



Long-term transients and complex dynamics of a stage-structured population with time delay and the Allee effect



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HIGHLIGHTS

- Long term transients (LTT) are known to play a crucial role in the dynamics of populations.
- LTT can be an alternative mechanism of ecological regime shifts as compared to the classical attractor-based explanation.
- Interplay between delay and the Allee effect can result in LTT leading to sudden regime shifts in a single species model.
- Our model shows a high complexity both in terms of its asymptotic dynamics and the basins of attraction of final states.

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ABSTRACT

Traditionally, mathematical modeling in population ecology is mainly focused on asymptotic behavior of the model, i.e. as given by the system attractors. Recently, however, transient regimes and especially long-term transients have been recognized as playing a crucial role in the dynamics of ecosystems. In particular, long-term transients are a potential explanation of ecological regime shifts, when an apparently healthy population suddenly collapses and goes extinct. In this paper, we show that the interplay between delay in maturation and a strong Allee effect can result in long-term transients in a single species system. We first derive a simple ‘conceptual’ model of the population dynamics that incorporates both a strong Allee effect and maturation delay. Unlike much of the previous work, our approach is not empirical since our model is derived from basic principles. We show that the model exhibits a high complexity in its asymptotic dynamics including multi-periodic and chaotic attractors. We then show the existence of long-term transient dynamics in the system, when the population size oscillates for a long time between locally stable stationary states before it eventually settles either at the persistence equilibrium or goes extinct. The parametric space of the model is found to have a complex structure with the basins of attraction corresponding to the persistence and extinction states being of a complicated shape. This impedes the prediction of the eventual fate of the population, as a small variation in the maturation delay or the initial population size can either bring the population to extinction or ensure its persistence.

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1. Introduction

Understanding the aspects and tendencies of complex population dynamics observed in natural ecosystems (Ellner and Turchin, 1995; Ranta et al., 1995; Widdicombe et al., 2010) as well as in the laboratory (Costantino et al., 1997; Yoshida et al., 2003; Becks et al., 2005) is important for both theoretical and practical reasons, and indeed it has been a central point of ecological research for several decades (Nicholson, 1954; Luckinbill, 1974; Turchin, 2003; Odum and Barrett, 2005; Begon et al., 2005). Whilst

empirical studies provide invaluable information such as, for instance, examples of different dynamics (Becks et al., 2005; Yoshida et al., 2003), a theoretical approach is necessary in order to generalize and systematize the results of field observations or lab experiments. In particular, mathematical modeling is proved to be an efficient research tool that helps to reveal ecosystem properties when replicated experiments under controlled conditions are not possible (Maynard Smith, 1974; Bjornstad and Grenfell, 2001; Turchin, 2003).

Mathematical analysis of population dynamics models usually focuses on asymptotic behavior, considering the existence and stability of steady states, limit cycles or more complex attractors. One reason for this is purely technical: mathematical models

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describing the system in the large time limit are often much simpler than the ‘full’ models accounting for transients. In particular, the first stage in a standard ‘protocol’ to explore the properties of a dynamical system is to reveal its stationary states; the corresponding ODEs become reduced to a system of algebraic equations. Another, more conceptual reason behind the traditional analysis is the assumption (often implicit) that the system will normally stay in the vicinity of an attractor, and hence the steady states’ analysis is representative of the system dynamics in general.

However, this traditional way of thinking has recently been challenged. There is a growing understanding that in natural ecosystems the asymptotic behavior is, in fact, rarely seen and their dynamics are essentially transient (Cushing et al., 1998; Hastings, 2001; Ims et al., 2008). Correspondingly, a big new challenge for theoretical ecology is to understand the implications of the transient dynamics (Hastings, 2004). This difficult task is exacerbated by the possibility of long-living transients and “ghost attractors” – when the population dynamics mimic the asymptotic behavior of one kind for a very long time before a sudden fast convergence to a different attractor (Lai and Winslow, 1995; Rodrigues et al., 2011).

Recently, considerable attention has been paid to the identification and prediction of “regime shifts” (Scheffer et al., 2001; Kéfi et al., 2014) – sudden changes that often result in species extinction and biodiversity loss. Understanding the mechanisms and scenarios of such shifts is thought to be important for efficient ecosystem management and nature conservation. There have been many reported cases when a species that has been present in apparently safe numbers goes extinct suddenly and seemingly without any warning (Scheffer et al., 2001, 2009; Carpenter, 2003). One general way to explain these cases might be to relate them to catastrophic changes in the ecosystem properties such as, in mathematical terms, the disappearance of a steady state as a result of saddle-node bifurcation (Scheffer et al., 2009; Boettiger and Hastings, 2012). Another scenario of regime shifts can be the existence of long-living transients, which provides an alternative explanation of sudden species extinction (Tilman et al., 1994; Schreiber, 2003). However, specific biological mechanisms and factors resulting in long living transients in various models using different mathematical frameworks often remain obscure (Hastings, 2004). Similarly, it remains unclear how model parameterization can affect its property to exhibit long-living transients as many widely used population dynamics models appear to be structurally unstable with regard to a small change in the constituent model functions (Fussmann and Blasius, 2005; Adamson and Morozov, 2013). In this paper our goal is to show that long-living transients mimicking complex dynamics are likely to be a common property of a conceptual, baseline single species population dynamics model.

