vanishes is given by

$$T^* = \frac{1}{\omega} \arccos \frac{\omega^2}{\alpha(1 - \frac{v}{2}\omega^2)} \tag{9}$$

and

$$\omega = \begin{cases} \sqrt{\omega_+^2} & \text{if } \alpha v < 2 \\ \sqrt{\frac{\alpha^2}{2\alpha + \beta^2}} & \text{if } \alpha v = 2 \\ \sqrt{\omega_\pm^2} & \text{if } \alpha v > 2 \end{cases}, \tag{10}$$

where

$$\omega_\pm^2 = \frac{2(\alpha^2 v + \beta^2)}{\alpha^2 v^2 - 4} \pm \sqrt{\frac{4(\alpha^2 v + \beta^2)^2}{(\alpha^2 v^2 - 4)^2} - \frac{4\alpha^2}{\alpha^2 v^2 - 4}}. \tag{11}$$

Figure 1 shows the critical values T^* as a function of αv. The upper branch (bold line) is the stability boundary. It is composed of the solution with ω_+^2 for $\alpha v < 2$ and ω_-^2 for $\alpha v > 2$ and includes the value for $\alpha v = 2$ from (10). Indeed, a rather tedious calculation shows that for this branch $dT^*/dv \geq 0$ for all $\alpha, \beta > 0$: The stability boundary is pushed to larger values as the variance v of the gamma distribution increases, resulting in a larger parameter range with asymptotically stable behavior.
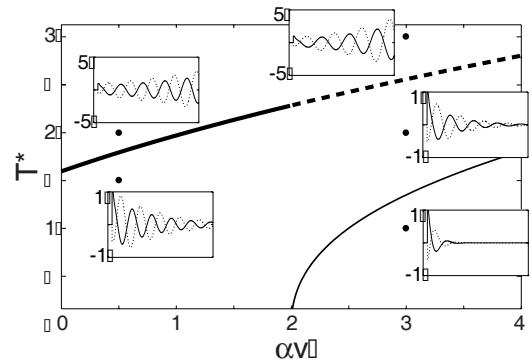

FIG. 1: *Average delay T^* of a gamma distribution which yields a vanishing real part μ of an eigenvalue λ. For $\alpha v < 2$, a single solution exists resulting from ω_+^2 in (10). For $\alpha v > 2$, two solutions resulting from ω_+^2 (solid line) and ω_-^2 (dashed line) exist. The two solution branches ω_+^2 for $\alpha v < 2$ and w_-^2 for $\alpha v > 2$ form a continuous function (bold line) with a value at $\alpha v = 2$ given by (10). Insets show simulated time courses of deviations from the steady state for various combinations of αv and T^* illustrating the changes in the system's dynamics as manifolds for $\mu = 0$ are crossed (abscissae: 50 time units). In all cases, $\alpha = 1$, $\beta = 1.3$.*

Finally, the dynamical system (1,2) is studied for the gamma distribution (6) in the limit of large variance, $v \to \infty$. Equation (7) simplifies to

$$\lambda^2 + \beta\lambda + \alpha = 0.$$

The resulting steady states are always stable, with an oscillatory approach for $\alpha > \beta^2/4$ and a non-oscillatory approach for $\alpha < \beta^2/4$.

Similar phenomena occur also in other predator-prey systems. For example, one can replace (2) by the dynamics of a polyphagous predator which survives also for

$N_1 \equiv 0$:

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\Big(1 - \frac{1}{K_2}N_2(t) + f_{12}\mathcal{N}_\xi(N_1(t))\Big), \quad (12)$$

where K_2 is the capacity of the predator population. The system (1,12) has a nontrivial steady state at $(N_1^0, N_2^0) = \big(\frac{K_1 - f_{21}K_1K_2}{1 + f_{12}f_{21}K_1K_2}, \frac{K_2 + f_{12}K_1K_2}{1 + f_{12}f_{21}K_1K_2}\big)$ which exists for $f_{21}K_2 < 1$. For the delay kernels considered above, the stability regime of this fixed point also grows as a function of the variance.

