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DISCRETE OR DISTRIBUTED DELAY? EFFECTS ON STABILITY OF POPULATION GROWTH

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Abstract. The growth of a population subject to maturation delay is modeled by using either a discrete delay or a delay continuously distributed over the population. The occurrence of stability switches (stable-unstable-stable) of the positive equilibrium as the delay increases is investigated in both cases. Necessary and sufficient conditions are provided by analyzing the relevant characteristic equations. It is shown that for any choice of parameter values for which the discrete delay model presents stability switches there exists a maximum delay variance beyond which no switch occurs for the continuous delay model: the delay variance has a stabilizing effect. Moreover, it is illustrated how, in the presence of switches, the unstable delay domain is as larger as lower is the ratio between the juveniles and the adults mortality rates.

1. **Introduction.** In population dynamics, processes like maturation are often modeled by introducing a discrete time delay into the equations. This means that it is implicitly assumed that the maturation delays are distributed over the population by a δ-Dirac distribution or, in other words, that each individual within the population is subject to the same maturation delay. The resulting Delay Differential Equations (DDEs) with discrete delay are then studied to derive the qualitative mathematical properties of the model, like stability of equilibria or existence of stability switches, as function of the discrete delay taken as parameter.

The use of a discrete delay, sometimes, might be seen as a rough approximation in modeling the delay distribution over a large size population. Of course, it may look much more realistic to assume the delay continuously distributed by a continuous distribution function, with a mean delay equal to the discrete delay and a positive variance giving account for the delay difference among individuals.

A question arises: are these two approaches for modeling the delay, i.e., *discrete* and *continuous*, equivalent from the point of view of the qualitative dynamical properties of the model? More precisely, the same biological model will have the same qualitative dynamical properties if modeled either by a discrete delay or by a

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continuously distributed delay function with mean value equal to the discrete delay but with a positive delay variance?

To answer we consider a quite widely studied population model with nonlinear Ricker birth rate function and discrete maturation delay τ, where the positive equilibrium undergoes stability switches like stability-instability-stability as τ increases (see [4, 6, 8] and the references therein). We formulate it as a sequence of models, each with maturation delay distributed by the continuous Gamma distributions [5], all with the same mean delay value equal to the discrete delay value τ, but with a decreasing variance as the Gamma shape parameter n increases. As $n \to \infty$ we recover the discrete delay model.

Besides the natural differences concerning the equilibrium values and their existence domains, we show that a threshold value n^* exists s.t. for $n \le n^*$, that means for a sufficiently large delay variance, the stability switches behavior is lost and the equilibrium remains asymptotically stable for all mean delay values τ in the equilibrium existence domain. The stability switches behavior of the discrete delay model reappears as the shape parameter becomes larger than n^* or, equivalently, as the delay variance becomes sufficiently small. In other words, it looks like that large delay variances stabilize the equilibrium. In addition, we show existence of parameters thresholds on stability that are independent of n, i.e., they hold for both the discrete and the continuous delay models.

The paper is organized as follows. In Section 2 we present the model of interest from [6], where a discrete delay is considered. Then we show how to interpret this model as the limit of a sequence of models with continuously distributed delay. In Section 3 we tackle the local stability analysis of both the trivial and positive equilibria for the model with discrete delay, proving the existence of the thresholds mentioned above. In Section 4 we perform the same analysis on the sequence of models with continuously distributed delay, illustrating the effects of the delay variance on the stability properties. Some concluding remarks end the work in Section 5.

2. The single species delay model.

In [6] the DDE

$$N'(t) = B(N(t-\tau))N(t-\tau)e^{-d_1\tau} - dN(t) \tag{1}$$

is proposed to model the time evolution of a single species adult population. $B(N)N$ is the birth rate function, $d \in (0,+\infty)$ is the death rate constant of the adult population, $d_1 \in (0,+\infty)$ is the death rate constant during the maturation life stage and $\tau \in [0,+\infty)$ is the constant maturation time of new born individuals. Furthermore, $B(N)$ is assumed to be the Ricker function $B(N) = be^{-aN}$ [4] with constants $a, b \in (0,+\infty)$. Thus (1) takes the form

$$N'(t) = be^{-aN(t-\tau)}N(t-\tau)e^{-d_1\tau} - dN(t). \tag{2}$$

For convenience we introduce the parameter $\eta := \log(b/d)$ in place of b and assume

(A1) $\eta > 0$,

which is the same as $b > d$. Then (2) reads

$$N'(t) = de^{\eta - d_1\tau - aN(t-\tau)}N(t-\tau) - dN(t). \tag{3}$$

Of course (3) can also be written as

$$N'(t) = d\int_0^{+\infty} F(s)e^{\eta - d_1 s - aN(t-s)}N(t-s)ds - dN(t), \tag{4}$$

where $F(s)$ is the δ-Dirac distribution at τ, namely $F(s) = \delta(s-\tau)$.

Alternatively, for the distribution function $F(s)$ we can choose from the Gamma distributions

$$F_{\alpha}^{(n)}(s) = \frac{\alpha^n s^{n-1} e^{-\alpha s}}{(n-1)!}, \quad s \in [0, +\infty), \tag{5}$$

with *shape* parameter $n \in \mathbb{N} := \{1, 2, \dots\}$ and *rate* parameter $\alpha \in (0, +\infty)$. Every element of the two-parameters family (5) is a continuous distribution, normalized as

$$\int_0^{+\infty} F_{\alpha}^{(n)}(s) ds = 1, \tag{6}$$

with mean value

$$\mu := \int_0^{+\infty} s F_{\alpha}^{(n)}(s) ds = \frac{n}{\alpha}$$

and variance

$$\sigma^2 := \int_0^{+\infty} (s-\mu)^2 F_{\alpha}^{(n)}(s) ds = \frac{n}{\alpha^2}.$$

By choosing $\alpha = n/\tau$ for $\tau > 0$ in (5), we obtain a sequence $\{F_{n/\tau}^{(n)}(s)\}_{n \in \mathbb{N}}$ of continuous distribution functions with constant mean value τ and decreasing variance τ^2/n as n increases. Correspondingly, the substitution of $F(s)$ in (4) by $F_{n/\tau}^{(n)}(s)$ leads to the family of DDEs

$$N'(t) = d \int_0^{+\infty} F_{n/\tau}^{(n)}(s) e^{\eta - d_1 s - aN(t-s)} N(t-s) ds - dN(t), \quad n \in \mathbb{N}, \tag{7}$$

where the delay is continuously distributed around the mean maturation time τ with variance τ^2/n. Since

$$\lim_{n \to \infty} F_{n/\tau}^{(n)}(s) = \delta(s-\tau),$$

the sequence of DDEs (7) with continuously distributed delay tends to the DDE (3) with discrete distributed delay as $n \to \infty$. In the sequel, we call (3) the *discrete* delay model and (7) the *continuous* delay model. Moreover, τ is considered as a varying parameter, w.r.t. which we aim at studying the qualitative properties of the equilibria such as existence, stability and stability switches.

3. **The discrete delay model.** The DDE (3) describes the single species model with a discrete delay. Its equilibria are the solutions N^{∞} of

$$dN \left(e^{\eta - d_1 \tau - aN} - 1 \right) = 0.$$

The trivial equilibrium $N_0^{\infty} = 0$ exists for all values of the parameters. A nontrivial equilibrium

$$N_+^{\infty}(\tau) = \frac{\eta - d_1 \tau}{a}$$

exists positive iff $\tau \in [0, \tau_+^{\infty})$ for

$$\tau_+^{\infty} := \frac{\eta}{d_1}. \tag{8}$$

The latter justifies assumption (A1), by which $\tau_+^\infty > 0$. Notice also that $N_+^\infty(\tau_+^\infty) = N_0^\infty$. We use the superscript ∞ to remember that (3) is the limit case of (7) as $n \to \infty$.

Linearization of (3) at an equilibrium N^∞ leads to the DDE

$$x'(t) = -dx(t) - d(aN^\infty - 1)e^{\eta - d_1\tau - aN^\infty} x(t-\tau)$$

and to the associated characteristic equation

$$\lambda + d + d(aN^\infty - 1)e^{\eta - d_1\tau - aN^\infty} e^{-\lambda\tau} = 0, \tag{9}$$

whose solutions $\lambda \in \mathbb{C}$ are called characteristic roots. At the trivial equilibrium N_0^∞, (9) becomes

$$G_0^\infty(\lambda;\tau) = 0 \tag{10}$$

for

$$G_0^\infty(\lambda;\tau) := \lambda + d - de^{\eta - d_1\tau} e^{-\lambda\tau}, \quad \tau \in [0, +\infty). \tag{11}$$

At the positive equilibrium N_+^∞, (9) becomes

$$G_+^\infty(\lambda;\tau) = 0 \tag{12}$$

for

$$G_+^\infty(\lambda;\tau) := \lambda + d + d(\eta - d_1\tau - 1)e^{-\lambda\tau}, \quad \tau \in [0, \tau_+^\infty). \tag{13}$$

3.1. **Stability and bifurcation analysis of the equilibria N^∞.** For the trivial equilibrium the following holds.

Theorem 3.1. *If $\tau \in [0, \tau_+^\infty)$ then N_0^∞ is unstable. If $\tau \in (\tau_+^\infty, +\infty)$ then N_0^∞ is locally asymptotically stable.*

Proof. Let τ be fixed in $[0, \tau_+^\infty)$, i.e., $\eta - d_1\tau > 0$ by (8). By considering (11) as a continuous function of the real variable $\lambda \in [0, +\infty)$, we have $G_0^\infty(0;\tau) < 0$ and $\lim_{\lambda\to+\infty} G_0^\infty(\lambda;\tau) = +\infty$. Continuity then implies the existence of at least one positive λ_+ s.t. $G_0^\infty(\lambda_+;\tau) = 0$, thus proving the first statement.

Now let τ be fixed in $(\tau_+^\infty, +\infty)$, i.e., $\eta - d_1\tau < 0$ by (8). Let $\lambda = \mu \pm \mathrm{i}\omega$ be a root of (10). Hence μ must satisfy $\mu = d(e^{\eta - d_1\tau} e^{-\mu\tau} \cos\omega\tau - 1)$ and $\mu \geq 0$ gives raise to a contradiction, thus proving the second statement. □

For the positive equilibrium we proceed as follows. In Theorem 3.2 we analyze the stability at $\tau = 0$. In Theorem 3.3 we show that, as τ increases, stability switches may occur only through imaginary conjugate roots crossings. Then, we characterize these switching values of τ as zeros of suitable functions in Theorem 3.4, showing in Theorem 3.5 that they can actually occur and in Theorem 3.6 that they give raise to Hopf bifurcations. Till here, the analysis follows the lines of [1, 4, 6]. Instead, in the last part of this section, we derive additional results by using a different function. This second approach is the one adopted also in Section 4.1 for the continuous model. In the sequel we assume

(A2) $\eta > 2$.