The question that immediately arises is what sort of population dynamics model can be regarded as conceptual, but still realistic. Such a model should take into account some common, typical features of real-world populations but describe them in the simplest possible way, avoiding unnecessary details. Arguably, two typical properties of realistic populations are a *time delay* in reproduction and the *Allee effect*.

Time delays are widely recognized as an inherent feature of population dynamics (Beretta and Kuang, 1998; Hansen et al., 1998; May, 2001; Murdoch et al., 2003; Ruan, 2006). Triggered by Hutchinson seminal work (Hutchinson, 1948), there have been a large number of theoretical studies concerned with the implications of time delays for populations and communities (Hastings, 1984; Aiello and Freedman, 1990; Murdoch et al., 2003; Ruan, 2009). Time delays are thought to have a destabilizing effect as a sufficiently long delay often turns an otherwise stable positive steady state

unstable (Kuang, 1993; May, 2001; Ruan, 2006, 2009), and hence converts steady population densities into population cycles, although the generality of this scenario remains controversial, e.g. see Jankovic and Petrovskii (2014) and Sen et al. (2014).

Interestingly, in spite of the vast existing literature on time delayed population dynamics, some important issues remain poorly studied. Firstly, it remains unclear which modeling frameworks are biologically reasonable and, correspondingly, what should be the baseline model of single-species population dynamics. Earlier studies (Hutchinson, 1948; Aiello and Freedman, 1990; also Ruan, 2006 and references therein) were based on extensions of the logistic equation. However, as we will show below, this is only relevant if the maturation time is short. Secondly, the limits of dynamical complexity of time delayed dynamics remain unclear. Whilst delay-induced periodic population cycles are well known and well understood, it is still unclear whether a simple single species delayed system is capable to produce more interesting dynamics such as chaos and long-living transients.

The Allee effect, defined as a decrease in the per capita population growth rate at small values of the population density (cf. Dennis, 1989), is a common feature of ecological populations as it can result from several different mechanisms (Courchamp et al., 1999; Stephens and Sutherland, 1999). It is well known that its inclusion can modify the population dynamics significantly (Courchamp et al., 2008), leading to the emergence of long-living transients in particular (Rodrigues et al., 2011). However, most of the previous theoretical studies were done using instantaneous non-delayed models, leaving the interplay between the strong Allee effect and the time delay poorly understood (but see Jankovic and Petrovskii, 2014). Recently, a model incorporating both time delay and the Allee effect was considered by Liz and Ruiz-Herrera (2015) and the existence of long living transients for some specific values of delay and initial conditions was observed. However, the generality of their results remained unclear, in particular due to the phenomenon of sensitivity of biological models to parameterizations (Cordoleani et al., 2011).

In this paper, we show that the interplay between time lag and the Allee effect can result in complex dynamics and long-term oscillatory transient regimes in a single-species continuous-time population model. Depending on the parameter values and the initial conditions, the population size can exhibit oscillations around the unstable equilibrium keeping constant amplitude for a long time until it eventually settles to one of the two steady states of the system: extinction or persistence. In the context of real-world ecosystems, this means that a population showing apparently ‘healthy’ dynamics over years of observation can suddenly collapse and go extinct even in a perfectly stationary environment. This is in good agreement with previous studies (cf. Schreiber, 2003; Liz and Ruiz-Herrera, 2015). However, we also show that the parametric space of the system has a complicated structure, and the basins of attraction corresponding to persistence and extinction have complicated shapes, so that small variation of the time delay or the initial conditions can turn extinction to persistence and vice versa. Moreover, we show that the simple time-continuous single species system with the time delay and the Allee effect can exhibit long-living *chaotic transients*. Along with the transient dynamics we also investigate the long term asymptotic behavior of the model and show that it can exhibit a wide array of complex dynamics including multiple cycles, intermittent dynamic and chaos.

We also mention here that the population dynamics model that we use in this study is not empirical; instead, it is derived from certain first principles of the population dynamics. Contrary to the over-simplified Hutchinson model, it takes into account the existence of different life stages such as juveniles and adults, the rate of transition between the stages being affected by the maturation lag. Therefore, in our model the time delay appears naturally as a

result of a careful description of the population, rather than being “plugged in” based on purely heuristic arguments, as is often done in the literature (see [Sen et al., 2014](#) for some examples).

The paper is organized as follows. In [Section 2](#), we introduce our conceptual population dynamics model. In [Section 3](#) we study the properties of the model. Firstly, we fulfill a complete bifurcation analysis of the system's attractors ([Section 3.1](#)). Then, as adequate mathematical tools for analyzing transients are currently under-developed, we perform an exhaustive study of transients by extensive numerical simulations ([Section 3.2](#)). Finally, [Section 4](#) provides a discussion of our findings and concluding remarks.