As a result, the study of two-species systems shows that distributed delays stabilize ecological systems by increasing the stability regime of asymptotically stable steady states.

Food chains and food webs. In this paragraph we study the impact of distributed delays on the stability of larger ecological systems. From an ecological perspective, it is usually not sufficient to study local stability properties of steady states [8]. For example, small-amplitude oscillations in the species' densities may also yield stability in the sense that species do not become extinct. Here we focus on stability measures associated with the extinction of species, which are evaluated numerically. Due to the ecological relevant Allee-effect [18], species typically cannot recover when their densities fall below a certain threshold (critical depensation). For this reason a species is considered extinct in our systems when its density is reduced to less than 1‰ of its equilibrium density in the non-delayed case.

First, consider a typical three-species food chain of the Lotka-Volterra type:

$$\frac{dN_1(t)}{dt} = r_1 N_1(t)\Big(1 - \frac{N_1(t)}{K_1} - f_{21}N_2(t)\Big)$$

$$\frac{dN_2(t)}{dt} = r_2 N_2(t)\Big(1 - \frac{N_2(t)}{K_2} + f_{12}\mathcal{N}_{\xi_1}(N_1(t)) \quad (13)$$
$$- f_{32}N_3(t)\Big)$$

$$\frac{dN_3(t)}{dt} = r_3 N_3(t)\Big(1 - \frac{N_3(t)}{K_3} + f_{23}\mathcal{N}_{\xi_2}(N_2(t))\Big)$$

where $\mathcal{N}_{\xi_i}(N_i(t))$ and the delay functions $\xi_i(t)$ $(i = 1, 2)$ read like (3) and (6), respectively, with given mean T_i and variance $v_i \equiv \sigma_i^2$. Here, the top predator N_3 feeds on the prey N_2 which itself feeds on the base prey N_1. As a stability measure, we use the fraction of surviving species, averaged over random realizations of the food chain. Figure 2 shows that large species density fluctuations (demonstrated in b) and subsequent extinctions are prevented by distributed delayed interactions (c), resulting in solutions that resemble those of a non-delayed system (a). This mechanism makes species survival more likely, even in presence of large mean interaction delays (d). Analog results are obtained for monophagous predators with constant per capita growth rate. Enhanced stability was also found in simulations using a Holling type II functional response [5] (data not shown).
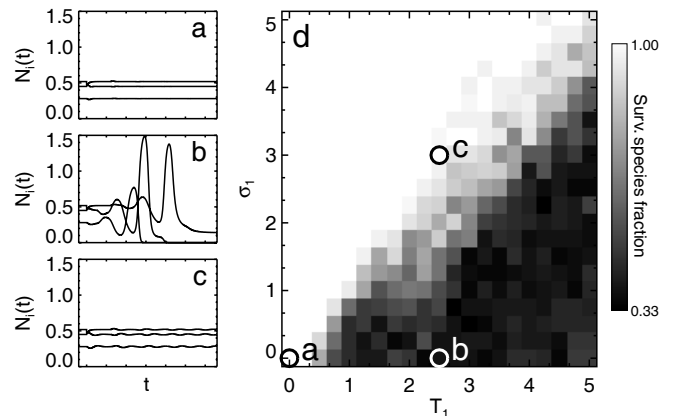

FIG. 2: Dynamics of three-species system (13). a–c: time courses for three combinations of mean delay T_1 and width σ_1 of the delay distribution ξ_1, marked in d. (a: $T_1 = 0.0$, $\sigma_1 = 0.1$; b: $T_1 = 2.5$, $\sigma_1 = 0.0$; c: $T_1 = 2.5$, $\sigma_1 = 3.0$). d: Mean survival ratio as a function of T_1 and σ_1. In all cases, $K_1 = 1$, $K_2 = 0.4$, $K_3 = 0.14$, $r_1 = 5$, $r_2 = 2$, $r_3 = 0.5$, $T_2 = 6$, $\bar{f}_{12} = 6$, $\bar{f}_{21} = 1.6$, $\bar{f}_{23} = 6$, $\bar{f}_{32} = 3$. Simulation time: 200 time units. Sample sizes: 20 food chains. See [19] for details.