Theorem 3.2. *$N_+^\infty(0)$ is locally asymptotically stable.*

Proof. For $\tau = 0$ (13) becomes $G_+^\infty(\lambda;0) = \lambda + d\eta$, whose only root is $\lambda = -d\eta < 0$ thanks to (A1). □

Theorem 3.3. *$N_+^\infty(\tau)$ may have a stability switch in $(0,\tau_+^\infty)$ only if (12) admits a pair of imaginary conjugate roots $\lambda_\omega(\tau) := \pm\mathrm{i}\omega(\tau)$ in some nonempty set in $(0,\tau_+^\infty)$. Then, necessarily, this set is $(0,\tau_\omega^\infty)$ for*

$$\tau_\omega^\infty := \frac{\eta-2}{d_1} \tag{14}$$

and $\omega(\tau)=\omega^\infty(\tau)$ for

$$\omega^\infty(\tau) := d\sqrt{(\eta-d_1\tau)(\eta-d_1\tau-2)}. \tag{15}$$

Proof. By Theorem 3.2, $N_+^\infty(\tau)$ can lose stability in $(0,\tau_+^\infty)$ only if by increasing τ above zero a characteristic root $\lambda(\tau)$ crosses the imaginary axis left to right. Since $G_+^\infty(0;\tau) = d(\eta-d_1\tau) = daN_+^\infty(\tau) > 0$ for all $\tau\in(0,\tau_+^\infty)$, only complex conjugate pairs can possibly cross the imaginary axis. Let then consider (12) for $\lambda=\lambda_\omega(\tau) := \mathrm{i}\omega(\tau)$ for $\omega(\tau)\in(0,+\infty)$ without loss of generality, which gives

$$(\mathrm{i}\omega(\tau)+d)e^{\mathrm{i}\omega(\tau)\tau} = -d(\eta-d_1\tau-1). \tag{16}$$

Following the approach in [1], a necessary condition is that $\omega(\tau)$ satisfies

$$\omega(\tau)^2+d^2 = d^2(\eta-d_1\tau-1)^2 \tag{17}$$

for some $\tau\in(0,\tau_+^\infty)$. Under Assumption (A2), τ_ω^∞ in (14) is positive, hence (15) is well defined for $\tau\in(0,\tau_\omega^\infty)$ and it is the unique solution of (17). ☐

Prior to go on we notice that the function ω^∞ defined in (15) is continuous and positive in $(0,\tau_\omega^\infty)$. It can be continuously extended by setting

$$\omega^\infty(0) = d\sqrt{\eta(\eta-2)} > 0 \tag{18}$$

and $\omega^\infty(\tau_\omega^\infty)=0$. Moreover,

$$\omega^{\infty\prime}(\tau) = -\frac{d^2d_1(\eta-d_1\tau-1)}{\omega^\infty(\tau)} < 0 \tag{19}$$

for $\tau\in(0,\tau_\omega^\infty)$,

$$\omega^{\infty\prime}(0) = -\frac{dd_1(\eta-1)}{\sqrt{\eta(\eta-2)}} < 0$$

and

$$\lim_{\tau\uparrow\tau_\omega^\infty}\omega^{\infty\prime}(\tau) = -\infty. \tag{20}$$

Finally,

$$\omega^{\infty\prime\prime}(\tau) = -\frac{d^4d_1^2}{\omega^\infty(\tau)^3} < 0. \tag{21}$$

Theorem 3.4. *A pair of simple imaginary conjugate roots $\lambda_*^\infty := \pm\mathrm{i}\omega^\infty(\tau_*^\infty)$ of (12) exists at $\tau=\tau_*^\infty$ iff $S_k^\infty(\tau_*^\infty)=0$ for some $k\in\mathbb{N}_0$, where*

$$S_k^\infty(\tau) := \tau - \frac{(2k+1)\pi}{\omega^\infty(\tau)} + \frac{1}{\omega^\infty(\tau)}\arctan\left(\frac{\omega^\infty(\tau)}{d}\right) \tag{22}$$

is defined in $(0,\tau_\omega^\infty)$ and ω^∞ is given by (15). As τ crosses τ_*^∞ left to right, this pair crosses the imaginary axis left to right if $\delta^\infty(\tau_*^\infty)=1$ or right to left if $\delta^\infty(\tau_*^\infty)=-1$, where

$$\delta^\infty(\tau) := \mathrm{sign}\left(\left.\frac{d\mathrm{Re}(\lambda)}{d\tau}\right|_{\lambda=\lambda_*^\infty}\right) = \mathrm{sign}\left(\left.\frac{dS_k^\infty(\tau)}{d\tau}\right|_{\tau=\tau_*^\infty}\right). \tag{23}$$

Proof. Theorem 3.3 states that possible imaginary conjugate roots necessarily have imaginary part given by (15). Its proof is based on the necessary condition (17) obtained by equating the squared moduli of both sides of (16). Then sufficiency follows from an argument condition on (16), namely

$$\arg\left((\mathrm{i}\omega^\infty(\tau)+d)e^{\mathrm{i}\omega^\infty(\tau)\tau}\right)=(2k+1)\pi \tag{24}$$

for some $k\in\mathbb{Z}$. Since

$$\arg\left((\mathrm{i}\omega^\infty(\tau)+d)e^{\mathrm{i}\omega^\infty(\tau)\tau}\right)=\arctan\left(\frac{\omega^\infty(\tau)}{d}\right)+\omega^\infty(\tau)\tau, \tag{25}$$

the first statement follows by defining (22) and by observing that $k\in\mathbb{N}_0$ since ω^∞ is positive. The second statement follows from [1, Theorem 4.1] and [6, Theorem 2.1]. $\square$

The following result gives a sufficient condition to guarantee the existence of zeros of (22). It is based on observing that $S_0^\infty(\tau)>S_k^\infty(\tau)$ for $\tau\in(0,\tau_\omega^\infty)$ and $k\in\mathbb{N}$ and that

$$S_0^\infty(0):=\frac{1}{\omega^\infty(0)}\left[\arctan\left(\frac{\omega^\infty(0)}{d}\right)-\pi\right]<0. \tag{26}$$

Then if S_0^∞ has no zeros in $(0,\tau_\omega^\infty)$, $N_+^\infty(\tau)$ is locally asymptotically stable for all $\tau\in[0,\tau_+^\infty)$ by virtue of Theorem 3.4. Otherwise, to guarantee the existence of zeros, it is sufficient to prove that S_0^∞ is positive in some nonempty set in $(0,\tau_\omega^\infty)$ since

$$\lim_{\tau\uparrow\tau_\omega^\infty}S_0^\infty(\tau)=-\infty, \tag{27}$$

as it follows from (22). This can actually occur as shown next.

Theorem 3.5. *If η, d and d_1 satisfy*

$$\left(\frac{d}{d_1}\right)^2\bar{y}^2(\eta-\bar{y})(\eta-\bar{y}-2)>\pi^2 \tag{28}$$

for

$$\bar{y}:=\frac{3(\eta-1)-\sqrt{(\eta-1)^2+8}}{4}, \tag{29}$$

then S_0^∞ is positive in some nonempty set in $(0,\tau_\omega^\infty)$.

Proof. The simplest sufficient condition to have S_0^∞ positive in some nonempty set in $(0,\tau_\omega^\infty)$ is $\tau\omega^\infty(\tau)>\pi$ or, equivalently by (15),

$$d^2\tau^2(\eta-d_1\tau)(\eta-d_1\tau-2)>\pi^2.$$

The latter can be rewritten as $f(y)>\pi^2$ for

$$f(y):=\left(\frac{d}{d_1}\right)^2y^2(\eta-y)(\eta-y-2)$$

and $y:=d_1\tau$. Notice that $\tau\in(0,\tau_\omega^\infty)$ implies $y\in(0,\eta-2)$. It is not difficult to show that f is positive in $(0,\eta-2)$ and reaches its unique relative and absolute maximum at $\bar{y}$ given in (29), thus proving that (28) is sufficient for the final statement. $\square$

Notice that it is always possible to satisfy (28) since the left-hand side is an increasing function of η and d_1 can be chosen independently. Moreover, Theorem 3.5 can be generalized to provide a sufficient condition for the existence of zeros of S_k^∞ for any $k \in \mathbb{N}$: it is enough to rework the proof given for $k = 0$ by substituting $(2k+1)\pi$ for π in the right-hand side of (28).

Theorem 3.6. *If η, d and d_1 satisfy (28), then there exist $\tau_{*1}^\infty, \tau_{*2}^\infty \in (0, \tau_\omega^\infty)$ with $\tau_{*1}^\infty < \tau_{*2}^\infty$ s.t. $N_+^\infty(\tau)$ is locally asymptotically stable for $\tau \in [0, \tau_{*1}^\infty) \cup (\tau_{*2}^\infty, \tau_+^\infty)$, unstable for $\tau \in (\tau_{*1}^\infty, \tau_{*2}^\infty)$ and two Hopf bifurcations occur for τ increasing in $[0, \tau_+^\infty)$, the first at τ_{*1}^∞ towards instability and the second at τ_{*2}^∞ towards stability.*

Proof. From (26), (27) and Theorem 3.5 we know that S_0^∞ has at least two zeros $\tau_{*1}^\infty < \tau_{*2}^\infty$ in $(0, \tau_\omega^\infty)$. From (22) we have

$$S_0^{\infty\prime}(\tau) = 1 + \frac{\omega^{\infty\prime}(\tau)}{\omega^\infty(\tau)^2}\left[\pi - \arctan\left(\frac{\omega(\tau)}{d}\right) + \frac{d\omega^\infty(\tau)}{d^2 + \omega^\infty(\tau)^2}\right]$$

and

$$\begin{aligned} S_0^{\infty\prime\prime}(\tau) \quad = \quad & \frac{\omega^{\infty\prime\prime}(\tau)\omega^\infty(\tau) - 2\omega^{\infty\prime}(\tau)^2}{\omega^\infty(\tau)^3}\left[\pi - \arctan\left(\frac{\omega(\tau)}{d}\right) + \frac{d\omega^\infty(\tau)}{d^2 + \omega^\infty(\tau)^2}\right] \\ & - \frac{2d\omega^{\infty\prime}(\tau)^2}{[d^2 + \omega^\infty(\tau)^2]^2}. \end{aligned}$$

The latter is negative by (21). This implies uniqueness of the two zeros $\tau_{*1}^\infty, \tau_{*2}^\infty$ and, moreover, that $S_0^{\infty\prime}(\tau_{*1}^\infty) > 0$ and $S_0^{\infty\prime}(\tau_{*2}^\infty) < 0$. Then, according to (23) and by considering $\tau \in [0, \tau_\omega^\infty)$ as a bifurcation parameter, Theorem 3.4 provides transversality conditions for two potential Hopf bifurcations, see [7, Section 6.2]: the first at τ_{*1}^∞ towards instability and the second at τ_{*2}^∞ towards stability. To conclude that these are indeed Hopf bifurcations, hypothesis (H) in the same reference has to be verified, i.e., there are no characteristic roots which are integer multiples of $\pm i\omega^\infty(\tau_{*1}^\infty)$, respectively of $\pm i\omega^\infty(\tau_{*2}^\infty)$. But this is easily checked by noticing that the necessary condition (17) cannot be satisfied for both $\pm i\omega^\infty(\tau_{*1}^\infty)$ and $\pm ik\omega^\infty(\tau_{*1}^\infty)$ for any $k > 1$ since the right-hand side is independent of ω^∞ (the same holds at τ_{*2}^∞).