2. Model equations

We use the general framework of age-structured populations by [Gurney et al. \(1983\)](#). Let us consider a single-species population with continuous reproduction, i.e. new offspring can appear at any time t . In order to take into account the effect of maturation, we develop a conceptual continuous-time model of a stage-structured population that consists of juveniles and adults. Adults are capable of reproduction and juveniles are not. Juveniles become adults after a maturation time τ .

Let us denote the densities of juveniles and adults at time t as $x(t)$ and $y(t)$, respectively. The rate of replenishment of the juveniles due to the reproduction of adults at time t (denoted by $[dx/dt]^+$ because it only takes into account replenishment, and not mortality of juveniles) is:

$$\left[\frac{dx(t)}{dt}\right]^+ = ry(t), \quad (1)$$

where r is the per capita reproduction rate that, in a general case, depends on the population density of adults (e.g. due to effects of competition). Correspondingly, the increase $\Delta x(t)$ in the density of juveniles because of the reproduction of the adults occurring over a small interval of time Δt is given by the following equation:

$$\Delta x(t) \approx \left[\frac{dx(t)}{dt}\right]^+ \Delta t = ry(t)\Delta t. \quad (2)$$

Let us now consider the change $\Delta y(t)$ in the population density of adults that occurs over the time between t and $t + \Delta t$. Obviously,

$$\Delta y(t) = \Delta y^+(t) - \Delta y^-(t), \quad (3)$$

where $\Delta y^+(t)$ is the increase in the density of adults due to the maturation of the juveniles and $\Delta y^-(t)$ is the decrease in the density of adults due to their mortality. We assume that the adults mortality is density independent with mortality rate D , so that

$$\Delta y^-(t) = Dy(t)\Delta t. \quad (4)$$

An increase in the density of adults occurs because of the maturation of juveniles. In the course of maturation, juveniles die with mortality rate δ . From the individuals $\Delta x(t)$ that are born between t and $t + \Delta t$, only a certain fraction survives and reaches the state of maturity:

$$\Delta x^+(t + \tau) = \Delta x(t)e^{-\delta\tau},$$

or, similarly,

$$\Delta x^+(t) = \Delta x(t - \tau)e^{-\delta\tau}. \quad (5)$$

Those who survive will leave the class of juveniles and enter the class of adults; therefore

$$\Delta y^+(t) = \Delta x^+(t). \quad (6)$$

From Eqs. (3)–(7), we obtain:

$$\Delta y(t) = \Delta x^+(t) - Dy(t)\Delta t = \Delta x(t - \tau)e^{-\delta\tau} - Dy(t)\Delta t. \quad (7)$$

Taking now into account (2), Eq. (7) takes the following form:

$$\Delta y(t) = ry(t - \tau)e^{-\delta\tau}\Delta t - Dy(t)\Delta t. \quad (8)$$

Recall that we have assumed Δt to be small, therefore $\Delta y/\Delta t \approx dy/dt$. From (7) and (8), we obtain the following delayed differential equation describing the population dynamics of the stage-structured population:

$$\frac{dy(t)}{dt} = re^{-\delta\tau}y(t - \tau) - Dy(t) \quad (9)$$

Note that Eq. (9) does not contain the density $x(t)$ of juveniles. Therefore, although a full description of the structured population dynamics should also include the equation for $x(t)$ (e.g. see [Aiello and Freedman, 1990](#)), the main properties of the system can be revealed based on the single Eq. (9). Once the solution of (9) is known, the density of juveniles can be obtained from Eq. (1). It is worth mentioning here that in the special case where the maturation time is negligible, i.e. $\tau = 0$, Eq. (9) coincides with the standard single species model of unstructured population dynamics.

The last issue to decide is the type of the density dependence in the per capita reproduction rate, i.e. the parametrization of function $r(y)$. A generic property of the population dynamics is that, for sufficiently large values of the population density y , the per capita reproduction rate r should be a decreasing function of y as a result of the competition for resources and/or space (e.g. [Begon et al., 2005](#)). Furthermore, we recall that, for the reasons explained in the introduction, we want our model to take into account the Allee effect. The defining property of the Allee effect is that the per capita reproduction rate reaches its maximum value at a positive value of the population density (i.e. not for $y \rightarrow +0$ as it happens in the case of logistic growth). Therefore, for the purposes of this study, function $r(y)$ should have a local maximum, which means that the graph of the function is dome-shaped.

There are numerous mathematical parameterizations of the per capita reproduction rate $r(y)$ that satisfy the above requirements, e.g. see [Boukal and Berec \(2002\)](#). In order to make our results comparable with some other relevant studies, we consider function $r(y)$ as follows:

$$r(y) = \frac{\alpha y^{n-1}}{1 + \beta y^m}, \quad n < m, \quad (10)$$

where α , β , n and m are positive parameters. Function (10) is therefore an immediate generalization of the parameterizations earlier used by [Jacobs \(1984\)](#) and [Takeuchi \(1996\)](#). Here the coefficient α characterises the reproduction rate at low population level and the coefficient β characterises the strength of intraspecific competition. The exponents n and m quantify the strength of the density dependence at small and large population density, respectively; the condition $m > n$ is required to ensure that the reproduction rate vanishes at large y . It is readily seen that, in order to make sure that our models (9) and (10) includes the strong Allee effect in the limiting case $\tau = 0$, the exponent n must be larger than one; correspondingly, below we choose $n = 2$. Thus, we arrive at the following equation for the population density of adults:

$$\frac{dy(t)}{dt} = \alpha \frac{y^2(t - \tau)}{1 + \beta y^m(t - \tau)} \exp(-\delta\tau) - Dy(t) \quad (11)$$