As a generalization of food chains we study food webs of the form

$$\frac{dN_i(t)}{dt} = r_i N_i(t)\Big(1 - \frac{N_i(t)}{K_i} + \sum_{j=1, i\neq j}^{M} f_{ji}\mathcal{N}_j(t)\Big). \quad (14)$$

The coupling constants f_{ji} read

$$f_{ji} = \begin{cases} 0 & \text{if } |j - i| > C \\ f_0 R_{ji} & \text{if } |j - i| \leq C \text{ and } j < i \\ -1.5 f_0 R_{ji} & \text{if } |j - i| \leq C \text{ and } j > i \end{cases}, \quad (15)$$

where $R_{ji} \in [0, 1[$ sets the interaction strength and f_0 is a scaling constant. C denotes the range of interaction in the web. Species with higher index prey on those with a lower index. The interaction terms $\mathcal{N}_j(t)$ are modeled as

$$\mathcal{N}_j(t) = \begin{cases} N_j(t) & \text{if } j > i \\ \int_0^\infty N_j(t - t')\xi_j(t')dt' & \text{if } j < i \end{cases}, \quad (16)$$

where again a prey population is instantaneously reduced by predators, but the increase in predators is delayed. For reasons of simplicity, $\xi_i \equiv \xi$ are chosen identical for all species. We employ two measures for stability: First, the survival ratio, that is the number of surviving species related to the corresponding number in the non-delayed case. Second, the species deletion stability which indicates the proportion of species that can be removed from the system without subsequent extinctions in the system [21]. Figure 3 shows both measures as a function of the width σ of the delay kernel for ten-species food webs. We find a higher stability, hence more robust systems, as σ is increased. For large σ, the mean survival ratio approaches 1 indicating that the stability resembles that
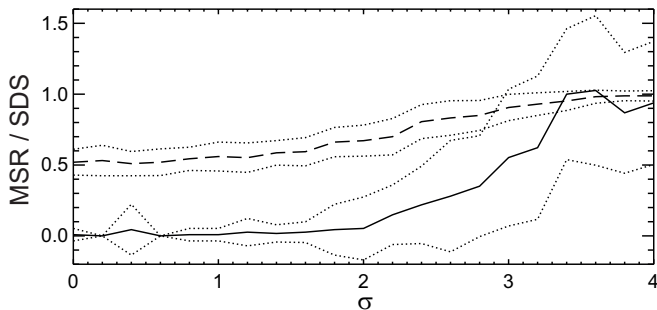
FIG. 3: Mean survival ratio (MSR; dashed line) and species deletion stability (SDS; solid line) for ten-species food webs (14). Standard deviations are given by dotted lines. $K_{1...10} = 10, 9, 8 ... 1$, $r_{1...10} = 5, 4.5, 4 ... 0.5$, $T = 5$, $C = 5$, $f_0 = 0.2$. Simulation time: 100 time units (MSR), 200 time units (SDS). Sample sizes: 50 networks (MSR), 25 networks (SDS). See [19] for details.

of the non-delayed system. Analog results are obtained for a ten-species food chain ($C = 1$, data not shown).

To summarize, our findings demonstrate the stabilizing effect of distributed delays for various types of dynamical predator-prey systems. A sufficiently great width of the memory kernel yields linear and nonlinear stability properties that can otherwise be found only in non-delayed systems. The necessary variance of the kernel typically lies in the same range as the corresponding mean of the distribution, which is in a biologically plausible range. In contrast, single delay models have a smaller stability regime and often predict oscillatory behavior and the extinction of species. In addition to other known factors [22], distributed delays may therefore play a crucial role in the stability of food webs. Our results apply also to other dynamical feedback systems. We suggest that more attention should be drawn to the stabilizing effect of a memory distribution in delayed dynamical systems.

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