The proof is completed by virtue of Theorem 3.2 and by the above analysis of S_0^∞, which implies that no other crossing is possible in $[0, \tau_\omega^\infty)$, nor in $[\tau_\omega^\infty, \tau_+^\infty)$, where (15) is not positive or neither defined. □

Example 1. Some values of the parameters of (2) satisfying (28) are $a = 7$, $d = 0.5$, $d_1 = 1$ and $b = 350$. In fact, it follows that $\eta = 6.5510\ldots$, $\bar{y} = 2.6057\ldots$ and $d^2\bar{y}^2(\bar{y} - \eta)[\bar{y} - (\eta - 2)]/d_1^2 = 13.0281\ldots > 9.8696\ldots = \pi^2$. The thesis of Theorem 3.6 is represented in Figure 1, where the real part of the rightmost root of (12) is plotted as a function of τ. The computation of the characteristic roots is done with the numerical method in [2, 3]. For $\tau = 0$ we have $\lambda = -3.2755\ldots$, according to (the proof of) Theorem 3.2 the only root is indeed $-d\eta$. The Hopf bifurcations occur at $\tau_{*1}^\infty = 0.7602\ldots$ and $\tau_{*2}^\infty = 4.0379\ldots$. Eventually, $N_+^\infty(\tau)$ exists positive up to $\tau_+^\infty = 6.5510\ldots$, value at which it undergoes a transcritical bifurcation with the trivial equilibrium. In fact, the rightmost root is $\lambda = 0$ (and it becomes positive beyond τ_+^∞).

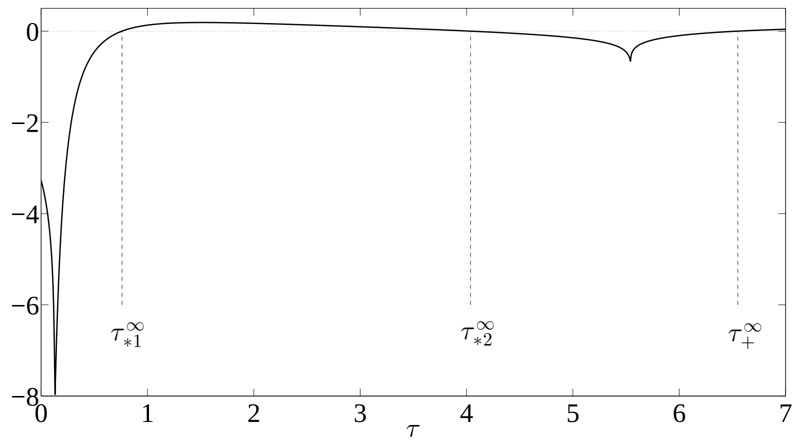

FIGURE 1. real part of the righmost root of (12) for varying τ and for the values of the parameters in Example 1.

Now, as anticipated, we follow a similar approach but based on a function different from (22). We define from (25) the function

$$\varphi^{\infty}(\tau) := \omega^{\infty}(\tau)\tau + \arctan\left(\frac{\omega^{\infty}(\tau)}{d}\right) \tag{30}$$

for $\tau \in (0, \tau^{\infty}_{\omega})$. The search for stability switches through the zeros of (22) is equivalent to look for the solutions of

$$\varphi^{\infty}(\tau) = (2k+1)\pi. \tag{31}$$

This is clear either from (24) or from (22) given that ω^{∞} is positive, in fact:

$$\omega^{\infty}(\tau)S^{\infty}_{k}(\tau) = \varphi^{\infty}(\tau) - (2k+1)\pi. \tag{32}$$

Then it immediately follows that all the previous results based on S^{∞}_{k} can be equivalently proved by using φ^{∞}. In particular, the crossing rule (23) becomes

$$\delta^{\infty}(\tau) := \operatorname{sign}\left(\left.\frac{d\mathrm{Re}(\lambda)}{d\tau}\right|_{\lambda=\lambda^{\infty}_{*}}\right) = \operatorname{sign}\left(\left.\frac{d\varphi^{\infty}(\tau)}{d\tau}\right|_{\tau=\tau^{\infty}_{*}}\right) \tag{33}$$

as it follows by differentiating (32) w.r.t. τ at $\tau = \tau^{\infty}_{*}$.

The advantage now is that φ^{∞} is independent of $k \in \mathbb{N}$ and that we can also prove additional stability properties. To this aim observe first that φ^{∞} is continuous and positive in $(0, \tau^{\infty}_{\omega})$. It can be continuously extended by setting $\varphi^{\infty}(0) = \arctan\sqrt{\eta(\eta-2)} > 0$ and $\varphi^{\infty}(\tau^{\infty}_{\omega}) = 0$. Moreover,

$$\varphi^{\infty\prime}(\tau) = \omega^{\infty}(\tau) + \omega^{\infty\prime}(\tau)\tau + \frac{d\omega^{\infty\prime}(\tau)}{d^2 + \omega^{\infty}(\tau)^2}$$

for $\tau \in (0, \tau^{\infty}_{\omega})$,

$$\varphi^{\infty\prime}(0) = \frac{d\eta(\eta-1)(\eta-2) - d_1}{(\eta-1)\sqrt{\eta(\eta-2)}} \tag{34}$$

follows from (18) and from the fact that ω^{∞} is the unique solution of (17) by Theorem 3.3 and

$$\lim_{\tau\uparrow\tau_{\omega}^{\infty}} {\varphi^{\infty}}'(\tau) = -\infty \tag{35}$$

follows from (20). Finally,

$$\varphi^{\infty\prime\prime}(\tau) = 2{\omega^{\infty}}'(\tau) + \omega^{\infty\prime\prime}(\tau)\tau + \frac{d\omega^{\infty\prime\prime}(\tau)}{d^2+\omega^{\infty}(\tau)^2} - \frac{2d\omega^{\infty}(\tau){\omega^{\infty}}'(\tau)^2}{[d^2+\omega^{\infty}(\tau)^2]^2} < 0 \tag{36}$$

follows from (19) and (21). Now, the two complementary assumptions

(A4) $\eta(\eta-1)(\eta-2) \leq d_1/d$;

(A5) $\eta(\eta-1)(\eta-2) > d_1/d$;

decide the monotonicity of $\varphi^{(n)}$ according to the following.

Lemma 3.7. *Under (A4) φ^{∞} monotonically decreases from its absolute maximum $\varphi^{\infty}(0)$ at $\tau = 0$. The latter is also relative iff (A4) holds with equality.*

Proof. ${\varphi^{\infty}}'$ is monotone decreasing by virtue of (36). Since (A4) implies ${\varphi^{\infty}}'(0) \leq 0$ thanks to (34), it follows that also φ^{∞} is monotone decreasing. The second statement is then trivial. □

Lemma 3.8. *Under (A5) there exists a unique $\bar{\tau}^{\infty} \in (0, \tau_{\omega}^{\infty})$ s.t. ${\varphi^{\infty}}'(\bar{\tau}^{\infty}) = 0$. Moreover, $\varphi^{\infty}(\bar{\tau}^{\infty}) = \max_{\tau\in[0,\tau_{\omega}^{\infty}]} \varphi^{\infty}(\tau)$.*

Proof. Again, ${\varphi^{\infty}}'$ is monotone decreasing by virtue of (36). Thanks to (34), (A5) now implies ${\varphi^{\infty}}'(0) > 0$ which, together with (35), gives the thesis. □

Finally, additional stability results follow directly from Lemma 3.7 and Lemma 3.8.

Theorem 3.9. *Under (A4) $N_{+}^{\infty}(\tau)$ is locally asymptotically stable for all $\tau \in [0, \tau_{+}^{\infty})$.*

Proof. For all $\tau \in (0, \tau_{\omega}^{\infty})$, Lemma 3.7 ensures $\varphi^{\infty}(\tau) \leq \varphi^{\infty}(0)$. Since $\varphi^{\infty}(0) = \arctan\sqrt{\eta(\eta-2)} < \pi/2$, it follows that for any $k \in \mathbb{N}_0$ (31) cannot have solutions and hence stability switches cannot occur. The proof is completed by Theorem 3.2. □

Theorem 3.10. *Under (A5) let $\bar{k}^{\infty} \in \mathbb{Z}$ be the largest integer s.t. $\varphi^{\infty}(\bar{\tau}^{\infty}) > (2\bar{k}^{\infty}+1)\pi$ for $\bar{\tau}^{\infty}$ in Lemma 3.8. If $\bar{k}^{\infty} < 0$ then $N_{+}^{\infty}(\tau)$ is locally asymptotically stable for all $\tau \in [0, \tau_{+}^{\infty})$. If $\bar{k}^{\infty} \geq 0$ then there exist two sequences of delays $\{\tau_{*1,k}^{\infty}\}_{k=0,1,\ldots,\bar{k}^{\infty}}$ and $\{\tau_{*2,k}^{\infty}\}_{k=0,1,\ldots,\bar{k}^{\infty}}$, respectively increasing and decreasing in $(0, \tau_{\omega}^{\infty})$ and separated by $\bar{\tau}^{\infty}$, i.e.,*

$$\tau_{*1,0}^{\infty} < \tau_{*1,1}^{\infty} < \cdots < \tau_{*1,\bar{k}^{\infty}}^{\infty} < \bar{\tau}^{\infty} < \tau_{*2,\bar{k}^{\infty}}^{\infty} < \cdots < \tau_{*2,1}^{\infty} < \tau_{*2,0}^{\infty}, \tag{37}$$

s.t.

$$\operatorname{sign}\left(\left.\frac{d\varphi^{\infty}(\tau)}{d\tau}\right|_{\tau=\tau_{*1,k}^{\infty}}\right) = 1, \quad k = 0, 1, \ldots, \bar{k}^{\infty},$$

and

$$\operatorname{sign}\left(\left.\frac{d\varphi^{\infty}(\tau)}{d\tau}\right|_{\tau=\tau_{*2,k}^{\infty}}\right) = -1, \quad k = 0, 1, \ldots, \bar{k}^{\infty},$$

so that $N_{+}^{\infty}(\tau)$ is locally asymptotically stable for $\tau \in [0, \tau_{*1,0}^{\infty}) \cup (\tau_{*2,0}^{\infty}, \tau_{+}^{\infty})$, unstable for $\tau \in (\tau_{*1,0}^{\infty}, \tau_{*2,0}^{\infty})$ and two Hopf bifurcations occur for τ increasing in $[0, \tau_{+}^{\infty})$, the first at $\tau_{*1,0}^{\infty}$ towards instability and the second at $\tau_{*2,0}^{\infty}$ towards stability.