For the sake of simplicity, we keep the adult mortality rate D to be constant. Also, for convenience, in the rest of the paper we consider $A = \alpha \exp(-\delta\tau)$ as a fixed parameter. This will allow us to complete an exhaustive analysis of possible dynamical regimes. Note that fixing $A = \text{const}$ can be also considered as a particular ecological scenario in which the mortality of juveniles is assumed to be small, i.e. $\tau\delta \ll 1$, so that $A \approx \alpha$.

Finally, to reduce the number of parameters in the model we shall consider a dimensionless version of (11) with only three

parameters g , τ and m :

$$\frac{dy(t)}{dt} = \frac{y^2(t-\tau)}{1+y^m(t-\tau)} - gy(t), \quad (12)$$

where $g = D\beta^{1/m}/A$ and the 'new' dimensionless delay is obtained from the original dimensional delay by multiplying it by factor $A/(D\beta^{1/m})$.

Eq. (12) must be complemented with the initial conditions, or "history", given by $y(t) = \theta(t)$, $-\tau < t \leq 0$, where $\theta(t)$ is a non-negative function. In the numerical simulations, for the sake of simplicity, we consider the case where the population was initially in a steady state, so that $\theta(t) = y_0 = \text{const}$. Numerical simulations of (12) were performed using a standard explicit Euler scheme with a sufficiently small time step ($h = 0.0001$): the required accuracy was verified by reducing the time step and comparison of the simulation results.

3. Simulations and results

3.1. Dynamical attractors of the model

We start our investigation of the model by exploring the system attractors, which describe the population dynamics in the large-time limit.

The model may have up to three stationary states y_1 , y_2 and y_3 (see Appendix A). The extinction state $y_1 = 0$ always exists and is always locally attractive for any $\tau \geq 0$. This signifies that the population will eventually go extinct if its density during time τ is low. In the case where the mortality g is sufficiently small, there can be two extra stationary states: y_2 and y_3 ($y_2 < y_3$). The intermediate state y_2 is always unstable, whereas the upper state y_3 (we shall call it the persistence stationary state) can be either stable or unstable depending on the magnitude of the delay. In the absence of delay, y_3 is always stable and we thus have a bi-stable model, which is equivalent to the classical population model with a strong Allee effect based on the cubic polynomial parametrization (cf. Lewis and Kareiva, 1993). For a supercritical delay τ , the persistence stationary state y_3 may lose its stability. This occurs only for small and intermediate mortality rates g (Appendix A), whereas for larger values of g (in the case where y_3 still exists) this state remains stable for any delay τ , thus it is absolutely stable.

The bifurcation portrait of the model in the (g, τ) plane is shown in Fig. 1, which is constructed for $m = 4$. The portrait is obtained from numerical simulation of (12) over a long time ($t > 2000$) after removing the initial transient dynamics. Also, we use analytical results to plot the local bifurcation curves H and L (see Appendix A). Different colors and numbers of the domains correspond to different dynamical regimes. The vertical line L is a saddle-node bifurcation curve: in domain 1 only the stationary state is the extinction $y_1 = 0$. In domain 2, the system is bi-stable with locally stable states y_1 and y_3 . Delay-induced destabilization of y_3 takes place on the Hopf bifurcation curve H , when entering domain 3, and results into the appearance of a stable limit cycle around y_3 . A further increase in τ results in complex sustained oscillations around y_3 . The complexity of the oscillatory dynamics can be characterized by the number of consecutive local maxima of $y(t)$ through the oscillation period, which is depicted by various colors.

Fig. 2 provides the cross section of Fig. 1 constructed for $g = 0.15$ and shows the density of species at consecutive local maxima of oscillations. Two main types of bifurcations are observed in the delay destabilized model: (i) peak-adding bifurcations and (ii) period-doubling bifurcations. Examples of the two types of bifurcations are shown in Fig. 3. In a peak-adding bifurcation a supplementary local maximum of $y(t)$ emerges (Fig. 3a and b) and the period of oscillations is conserved at the moment when the

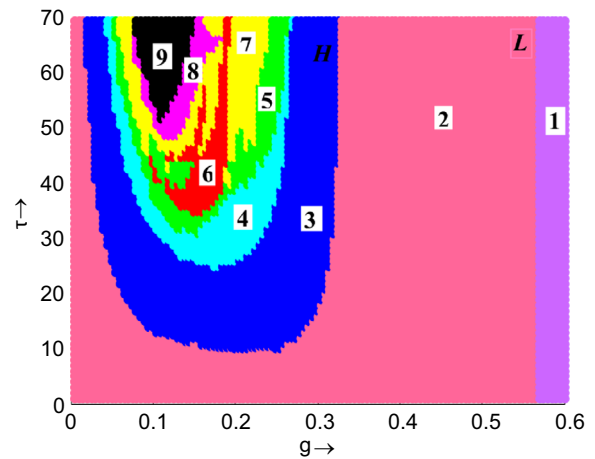


Fig. 1. Bifurcation diagram in the (g, τ) plane showing the attractors of the delay model (12) constructed for $m = 4$. The curve L is a saddle-node bifurcation curve and H is a Hopf bifurcation curve. The domains have the following meaning: domain 1 – the only stable stationary state is $y_1 = 0$; domain 2 – bi-stability with the stable stationary states being $y_1 = 0$ and y_3 ; domain 3 – stable stationary state y_1 and a stable limit cycle around y_3 ; domains 4–8 – stable stationary state y_1 and periodic oscillations around y_3 with the number of local maxima in the period is 2, 4, 6, 8 and > 8 , respectively; domain 9 – stable state y_1 and chaotic oscillations around the unstable stationary state y_3 . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

bifurcation occurs. The main benchmark of this bifurcation is the sudden, discontinuous appearance or disappearance of new branches of local maxima of $y(t)$ in Fig. 2. In the $y(t) - y(t - \tau)$ plane, a peak-adding bifurcation corresponds to a loop formation on the null-cline of the system shown in red (see Fig. S1 in Appendix B). On the other hand, a period doubling bifurcation is characterized by an increase of the period of oscillations by the factor of 2, which is shown in Fig. 3c and d. The corresponding $y(t) - y(t - \tau)$ plane diagrams are provided in Fig. S2 in Appendix B. The number of peaks in this bifurcation remains the same and a discontinuous appearance of new branches of local maxima of $y(t)$ is not observed.

An increase in the magnitude of the time lag τ results into a set of peak-adding bifurcations combined with period doubling bifurcations (see Fig. 2) and eventually, the interplay between these two types of bifurcation leads to highly irregular oscillations of species density, without any apparent periodicity. This is observed for intermediate time delays. A thorough investigation of those patterns reveals that the dynamics are highly sensitive to initial conditions, which indicates that the irregular oscillations of species density are chaotic (see Fig. S3 in Appendix C): initially close trajectories will eventually diverge exponentially because the leading Lyapunov exponent is positive. In the (g, τ) diagram (Fig. 1) the domain corresponding to chaotic regime is depicted in black. One can see that the delay-induced chaos in the system can be observed only within limited range of the other model parameter g . It is also worth noting that the boundaries of the domains corresponding to complex multi-periodic and chaotic regimes in the (g, τ) diagram appear to be simple, this is an effect of a coarse resolution. A finer resolution would reveal fractal boundaries between these domains, but research into the fractal structure of the (g, τ) diagram is a separate topic for investigation and should be done elsewhere.

Finally, we should emphasize that sustained oscillations occur only in the case where the initial species density is sufficiently high, otherwise, the population will eventually go extinct. In the infinite dimensional functional space given by $y(t) = y_0(t)$ for $-\tau < t \leq 0$, the basin of attraction of the extinction state and persistence dynamics is rather complex. We will address this interesting issue in the next section.

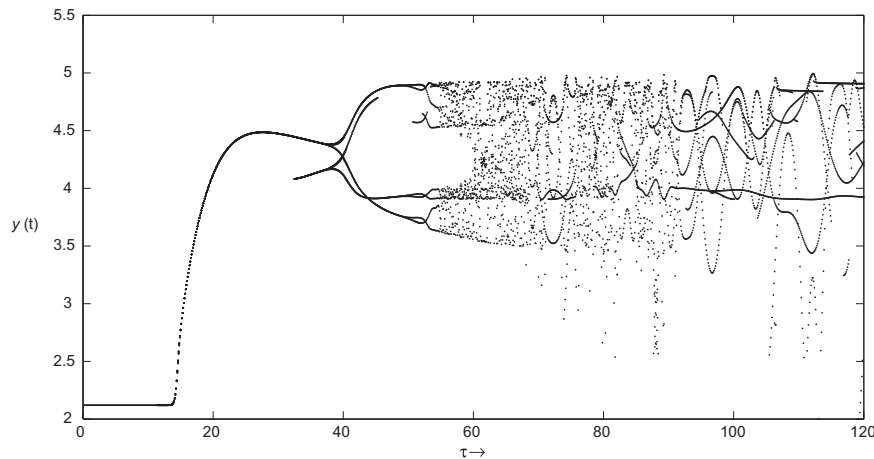


Fig. 2. Cross section of the diagram shown in Fig. 1 constructed for $g=0.15$. We show points of consecutive local maxima of $y(t)$ through oscillations. The two main types of bifurcations are illustrated in Fig. 3.