Proof. The proof is based on the equivalence of the existence of imaginary conjugate crossing roots to the existence of solutions of (31), which, in turn, follows from (32) and the first part of Theorem 3.4. Since $\varphi^\infty(\bar\tau)$ is the maximum of φ^∞ by virtue of Lemma 3.8, condition (36) provides the full statement. In fact, if $\bar k^\infty < 0$ then no crossing is possible and the thesis follows from Theorem 3.2. Otherwise, $2(\bar k^\infty + 1)$ crossings occur according to the delay values in (37). More precisely, by denoting with $\mu^\infty(a, b)$ the total multiplicity of characteristic roots in the right-hand side of the complex plane for $\tau \in (a, b)$, we have

$$\begin{aligned}
&\mu^\infty(0, \tau^\infty_{*1,0}) = 0,\\
&\mu^\infty(\tau^\infty_{*1,0}, \tau^\infty_{*1,1}) = 2,\\
&\mu^\infty(\tau^\infty_{*1,1}, \tau^\infty_{*1,2}) = 4,\\
&\dots\\
&\mu^\infty(\tau^\infty_{*1,\bar k^\infty-1}, \tau^\infty_{*1,\bar k^\infty}) = 2\bar k^\infty,\\
&\mu^\infty(\tau^\infty_{*1,\bar k^\infty}, \tau^\infty_{*2,\bar k^\infty}) = 2(\bar k^\infty + 1),\\
&\mu^\infty(\tau^\infty_{*2,\bar k^\infty}, \tau^\infty_{*2,\bar k^\infty-1}) = 2\bar k^\infty,\\
&\dots\\
&\mu^\infty(\tau^\infty_{*2,2}, \tau^\infty_{*2,1}) = 4,\\
&\mu^\infty(\tau^\infty_{*2,1}, \tau^\infty_{*2,0}) = 2,\\
&\mu^\infty(\tau^\infty_{*2,0}, \tau^\infty_{+}) = 0.
\end{aligned}$$

by virtue of (33), (23), the second part of Theorem 3.4 and together also with Theorem 3.2 and the fact that no crossing is possible in $[\tau^\infty_\omega, \tau^\infty_+)$. □

We illustrate Theorem 3.10 by way of two examples, one in Figure 2 for $d > d_1$ and the other in Figure 3 for $d < d_1$. The latter, in particular, refers to the same parameter values used in Example 1.

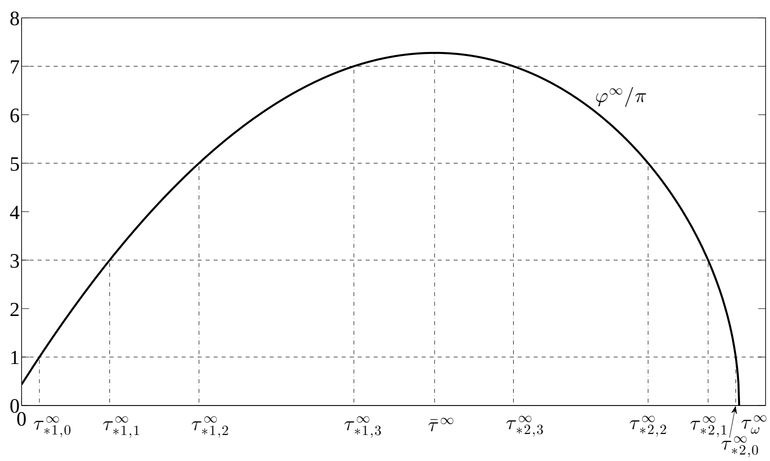

FIGURE 2. Theorem 3.10, intersections (37) of φ^∞ in (30) with $(2k+1)\pi$, $k = 0, 1, \dots, \bar k^\infty$, where $\bar k^\infty = 3$ for $a = 7$, $b = 350$, $d = 1$, $d_1 = 0.25$: $\tau^\infty_{*1,0} = 0.3828\dots$, $\tau^\infty_{*2,0} = 15.3584\dots$, $\tau^\infty_\omega = 15.4317\dots$.

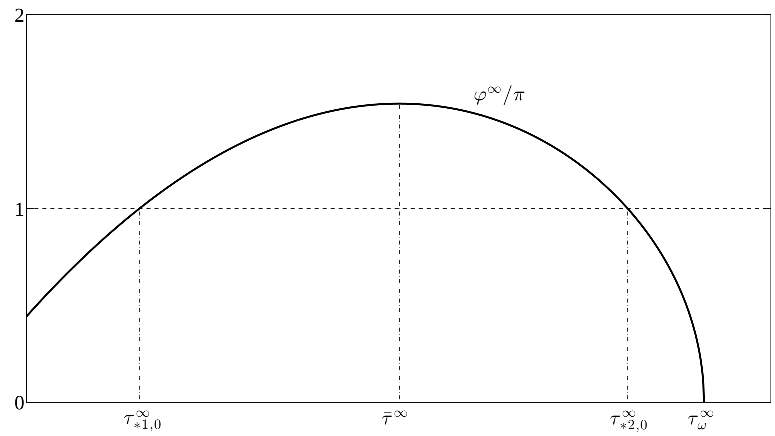

FIGURE 3. Theorem 3.10, intersections (37) of φ^∞ in (30) with $(2k+1)\pi$, $k = 0, 1, \ldots, \bar{k}^\infty$, where $\bar{k}^\infty = 0$ for $a = 7$, $b = 350$, $d = 0.5$, $d_1 = 1$: $\tau^\infty_{*1,0} = 0.7603\ldots$, $\tau^\infty_{*2,0} = 4.0379\ldots$, $\tau^\infty_\omega = 4.5511\ldots$.

4. **The continuous delay model.** The DDE (7) describes the single species model with a continuously distributed delay, according to the Gamma distribution (5) with shape parameter $n \in \mathbb{N}$ and rate parameter $\alpha = n/\tau \in (0, +\infty)$. The latter is meaningful only if the mean delay value τ is positive. Also the variance τ^2/n is positive then.

In the sequel, to compare the sequence of continuous models (7) with the discrete model (3) (i.e., Gamma distributions vs δ-Dirac distribution), we use the same parameters and the relevant assumptions of Section 3. Accordingly, we use the superscript (n) to remember that (3) is the limit case of (7) as $n \to \infty$.

Now let n be fixed. The equilibria of (7) are the solutions $N^{(n)}$ of

$$dN\left(\int_0^{+\infty} F^{(n)}_{n/\tau}(s)e^{\eta - d_1 s - aN}ds - 1\right) = 0.$$

The trivial equilibrium $N^{(n)}_0 = 0$ exists for all values of the parameters. A nontrivial equilibrium

$$N^{(n)}_+(\tau) = \frac{\eta - \log\left(1 + \frac{d_1\tau}{n}\right)^n}{a}, \tag{38}$$

exists positive iff $\tau \in (0, \tau^{(n)}_+)$ for

$$\tau^{(n)}_+ := \frac{n}{d_1}(e^{\eta/n} - 1). \tag{39}$$

The latter justifies again assumption (A1), by which $\tau^{(n)}_+ > 0$. Note that (38) follows from the normalization (6) of the Gamma distribution:

$$\int_0^{+\infty} F^{(n)}_{n/\tau}(s)e^{-d_1 s}ds = \left(\frac{n}{n + d_1\tau}\right)^n \int_0^{+\infty} F^{(n)}_{d_1 + n/\tau}(s)ds = \left(1 + \frac{d_1\tau}{n}\right)^{-n}.$$

Notice also that $N_+^{(n)}(\tau_+^{(n)}) = N_0^{(n)}$. Moreover, $\lim_{\tau\downarrow 0} N_+^{(n)}(\tau) = \eta/a = N_+^{\infty}(0)$: in fact, when the delay is absent, the discrete and the continuous models coincide. In this sense, we can continuously extend $N_+^{(n)}(\tau)$ at $\tau = 0$. Finally, for later convenience, we rewrite (38) as

$$N_+^{(n)}(\tau) = \frac{\eta - \log e_n(d_1\tau)}{a},$$

where e_n is the (possibly complex-valued) function

$$e_n(z) := \left(1 + \frac{z}{n}\right)^n \tag{40}$$

and, clearly,

$$\lim_{n\to\infty} e_n(z) = e^z. \tag{41}$$

Linearization of (7) at an equilibrium $N^{(n)}$ leads to the DDE

$$x'(t) = -dx(t) - d(aN^{(n)} - 1)\int_0^{+\infty} F_{n/\tau}^{(n)}(s)e^{\eta - d_1 s - aN^{(n)}}x(t-s)ds$$

and to the associated characteristic equation

$$\lambda + d + d(aN^{(n)} - 1)\int_0^{+\infty} F_{n/\tau}^{(n)}(s)e^{\eta - d_1 s - aN^{(n)}}e^{-\lambda s}ds = 0. \tag{42}$$

Besides constants, the integral in (42) is the Laplace transform of $F_{n/\tau}^{(n)}(s)e^{-d_1 s}$, which exists provided that

(A3) $\mathrm{Re}(\lambda) > -(n/\tau + d_1)$, $n \in \mathbb{N}$.

Under this assumption, (42) reads

$$\lambda + d + d(aN^{(n)} - 1)\frac{e^{\eta - aN^{(n)}}}{e_n((d_1+\lambda)\tau)} = 0. \tag{43}$$

At the trivial equilibrium $N_0^{(n)}$, (43) becomes

$$G_0^{(n)}(\lambda;\tau) = 0 \tag{44}$$

for

$$G_0^{(n)}(\lambda;\tau) := \lambda + d - d\frac{e^{\eta}}{e_n((d_1+\lambda)\tau)}, \quad \tau \in (0,+\infty). \tag{45}$$

At the positive equilibrium $N_+^{(n)}$, (43) becomes

$$G_+^{(n)}(\lambda;\tau) = 0 \tag{46}$$

for

$$G_+^{(n)}(\lambda;\tau) := \lambda + d + d(\eta - \log e_n(d_1\tau) - 1)\frac{e_n(d_1\tau)}{e_n((d_1+\lambda)\tau)}, \quad \tau \in (0,\tau_+^{(n)}). \tag{47}$$

The next result shows how equilibria and relevant characteristic equations of (7) vary by increasing the shape parameter $n \in \mathbb{N}$ at τ fixed or, equivalently, by decreasing the variance τ^2/n of the Gamma distribution.

Theorem 4.1. *The following limits hold:*

$$\begin{aligned}
&\lim_{n\to\infty} \tau_+^{(n)} = \tau_+^\infty, && &&\\
&\lim_{n\to\infty} N_+^{(n)}(\tau) = N_+^\infty(\tau), && && \tau\in[0,\tau_+^\infty),\\
&\lim_{n\to\infty} G_0^{(n)}(\lambda;\tau) = G_0^\infty(\lambda;\tau), && \lambda\in\mathbb{C}, && \tau\in[0,+\infty),\\
&\lim_{n\to\infty} G_+^{(n)}(\lambda;\tau) = G_+^\infty(\lambda;\tau), && \lambda\in\mathbb{C}, && \tau\in[0,\tau_+^\infty).
\end{aligned}$$

Proof. The first limit is trivial from (39), all the others follow by applying (41) to the relevant functions. Notice that the second and the last limits are well posed since the sequence $\{\tau_+^{(n)}\}_{n\in\mathbb{N}}$ is monotone decreasing, so that $\tau_+^\infty < \tau_+^{(n)}$ for all $n\in\mathbb{N}$. □

4.1. **Stability and bifurcation analysis of the equilibria $N^{(n)}$.** For the trivial equilibrium the analogous of Theorem 3.1 holds.

Theorem 4.2. *If $\tau\in(0,\tau_+^{(n)})$ then $N_0^{(n)}$ is unstable. If $\tau\in(\tau_+^{(n)},+\infty)$ then $N_0^{(n)}$ is locally asymptotically stable.*

Proof. Let τ be fixed in $(0,\tau_+^{(n)})$. Then $e_n(d_1\tau)<e^\eta$ easily follows from (39). By considering (45) as a continuous function of the real variable $\lambda\in[0,+\infty)$ we have

$$G_0^{(n)}(0;\tau) = d\left(1-\frac{e^\eta}{e_n(d_1\tau)}\right) < 0$$

and $\lim_{\lambda\to\infty} G_0^{(n)}(\lambda;\tau)=+\infty$. Continuity then implies the existence of at least one positive λ_+ s.t. $G_0^{(n)}(\lambda_+;\tau)=0$, thus proving the first statement.

Now let τ be fixed in $(\tau_+^{(n)},+\infty)$. Let $\lambda=\mu\pm \mathrm{i}\omega$ be a root of (44). Hence μ must satisfy

$$\mu = d\left(\frac{e^\eta}{\rho^n}\cos n\theta - 1\right) \tag{48}$$

for $\rho:=|z|$, $\theta:=\arg z$ and

$$z := 1+\frac{(d_1+\mu)\tau \pm \mathrm{i}\omega\tau}{n}.$$

Assume by contradiction that $\mu\ge 0$, which implies $|z|\ge 1+d_1\tau/n$ and hence $\rho^n\ge e_n(d_1\tau)$. Since $\tau>\tau_+^{(n)}$ ensures $e_n(d_1\tau)>e^\eta$ by (39), (48) gives the absurd $\mu<0$, thus proving the second statement. □

An analogous of Theorem 3.2 can also be proved, with the attention that (7) is not defined for $\tau=0$ since the rate parameter $\alpha=n/\tau\in(0,+\infty)$ of the Gamma distribution has sense only for $\tau>0$. Nevertheless, we have seen that $N_+^{(n)}(\tau)$ can be continuously extended at $\tau=0$. Hence, the following theorem concerns the limit $\tau\downarrow 0$ in $(0,\tau_+^{(n)})$ for all $n\in\mathbb{N}$.

Theorem 4.3. *$N_+^{(n)}(\tau)$ is locally asymptotically stable for $\tau\in(0,\tau_+^{(n)})$ sufficiently close to zero.*

Proof. From (47) and (41) we have $\lim_{\tau\downarrow 0} G_+^{(n)}(\lambda;\tau)=\lambda+d\eta$, whose only root is $\lambda=-d\eta<0$ thanks to (A1). □

Now we state and prove an analogous of Theorem 3.3.

Theorem 4.4. *$N_+^{(n)}(\tau)$ may have a stability switch in $(0,\tau_+^{(n)})$ only if (46) admits a pair of imaginary conjugate roots $\lambda_\omega := \pm\mathrm{i}\omega(\tau)$ in some nonempty set in $(0,\tau_+^{(n)})$. Then, necessarily, this set is $(0,\tau_\omega^{(n)})$ for*

$$\tau_\omega^{(n)} := \frac{n}{d_1}\left(e^{(\eta-2)/n}-1\right) \tag{49}$$

and $\omega(\tau)=\omega^{(n)}(\tau)$, where $\omega^{(n)}(\tau)$ is s.t. $t^{(n)}(\tau):=\omega^{(n)}(\tau)^2$ is the unique positive root of the polynomial equation

$$T_{n+1}(t;\tau)=0, \tag{50}$$

where

$$T_{n+1}(t;\tau) := \sum_{\nu=0}^{n+1} q_\nu(\tau)t^\nu$$

has coefficients

$$q_{n+1}(\tau) = \left(\frac{\tau}{n+d_1\tau}\right)^{2n}, \tag{51}$$

$$q_\nu(\tau) = \left[\frac{\nu}{n+1-\nu}+d^2\left(\frac{\tau}{n+d_1\tau}\right)^2\right]\binom{n}{\nu}\left(\frac{\tau}{n+d_1\tau}\right)^{2(\nu-1)} \tag{52}$$

for $\nu=n,\dots,1$ and

$$q_0(\tau) = -d^2[\eta-\log e_n(d_1\tau)][\eta-\log e_n(d_1\tau)-2]. \tag{53}$$

Proof. By Theorem 4.3, $N_+^{(n)}(\tau)$ can lose stability in $(0,\tau_+^{(n)})$ only if by increasing τ above zero a characteristic root $\lambda(\tau)$ crosses the imaginary axis left to right. Since $G_+^{(n)}(0;\tau)=d(\eta-\log e_n(d_1\tau))=daN_+^{(n)}(\tau)>0$ for all $\tau\in(0,\tau_+^{(n)})$, only complex conjugate pairs can possibly cross the imaginary axis. Let then consider (46) for $\lambda=\lambda_\omega(\tau):=\mathrm{i}\omega(\tau)$ for $\omega(\tau)\in(0,+\infty)$ without loss of generality, which gives

$$(\mathrm{i}\omega(\tau)+d)\frac{e_n((d_1+\mathrm{i}\omega(\tau))\tau)}{e_n(d_1\tau)} = -d(\eta-\log e_n(d_1\tau)-1). \tag{54}$$

A necessary condition is that $\omega(\tau)$ satisfies

$$(\omega(\tau)^2+d^2)\left|\frac{e_n((d_1+\mathrm{i}\omega(\tau))\tau)}{e_n(d_1\tau)}\right|^2 = d^2(\eta-\log e_n(d_1\tau)-1)^2$$

for some $\tau\in(0,\tau_+^{(n)})$. By using (40) the latter reads

$$(\omega(\tau)^2+d^2)\left[1+\left(\frac{\omega(\tau)\tau}{n+d_1\tau}\right)^2\right]^n = d^2(\eta-\log e_n(d_1\tau)-1)^2 \tag{55}$$

which, by applying the Newton binomial expansion, is transformed into (50) for $t=t(\tau)=\omega(\tau)^2$. Since all the coefficients (51) and (52) are positive functions of $\tau\in(0,\tau_+^{(n)})$, a positive root of (50) requires that the last coefficient (53) is negative. Hence it must be $\eta-\log e_n(d_1\tau)-2>0$, which holds true only if $\tau\in(0,\tau_\omega^{(n)})$ for $\tau_\omega^{(n)}$ in (49). Clearly, $\tau_\omega^{(n)}<\tau_+^{(n)}$, while $\tau_\omega^{(n)}>0$ by virtue of (A2). It remains to prove that under this condition (50) admits a unique positive solution. Indeed, $T_{n+1}(0;\tau)=q_0(\tau)<0$ and the positivity of all the coefficients (51) and (52) implies $\lim_{t\to+\infty}T_{n+1}(t;\tau)=+\infty$ and $T'_{n+1}(t;\tau)>0$ for all $t\geq 0$. □

Prior to go on we notice that the function $\omega^{(n)}(\tau) = \sqrt{t^{(n)}(\tau)}$ defined through the unique positive solution $t^{(n)}(\tau)$ of (50) for $\tau \in (0, \tau_\omega^{(n)})$ is known only implicitly. This is a major difference w.r.t. $\omega^\infty(\tau)$ in (15) of Theorem 3.3. Nevertheless, we can still recover some useful properties for a later use. First, $\omega^{(n)}(\tau)$ is continuous since roots of polynomials are continuous functions of the polynomial coefficients and it is positive by definition. Second, it can be continuously extended by setting $\omega^{(n)}(0) = d\sqrt{\eta(\eta-2)} > 0$ and $\omega^{(n)}(\tau_\omega^{(n)}) = 0$. The former can be seen either directly from (55) or by solving (50) explicitly when $\tau = 0$. The latter is a consequence of (53), since $q_0(\tau_\omega^{(n)}) = 0$. Finally, we differentiate (55) w.r.t. τ to find ${\omega^{(n)}}'(\tau)$. After lengthy calculations, we get

$$ {\omega^{(n)}}'(\tau) = -\frac{[d_1 A(\tau) + n\tau {\omega^{(n)}(\tau)}^2 C(\tau)] n B(\tau)}{\omega^{(n)}(\tau) C(\tau)(n + d_1\tau)[A(\tau) + n\tau^2 B(\tau)]}, \tag{56} $$

where, for brevity, we introduced the continuous and positive functions

$$ \begin{aligned} A(\tau) &:= (n + d_1\tau)^2 + (\omega^{(n)}(\tau)\tau)^2, \\ B(\tau) &:= d^2 + {\omega^{(n)}(\tau)}^2, \\ C(\tau) &:= \eta - \log e_n(d_1\tau) - 1. \end{aligned} $$

They are defined for $\tau \in (0, \tau_\omega^{(n)})$ with straightforward continuous extensions to the closed interval:

$$ \begin{aligned} A(0) &= n^2, & A(\tau_\omega^{(n)}) &= n^2 e^{2(\eta-2)/n}, \\ B(0) &= d^2(\eta-1)^2, & B(\tau_\omega^{(n)}) &= d^2, \\ C(0) &= \eta - 1, & C(\tau_\omega^{(n)}) &= 1. \end{aligned} $$

Notice that (56) proves that $\omega^{(n)}(\tau)$ is decreasing w.r.t. τ and, moreover,

$$ {\omega^{(n)}}'(0) = -\frac{dd_1(\eta-1)}{\sqrt{\eta(\eta-2)}} = {\omega^\infty}'(0) < 0 $$

and $\lim_{\tau \uparrow \tau_\omega^{(n)}} {\omega^{(n)}}'(\tau) = -\infty$.