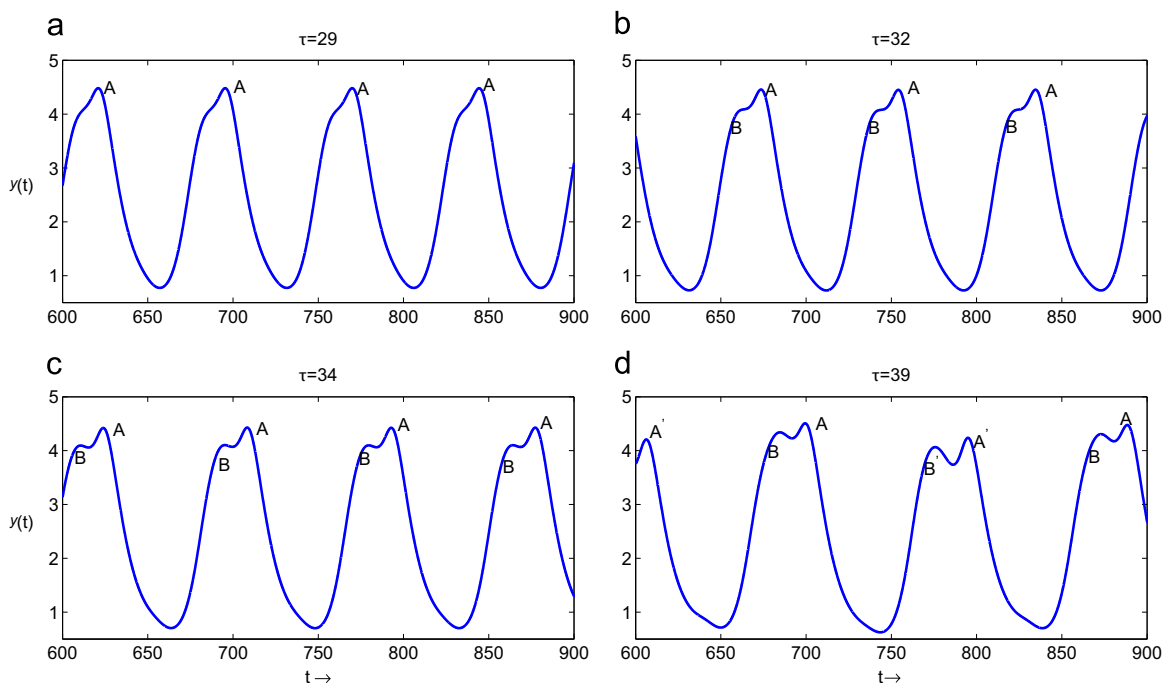


Fig. 3. Two main types of non-local bifurcations in the delay model. (a,b) peak-adding bifurcation: a supplementary local maximum emerges at point B. (c,d) period-doubling bifurcation: the period of oscillations increase by a factor of 2 with only small changes in the shape of the trajectory $y(t)$ (compare A, B and A', B'). The model parameters are $g=0.15$, $m=4$.

3.2. Long-term transient population dynamics

Extensive numerical simulation of the model shows that for large time interval – potentially up hundreds of generation times of the population, but of finite length – the patterns of population dynamics can be substantially different from those corresponding to the eventual system attractors.

We start our exploration of transient dynamics with the case that the persistence stationary state is absolutely stable, i.e. when the state y_3 cannot be destabilized for any $\tau > 0$. Thus, there can be only two long term outcomes of dynamics, depending on the initial conditions: (i) the system settles on the persistence state y_3 or (ii) goes towards the extinction state $y_1=0$. Since the initial conditions of the system belong to the infinite dimensional functional space $y(t)$, $-\tau < t \leq 0$, we consider for the sake of simplicity that $y(t) = y_0 = \text{const}$ for $-\tau < t \leq 0$. Our simulation shows that starting from very low initial densities y_0 , the trajectory quickly

approaches the extinction state since the mortality rate is higher than reproduction rate. The same holds for very high initial densities y_0 since the mortality rate again is larger than the reproduction rate and the population densities quickly drop to low values with a further extinction. On the other hand, for values of y_0 sufficiently close to y_3 , the trajectory quickly settles on this state.

On the other hand, for some intermediate range of initial densities y_0 the population dynamics exhibit substantially different behavior: the population size shows long term oscillations around the unstable state y_2 . Interestingly, after a few initial fluctuations (see Fig. 4) the amplitude of oscillations becomes quasi constant over a long time period (up to 20–40 periods of oscillations) and suddenly the trajectory returns to one of the final stationary states. This pattern of dynamics can be considered as a transient limit cycle, where the trajectory initially approaches the cycle, remains on it for a while with constant amplitude and finally leaves the cycle. The duration of the transient oscillations depends