Now, as anticipated, we complete the parallelism with the content of Section 3.1 by following the approach based on the similar function φ^∞ defined there in (30). In analogy, the function $\varphi^{(n)}$ defines the argument of the left-hand side of (54). Hence, by recalling (40), we set

$$ \varphi^{(n)}(\tau) := n \arctan\left(\frac{\omega^{(n)}(\tau)\tau}{n + d_1\tau}\right) + \arctan\left(\frac{\omega^{(n)}(\tau)}{d}\right) \tag{57} $$

for all $\tau \in (0, \tau_\omega^{(n)})$. The proof of the following result, which completes Theorem 4.1, is trivial.

Theorem 4.5. *The following limits hold:*

$$ \begin{aligned} &\lim_{n\to\infty} \tau_\omega^{(n)} = \tau_\omega^\infty, \\ &\lim_{n\to\infty} \varphi^{(n)}(\tau) = \varphi^\infty(\tau), \qquad \tau \in (0, \tau_\omega^\infty). \end{aligned} $$

The function $\varphi^{(n)}$ is continuous and positive in $(0, \tau_\omega^{(n)})$. It can be continuously extended by setting $\varphi^{(n)}(0) = \arctan\sqrt{\eta(\eta-2)} = \varphi^\infty(0) > 0$ and $\varphi^{(n)}(\tau_\omega^{(n)}) = 0$. Moreover, after some computations, direct differentiation and (56) lead to

$$ {\varphi^{(n)}}'(\tau) = \frac{n\omega^{(n)}(\tau)\Delta(\tau)}{(n + d_1\tau)C(\tau)[A(\tau) + n\tau^2 B(\tau)]}, \tag{58} $$

where, for brevity again, we introduced the continuous functions

$$\begin{aligned}
&\Delta(\tau) := C(\tau)n[n + (d_1 - d)\tau] - D(\tau),\\
&D(\tau) := E(\tau) + F(\tau)/\omega^{(n)}(\tau)^2,\\
&E(\tau) := n^2 d_1 \tau + n d_1^2 \tau^2 + d d_1 \tau^2,\\
&F(\tau) := (n + d_1\tau)(n d^2 d_1 \tau + n d d_1 + d d_1^2 \tau).
\end{aligned}$$

They are defined for $\tau \in (0, \tau_\omega^{(n)})$ with straightforward continuous extensions at $\tau = 0$:

$$\begin{aligned}
&\Delta(0) = \frac{n^2[d\eta(\eta-1)(\eta-2) - d_1]}{d\eta(\eta-2)},\\
&D(0) = \frac{n^2 d_1}{d\eta(\eta-2)},\\
&E(0) = 0,\\
&F(0) = n^2 d d_1.
\end{aligned}$$

On the other side E and F remains bounded and positive, while $\lim_{\tau \uparrow \tau_\omega^{(n)}} D(\tau) = +\infty$ and $\lim_{\tau\uparrow\tau_\omega^{(n)}} \Delta(\tau) = -\infty$. The next result is the analogous of Theorem 3.4, but based on the function $\varphi^{(n)}$.

Theorem 4.6. *A pair of simple imaginary conjugate roots $\lambda_*^{(n)} := \pm i\omega^{(n)}(\tau_*^{(n)})$ of (46) exists at $\tau = \tau_*^{(n)}$ iff*

$$\varphi^{(n)}(\tau_*^{(n)}) = (2k+1)\pi \tag{59}$$

for some $k \in \mathbb{N}_0$ and $\varphi^{(n)}$ in (57). As τ crosses $\tau_*^{(n)}$ left to right, this pair crosses the imaginary axis left to right if $\delta^{(n)}(\tau_*^{(n)}) = 1$ or right to left if $\delta^{(n)}(\tau_*^{(n)}) = -1$, where

$$\delta^{(n)}(\tau) := \operatorname{sign}\left(\left.\frac{d\mathrm{Re}(\lambda)}{d\tau}\right|_{\lambda=\lambda_*^{(n)}}\right) = \operatorname{sign}\left(\left.\frac{d\varphi^{(n)}(\tau)}{d\tau}\right|_{\tau=\tau_*^{(n)}}\right). \tag{60}$$

Proof. Theorem 4.4 states that possible imaginary conjugate roots necessarily have imaginary part given by $\omega^{(n)}(\tau) = \sqrt{t^{(n)}(\tau)}$, where $t^{(n)}(\tau)$ is the unique positive solution of (50) for $\tau \in (0, \tau_\omega^{(n)})$. Its proof is based on the necessary condition (55) obtained by equating the squared moduli of both sides of (54). Then sufficiency follows from an argument condition on (54), which is precisely (59) for some $k \in \mathbb{Z}$. Then the first statement follows by observing that $k \in \mathbb{N}_0$ since $\omega^{(n)}$ in (57) is positive. To prove the second statement, we compute directly both sides of (60). For the right-hand side, it is clear from (58) that

$$\begin{aligned}
&\operatorname{sign}\left(\left.\frac{d\varphi^{(n)}(\tau)}{d\tau}\right|_{\tau=\tau_*^{(n)}}\right)\\
=\ &\operatorname{sign}(\Delta(\tau_*^{(n)}))\\
=\ &\operatorname{sign}\Bigg(C(\tau_*^{(n)})n[n + (d_1 - d)\tau_*^{(n)}] - n^2 d_1 \tau_*^{(n)} - n d_1^2 {\tau_*^{(n)}}^2 - d d_1 {\tau_*^{(n)}}^2\\
&-\frac{(n + d_1\tau_*^{(n)})(n d^2 d_1 \tau_*^{(n)} + n d d_1 + d d_1^2 \tau_*^{(n)})}{\omega^{(n)}(\tau_*^{(n)})^2}\Bigg).
\end{aligned} \tag{61}$$

For the left-hand side of (60), let us first observe that

$$\operatorname{sign}\left(\left.\frac{d\mathrm{Re}(\lambda)}{d\tau}\right|_{\lambda=\lambda_*^{(n)}}\right) = \operatorname{sign}\left(\left.\mathrm{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\right|_{\lambda=\lambda_*^{(n)}}\right).$$

Consider now the characteristic equation (46). Since

$$G_+^{(n)}(\lambda_*^{(n)};\tau_*^{(n)})=0, \tag{62}$$

it also follows that the total derivative w.r.t. τ vanishes:

$$D_\tau\, G_+^{(n)}(\lambda;\tau)\Big|_{(\lambda;\tau)=(\lambda_*^{(n)};\tau_*^{(n)})}=0.$$

Then

$$\left(\frac{d\lambda}{d\tau}\right)^{-1}\Bigg|_{\lambda=\lambda_*^{(n)}}=-\frac{\left.\dfrac{\partial G_+^{(n)}(\lambda;\tau)}{\partial\lambda}\right|_{(\lambda,\tau)=(\lambda_*^{(n)};\tau_*^{(n)})}}{\left.\dfrac{\partial G_+^{(n)}(\lambda;\tau)}{\partial\tau}\right|_{(\lambda,\tau)=(\lambda_*^{(n)};\tau_*^{(n)})}}. \tag{63}$$

By using (62) it turns out that

$$\left.\frac{\partial G_+^{(n)}(\lambda;\tau)}{\partial\lambda}\right|_{(\lambda,\tau)=(\lambda_*^{(n)};\tau_*^{(n)})}=1+\frac{n\tau_*^{(n)}(\lambda_*^{(n)}+d)}{n+(d_1+\lambda_*^{(n)})\tau_*^{(n)}} \tag{64}$$

and

$$\left.\frac{\partial G_+^{(n)}(\lambda;\tau)}{\partial\tau}\right|_{(\lambda,\tau)=(\lambda_*^{(n)};\tau_*^{(n)})}=\frac{\lambda_*^{(n)}+d}{n+d_1\tau_*^{(n)}}\cdot\left[\frac{nd_1}{C(\tau_*^{(n)})}+\frac{n^2\lambda_*^{(n)}}{n+(d_1+\lambda_*^{(n)})\tau_*^{(n)}}\right]. \tag{65}$$

By considering that $\lambda_*^{(n)}=\mathrm{i}\omega^{(n)}(\tau_*^{(n)})$ without loss of generality, substitution of (64) and (65) into (63) leads, after suitable simplifications, to

$$\begin{aligned}\left(\frac{d\lambda}{d\tau}\right)^{-1}\Bigg|_{\lambda=\lambda_*^{(n)}} &= -\frac{C(\tau_*^{(n)})(n+d_1\tau_*^{(n)})}{n[d^2+\omega^{(n)}(\tau_*^{(n)})^2]}\\ &\quad\cdot\left\{\frac{d(n+d_1\tau_*^{(n)})+\tau_*^{(n)}[nd^2+(n+1)\omega^{(n)}(\tau_*^{(n)})^2]}{d_1(n+d_1\tau_*^{(n)})+\mathrm{i}\omega^{(n)}(\tau_*^{(n)})[d_1\tau_*^{(n)}+nC(\tau_*^{(n)})]}\right.\\ &\quad\left.-\mathrm{i}\frac{\omega^{(n)}(\tau_*^{(n)})[n+(d_1-d)\tau_*^{(n)}]}{d_1(n+d_1\tau_*^{(n)})+\mathrm{i}\omega^{(n)}(\tau_*^{(n)})[d_1\tau_*^{(n)}+nC(\tau_*^{(n)})]}\right\}.\end{aligned}$$