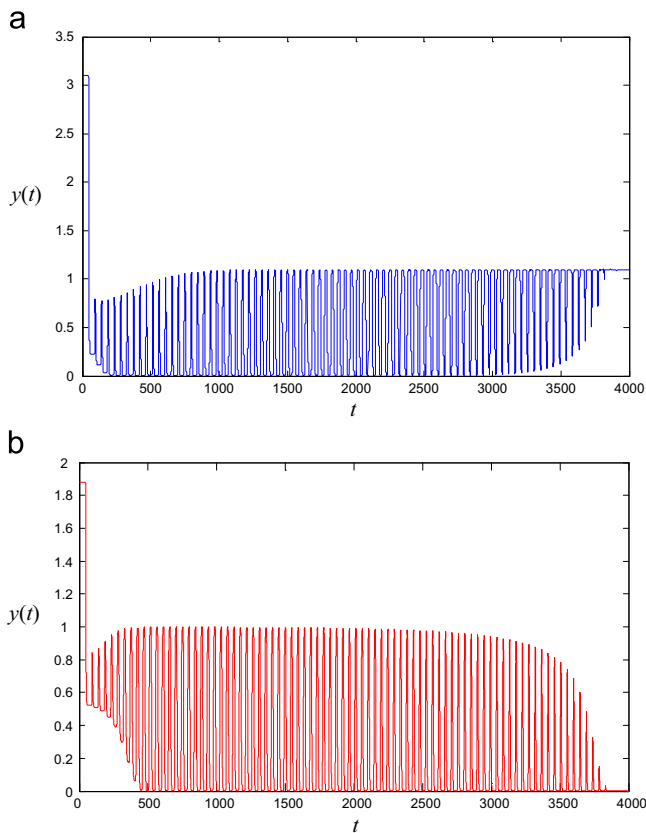


Fig. 4. Long term transient oscillations in the delay model in the case where the final attractors are stationary states. The population size exhibits long term oscillations with quasi-constant amplitude around the unstable equilibrium y_2 before finally approaching either the persistence equilibrium (a) or extinction equilibrium (b). The model parameters are $m=4$, $\tau=45$ for both curves. However, $g=0.45$ is for solution (a) and $g=0.5$ is for solution (b).

on the time delay τ and the initial condition y_0 . Fig. 5 (left column) shows how N , the number of transient oscillations before the trajectory finally settles on the stable state, depends on y_0 and τ . Note that when constructing Fig. 5 we count only large supercritical oscillations and disregard relaxation oscillations. From this figure, one can see that the dependence of N on the magnitude of the delay is not monotonic: for small τ the system behaves as a classical bi-stable population model and the population size quickly approaches to one of the stable states, depending on the initial density y_0 . For sufficiently large τ , the population sizes also quickly approach the stationary large, but for some intermediate delay values we should expect the existence of very long-term transient limit cycles.

It is interesting to consider how the final destinations of the trajectories depend on y_0 and τ , which is shown in the right column of Fig. 5. Dark blue corresponds to the eventual extinction of the population whereas red indicates that the system will be at the persistence state. Within the chosen range of the initial density y_0 , and given parameter values, the delay-free model always predicts persistence of the population since we always have $y_3 < y_0$, but adding a supercritical delay may cause the extinction of the population. The basins of attraction of y_1 and y_3 have a complex structure showing intermittency of red and blue stripes, thus a graduate increase in the magnitude of delay can potentially result in either extinction or rescue of the population.

We also investigated the dependence of the transients and long term asymptotic dynamics on the other model parameter m , which accounts for the strength of the Allee effect in the model. We found that an increase in m leads to shrinking of the whole

bifurcation diagram in the (g, τ) plane, but the main bifurcation structure remains qualitatively similar to the one shown in Fig. 1. We also found long-term transient oscillations for $m=6, 8, 10$ similar to those observed in Fig. 4. We can therefore conclude that the long-term transients in the model are robust to a variation of parameters in terms of τ and m as well as the initial condition y_0 .

Finally, long-term transient oscillations of the population size are not only observed in the case when the state y_3 is stable but also in the case where y_3 loses its stability and the final attractor is a limit cycle or chaotic attractor. Fig. 6 shows an example of a long-living transient population cycle around the unstable saddle state y_2 . In Fig. 6A, the final attractor is the periodic limit cycle. Here the amplitude of the transient oscillations remains constant whereas the shape of the oscillations gradually changes and finally the trajectory quickly approaches the system attractor- the stable limit cycle. More complex transient oscillations occur in the case where the eventual attractor is chaotic, as is shown in Fig. 6B. One can see that the shape of the transitional oscillations around y_2 is highly irregular, particularly concerning the population densities near the peaks; the drop of the population density to low values is still periodic, however. Analysis of time series of such transient dynamics can be a challenge since conclusions about the periodicity or chaoticity of the system will depend on the way the data points are chosen. The basins of attractions of the extinction and oscillatory states in the τ - y_0 plane also show a high degree of complexity, thus small fluctuations in τ or y_0 can substantially change the long term fate of the population. We do not show these basins of attraction in the τ - y_0 plane here for the sake of brevity.

4. Discussion

In this paper, we have explored how the interplay between effects of maturation and the strong Allee effect can shape the population dynamics. Our motivation for this study was to build a minimal model that would account for some of the most common features of population ecology whilst remaining capable of simulating sufficiently complex dynamics including long-living transients and chaos that are thought to play an important role in ecology. Our model is conceptual because it omits unnecessary details, yet it is realistic in the sense that it overcomes the shortcomings of the logistic equation where individuals start reproducing immediately after they are born, which is clearly unrealistic.