From the latter we recover by simple computations that

$$\begin{aligned}&\operatorname{sign}\left(\operatorname{Re}\left(\frac{d\lambda}{d\tau}\right)^{-1}\Bigg|_{\lambda=\lambda_*^{(n)}}\right)\\ =\;&-\operatorname{sign}\Bigg(d_1(n+d_1\tau_*^{(n)})\{d(n+d_1\tau_*^{(n)})+\tau_*^{(n)}[nd^2+(n+1)\omega^{(n)}(\tau_*^{(n)})^2]\}\\ &-\omega^{(n)}(\tau_*^{(n)})^2[n+(d_1-d)\tau_*^{(n)}][d_1\tau_*^{(n)}+nC(\tau_*^{(n)})]\Bigg)\\ =\;&\operatorname{sign}\Bigg(\omega^{(n)}(\tau_*^{(n)})^2C(\tau_*^{(n)})n[n+(d_1-d)\tau_*^{(n)}]\\ &-\omega^{(n)}(\tau_*^{(n)})^2\left[n^2d_1\tau_*^{(n)}+nd_1^2{\tau_*^{(n)}}^2+dd_1{\tau_*^{(n)}}^2\right]\\ &-(n+d_1\tau_*^{(n)})(nd^2d_1\tau_*^{(n)}+ndd_1+dd_1^2\tau_*^{(n)})\Bigg).\end{aligned}$$

The second statement is thus proved by comparison with (61). $\square$

By using the same arguments adopted in the proof of Theorem 3.6, it is clear that the crossings mentioned in Theorem 4.6 are indeed Hopf bifurcations. Hence, it is proved that possible stability switches of $N_+^{(n)}$ occur correspondingly to solutions of (59) and vice-versa. It is left to see whether such solutions exist. To this aim, we go back to the complementary assumptions (A4) and (A5) introduced in Section 3.1. Again, as we show next by mimicking Lemma 3.7 and Lemma 3.8, these assumptions decide the monotonicity of the function $\varphi^{(n)}$. Surprisingly, both results are independent of n. Recall from (58) that

$$\mathrm{sign}\left({\varphi^{(n)}}'(\tau)\right) = \mathrm{sign}(\Delta(\tau)).$$

Lemma 4.7. *Under (A4) and for any $n \in \mathbb{N}$, $\varphi^{(n)}$ monotonically decreases from its absolute maximum $\varphi^{(n)}(0)$ at $\tau = 0$. The latter is also relative iff (A4) holds with equality.*

Proof. Assumption (A4) ensures $\Delta(0) \leq 0$. To prove the result we show that Δ is always negative or at most it vanishes at $\tau = 0$ only when (A4) holds with equality. To this aim observe that

$$\Delta'(\tau) = C'(\tau)n[n + (d_1 - d)\tau] + C(\tau)n(d_1 - d) - D'(\tau) \tag{66}$$

where

$$C'(\tau) = -\frac{nd_1}{n + d_1\tau} < 0$$

and $D'(\tau) > 0$ since E and F are monotonically increasing whereas $\omega^{(n)}$ is monotonically decreasing, recall (56). Let us distinguish three cases:

(i) $d = d_1$: from (66) Δ' is always negative and the thesis follows.

(ii) $d > d_1$: let $\tilde{\tau} := n/(d - d_1)$. If $\tilde{\tau} \geq \tau_\omega^{(n)}$ then $\tau < \tilde{\tau}$ and $n + (d_1 - d)\tau > 0$ implies again that Δ' is always negative, giving the thesis. Otherwise, if $\tilde{\tau} < \tau_\omega^{(n)}$, then for $\tau \in [0, \tilde{\tau})$ we have $n + (d_1 - d)\tau > 0$ and Δ' is negative. So Δ decreases from $\Delta(0) \leq 0$ down to $\Delta(\tilde{\tau}) = -D(\tilde{\tau}) < 0$. Finally, for $\tau \in [\tilde{\tau}, \tau_\omega^{(n)})$ we have $n + (d_1 - d)\tau \leq 0$ and Δ remains negative. The thesis holds again.

(iii) $d < d_1$: it is not clear from the definition if Δ can change sign. Assume that τ_0 exists in $[0, \tau_\omega^{(n)})$ s.t. $\Delta(\tau_0) = 0$. This implies

$$C(\tau_0) = \frac{D(\tau_0)}{n[n + (d_1 - d)\tau]}.$$

Then (66) reads

$$\begin{aligned}\Delta'(\tau_0) &= -\frac{n^2 d_1}{n + d_1\tau_0}[n + (d_1 - d)\tau_0] + \frac{D(\tau_0)(d_1 - d)}{n + (d_1 - d)\tau_0} - D'(\tau_0) \\ &= \frac{A_1 + A_2 + A_3 + A_4}{n + (d_1 - d)\tau_0},\end{aligned}$$

where it is not difficult to recover

$$\begin{aligned}A_1 &= -\frac{n^2 d_1}{n + d_1\tau_0}[n + (d_1 - d)\tau_0]^2, \\ A_2 &= E(\tau_0)(d_1 - d) - E'(\tau_0)[n + (d_1 - d)\tau_0], \\ A_3 &= \frac{F(\tau_0)(d_1 - d) - F'(\tau_0)[n + (d_1 - d)\tau_0]}{{\omega^{(n)}(\tau_0)}^2}, \\ A_4 &= \frac{2F(\tau_0){\omega^{(n)}}'(\tau_0)}{{\omega^{(n)}(\tau_0)}^3}[n + (d_1 - d)\tau_0].\end{aligned}$$

The first addend A_1 is clearly negative. So is A_4 by recalling that F and $\omega^{(n)}$ are positive while $\omega^{(n)}$ is decreasing. As for A_2 and A_3, direct calculations show that

$$A_2 = -d_1\tau_0^2(d_1 - d)(nd_1 + d) - nd_1[n^2 + d\tau_0(nd_1 + d)] < 0$$

and

$$\begin{aligned} {\omega^{(n)}(\tau_0)}^2 A_3 &= -n(1+n)d^2 d_1(n + d_1\tau_0) \\ &\quad -d_1(nd^2 d_1\tau_0 + ndd_1 + dd_1^2\tau_0)[n + (d_1 - d)\tau] < 0. \end{aligned}$$

It follows that whenever Δ vanishes, it crosses zero from above. Since $\Delta(0) \leq 0$, the thesis follows.

Finally, in what above, the choice of $n \in \mathbb{N}$ is arbitrary. □

Lemma 4.8. *Under (A5) and for any $n \in \mathbb{N}$, there exists a unique $\bar{\tau}^{(n)} \in (0, \tau_\omega^{(n)})$ s.t. ${\varphi^{(n)}}'(\bar{\tau}^{(n)}) = 0$. Moreover, $\varphi^{(n)}(\bar{\tau}^{(n)}) = \max_{\tau \in [0,\tau_\omega^{(n)}]} \varphi^{(n)}(\tau)$.*

Proof. Assumption (A5) ensures $\Delta(0) > 0$. Since $\lim_{\tau\uparrow\tau_\omega^{(n)}} \Delta(\tau) = -\infty$, it follows that there exists $\bar{\tau}^{(n)} \in (0, \tau_\omega^{(n)})$ s.t. $\Delta(\bar{\tau}^{(n)}) = 0$. To show uniqueness it is enough to repeat the same arguments used for the three distinct cases in the proof of Lemma 4.7. In particular, the monotonicity of Δ is preserved, which keeps cases (i) and (iii) unchanged with the only difference that $\Delta(0)$ is shifted above zero, giving indeed the existence and uniqueness of the zero $\bar{\tau}^{(n)}$. Case (ii) holds as well by observing that $\Delta(\tilde{\tau}) = -D(\tilde{\tau})$ is still negative, giving existence and uniqueness of the zero $\bar{\tau}^{(n)} \in (0, \tilde{\tau})$. Finally, again, the choice of $n \in \mathbb{N}$ is arbitrary. □

Additional stability results follow directly from Lemma 4.7 and Lemma 4.8 exactly as Theorem 3.9 and Theorem 3.10 followed respectively from Lemma 3.7 and Lemma 3.8 in Section 3.1 (hence the proofs are omitted).

Theorem 4.9. *Under (A4) and for any $n \in \mathbb{N}$, $N_+^{(n)}(\tau)$ is locally asymptotically stable for all $\tau \in (0, \tau_+^{(n)})$.*

Theorem 4.10. *Under (A5) and for any $n \in \mathbb{N}$, let $\bar{k}^{(n)} \in \mathbb{Z}$ be the largest integer s.t. $\varphi^{(n)}(\bar{\tau}^{(n)}) > (2\bar{k}^{(n)} + 1)\pi$ for $\bar{\tau}^{(n)}$ in Lemma 4.8. If $\bar{k}^{(n)} < 0$ then $N_+^{(n)}(\tau)$ is locally asymptotically stable for all $\tau \in (0, \tau_+^{(n)})$. If $\bar{k}^{(n)} \geq 0$ then there exist two sequences of delays $\{\tau_{*1,k}^{(n)}\}_{k=0,1,\ldots,\bar{k}^{(n)}}$ and $\{\tau_{*2,k}^{(n)}\}_{k=0,1,\ldots,\bar{k}^{(n)}}$, respectively increasing and decreasing in $(0, \tau_\omega^{(n)})$ and separated by $\bar{\tau}^{(n)}$, i.e.,*

$$\tau_{*1,0}^{(n)} < \tau_{*1,1}^{(n)} < \cdots < \tau_{*1,\bar{k}^{(n)}}^{(n)} < \bar{\tau}^{(n)} < \tau_{*2,\bar{k}^{(n)}}^{(n)} < \cdots < \tau_{*2,1}^{(n)} < \tau_{*2,0}^{(n)},$$

s.t.

$$\operatorname{sign}\left(\left.\frac{d\varphi^{(n)}(\tau)}{d\tau}\right|_{\tau=\tau_{*1,k}^{(n)}} \right) = 1, \quad k = 0, 1, \ldots, \bar{k}^{(n)},$$

and

$$\operatorname{sign}\left(\left.\frac{d\varphi^{(n)}(\tau)}{d\tau}\right|_{\tau=\tau_{*2,k}^{(n)}} \right) = -1, \quad k = 0, 1, \ldots, \bar{k}^{(n)},$$

so that $N_+^{(n)}(\tau)$ is locally asymptotically stable for $\tau \in (0, \tau_{*1,0}^{(n)}) \cup (\tau_{*2,0}^{(n)}, \tau_+^{(n)})$, unstable for $\tau \in (\tau_{*1,0}^{(n)}, \tau_{*2,0}^{(n)})$ and two Hopf bifurcations occur for τ increasing in $(0, \tau_+^{(n)})$, the first at $\tau_{*1,0}^{(n)}$ towards instability and the second at $\tau_{*2,0}^{(n)}$ towards stability.

Let us warn the reader not to interpret the last result as a guarantee of existence of stability switches: this occur only if $\bar{k}^{(n)} \geq 0$ for the given n. Indeed, even under (A5) $N_+^{(n)}(\tau)$ may preserve its local asymptotic stability for all $\tau \in (0, \tau_+^{(n)})$. Take, e.g., $n = 1$: it is clear from (57) that (59) cannot be satisfied since $\varphi^{(1)}(\tau) < \pi$ for all $\tau \in (0, \tau_+^{(1)})$, hence no stability switch occurs. Given this, and considering Theorem 4.5 and the results of Section 3.1, we may ask which is the threshold shape parameter n^* below or equal to which stability switches *cannot* occur and beyond which stability switches *must* occur. Thanks to Theorem 4.10, we can give the following definition:

$$n^* := \max_{n \in \mathbb{N}} \left\{ \varphi^{(n)}(\bar{\tau}^{(n)}) \leq \pi < \varphi^{(n+1)}(\bar{\tau}^{(n+1)}) \right\}.$$

Therefore, for any parameters choice that ensures delay stability switches of $N_+^{\infty}(\tau)$, a threshold variance $\sigma^{*2} = \tau^2/n^*$ exists s.t. larger variances $\sigma^2 = \tau^2/n$ (i.e., for $n < n^*$) stabilize the corresponding equilibrium $N_+^{(n)}(\tau)$. In Figure 4 we show that $n^* = 2$ for the same parameter values used in Figure 2. Similarly, in Figure 5 we show that $n^* = 6$ for the same parameter values used in Figure 3. In Figure 6, instead, we illustrate Theorem 4.5 for the parameter values of Figure 2 and Figure 4. It can be appreciated how more crossings are correctly recovered by the continuous model as n increases. Nevertheless, it is interesting to observe that a very large n may be required to recover all the crossings, but a small n can suffice to recover with good agreement the important crossings, i.e., those (with π) that give raise to the only two possible stability switches as stated by Theorem 4.10.

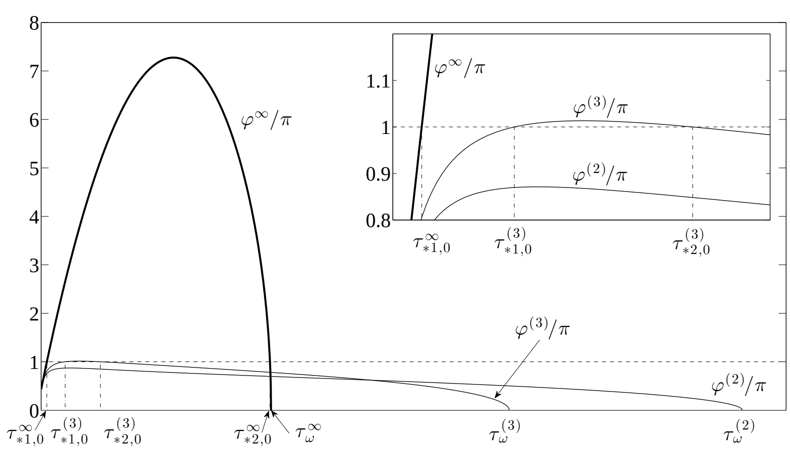

FIGURE 4. φ^∞ in (30) (solid thick) and $\varphi^{(n)}$ in (57) for $n = 2, 3$ (solid thin) and $a = 7$, $b = 350$, $d = 1$, $d_1 = 0.25$: $\tau_{*1,0}^{(3)} = 1.6116\ldots$, $\tau_{*2,0}^{(3)} = 3.9726\ldots$, $\tau_\omega^{(3)} = 31.4184\ldots$ and intersections with π show that $n^* = 2$ (inner panel: zoom of the left-bottom corner).

5. **Conclusions.** In this section we wish to point out which are the differences in modeling the juvenile stage delay in a single species growth model by a discrete delay τ through a δ-Dirac distribution or by a n-order Gamma distribution with mean delay the same value τ but positive variance $\sigma^2 = \tau^2/n$.

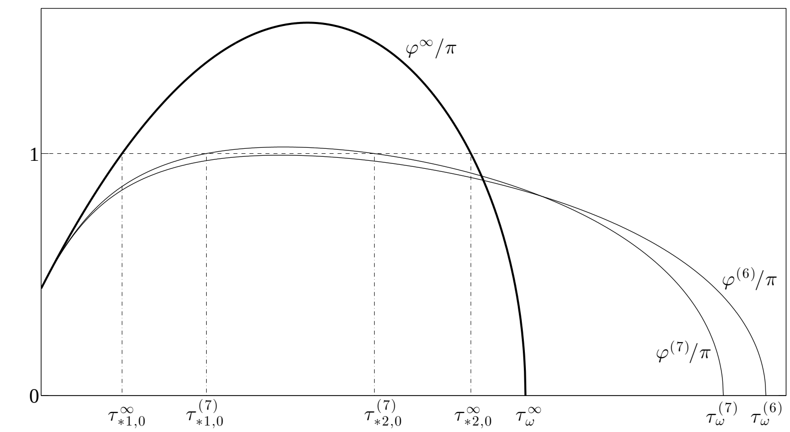

FIGURE 5. φ^{∞} in (30) (solid thick) and $\varphi^{(n)}$ in (57) for $n = 6, 7$ (solid thin) and $a = 7$, $b = 350$, $d = 0.5$, $d_1 = 1$: $\tau^{(7)}_{*1,0} = 1.5519\ldots$, $\tau^{(7)}_{*2,0} = 3.1303\ldots$, $\tau^{(7)}_{\omega} = 6.4109\ldots$ and intersections with π show that $n^* = 6$.

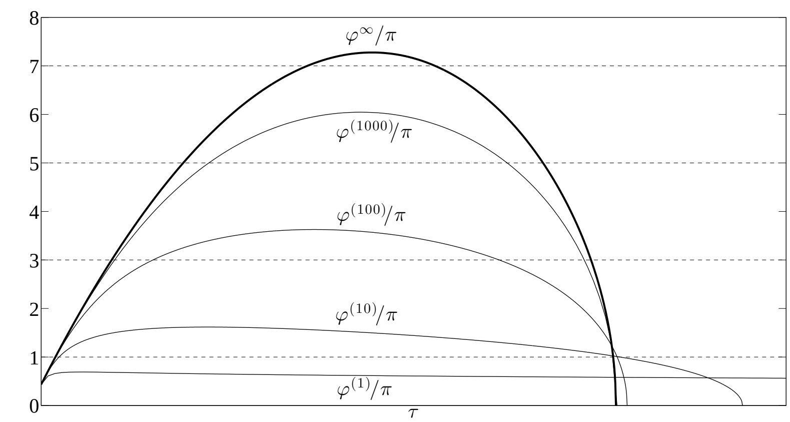

FIGURE 6. Theorem 4.5, φ^{∞} in (30) (solid thick) and $\varphi^{(n)}$ in (57) for $n = 1, 10, 100, 1000$ (solid thin) and $a = 7$, $b = 350$, $d = 1$, $d_1 = 0.25$.

First, a quantitative difference is evident: even if both the positive equilibria $N^{\infty}_{+}(\tau)$ and $N^{(n)}_{+}(\tau)$ assume the same value η/a for $\tau = 0$, it occurs that for any $n \in \mathbb{N}$, the existence domain of the latter is wider than that of the former being $\tau^{(n)}_{+} > \tau^{\infty}_{+}$ (and also $N^{(n)}_{+}(\tau) > N^{\infty}_{+}(\tau)$ for all $\tau \in (0, \tau^{\infty}_{+})$). This fact reflects on the relevant characteristic functions implying, e.g., that the delay domain where the stability switches may occur is wider for the continuous model rather than for the discrete one: $\tau^{(n)}_{\omega} > \tau^{\infty}_{\omega}$, see Figure 2 vs Figure 4 and Figure 3 vs Figure 5 and the relevant captions.

A more qualitative discussion follows. The equation ruling the evolution of the adults has a destabilizing contribution due to the maturation of the juveniles and a stabilizing contribution due to the death of the adults (with mortality d). The delay τ, responsible for the stability switches, is the juvenile maturation time. It cuts exponentially the juveniles contribution (with mortality d_1), either directly in the discrete model or through a distributed integral in the continuous model. Therefore, the destabilizing effect of the delay is as more evident as lower is the ratio d_1/d. This can be intuitively observed already by considering the complementary assumptions (A4) and (A5). Indeed they can be read as

(A4) $d_1/d \geq (d_1/d)_{\mathrm{c}}$;
(A5) $d_1/d < (d_1/d)_{\mathrm{c}}$;

for $(d_1/d)_{\mathrm{c}} := \eta(\eta-1)(\eta-2)$ and stability switches are possible only under the latter, while under the former both the positive equilibria $N_+^\infty(\tau)$ and $N_+^{(n)}(\tau)$ are locally asymptotically stable in their existence domains. Nevertheless, even when (A5) holds true, the effect of a reduced instability for increasing d_1/d can be appreciated. For the discrete model see Figure 2 and Figure 3 where, keeping $a = 7$ and $b = 350$ fixed, we have $d_1/d = 0.25$ in the former and $d_1/d = 2$ in the latter. In fact, in the former case the total multiplicity of roots with positive real part can reach the value $2(\bar{k}^\infty + 1) = 8$, whereas in the latter case the same value is bounded above by $2(\bar{k}^\infty + 1) = 2$. For the continuous model, the same phenomenon can be observed in Figure 4 and Figure 5 for the same values of the parameters: in the former $n = 3$ is sufficient to recover the stability switches for $d_1/d = 0.25$, whereas $n = 7$ is necessary in the latter for $d_1/d = 2$.

Moreover, given an adults mortality d, if the juveniles mortality d_1 is sufficiently high in the sense that (A4) holds, then the equilibria are asymptotically stable independently of the delay variance. Notice that in the inequality (A4) an essential role is played by the birth rate b through the parameter η. Opposite, when (A5) holds, which occurs by either increasing b or by diminishing d_1, the stabilizing effect of the delay variance increases as the ratio d_1/d decreases. Therefore, the difference in the stable/unstable behaviors of the discrete and continuous distributions is as lower as higher is the ratio d_1/d, keeping fixed all the other parameters.

Finally, let us give some further comments on the general validity of the presented study. The proposed research is based on the particular model (1), taken from [6] for its simplicity as a prototype of single species population growth. Therefore, we are not in the position of claiming general statements about general population growth and neither this was our intention. In fact, the present study is not sufficient to claim, e.g., that delay variance is *always* stabilizing. Opposite, the current outcome allows us to warn that in general, when data about delay variance and distribution are available, one should consider them carefully and incorporate them in the modeling process. Indeed, as shown for model (1), discrete and continuous formulations are not equivalent and the distributed framework appears more realistic and meaningful in the biological context. Instead, as for verifying a general potential stabilizing role of delay variance, we should extend the present investigation and relevant techniques to more general models such as, for instance, those systems typical of epidemiology (see, e.g., the SIS model in [4, §4]). We reserve to follow this direction in the future.

Future studies may be devoted also to the search of sharp estimates of n^* based solely on the values of the parameters.

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