Contemporary theoretical ecology relies heavily on predictions and inferences from mathematical modeling, and over the last several decades a great variety of models of various complexity have been developed ranging from very simple to very complicated. There has been considerable experience gained, and there is currently a good understanding as to what a “realistic” model should be (multi-species, multi-scale, hybrid, etc.) to describe the population dynamics of given species in sufficient detail, although the limits of modeling complexity remain a controversial issue (Pascual, 2005; Adamson and Morozov, 2014; Petrovskii and Petrovskaya, 2012; Morozov and Petrovskii, 2013).

Ironically, the situation appears to be less clear at the other end of the spectrum, i.e. with simple conceptual models. Such models do not claim to have much predictive power or to embrace all the details, but are instead used to reveal some basic, fundamental properties of the ecological dynamics. Talking specifically about the population dynamics of a species with overlapping generations, the logistic equation used to be regarded as a minimum sensible model, and does indeed well describe the properties of some simple systems such as, for instance, a single-species algae population with one limiting resource (Brezonik, 1993; Scheffer, 1998; Yang et al., 2011).

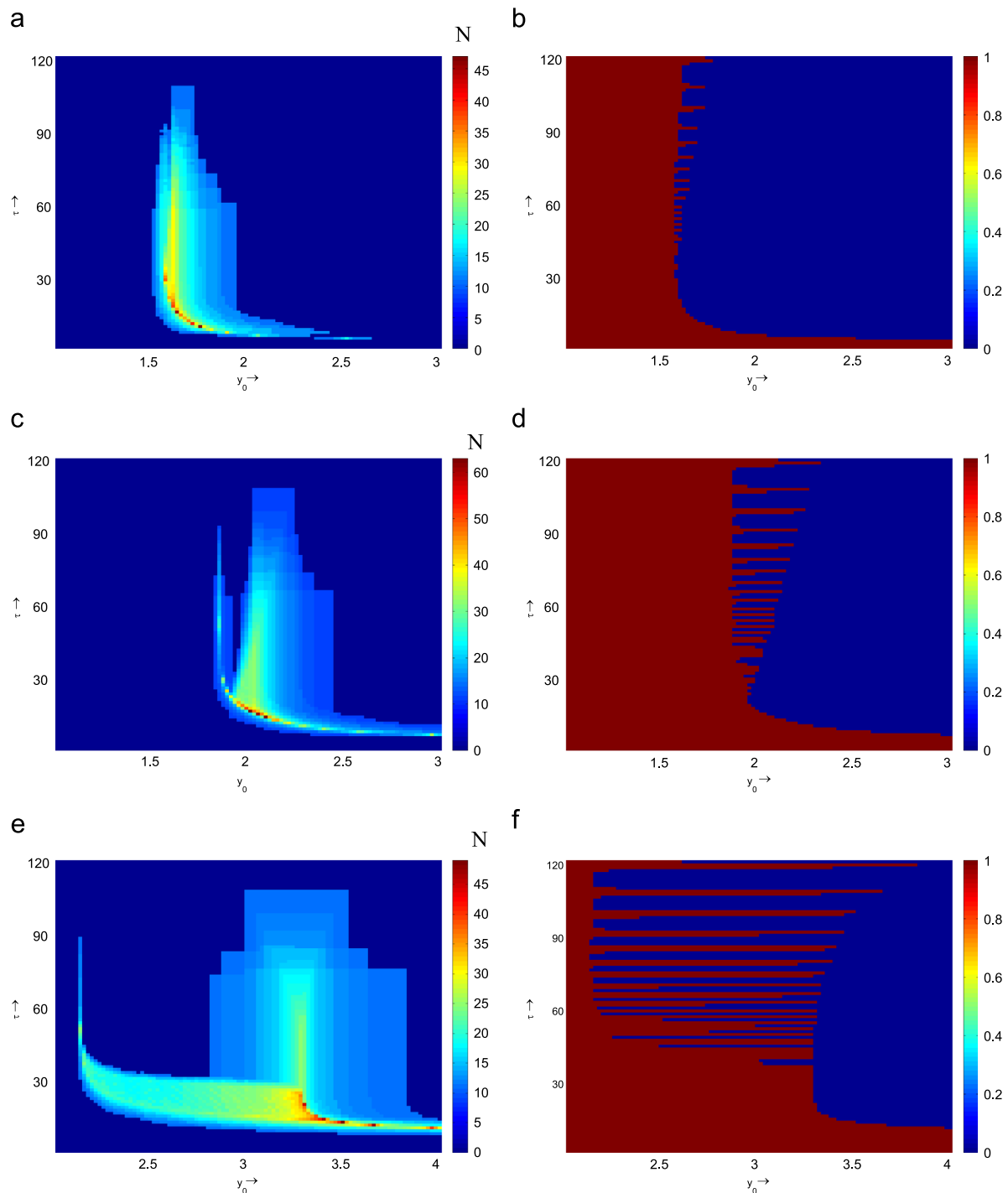


Fig. 5. Dependence of transient oscillations on the initial density y_0 and the value of delay τ . Left hand column: in each diagram the number N of large amplitude transient oscillations is shown. We count only those oscillations with $y_{\min}(t) < 0.95y_3$ and $y_{\max}(t) > 1.05y_3$, thus excluding small amplitude relaxation oscillations around the stationary states. The diagrams (a)–(c) are constructed for $g=0.55, g=0.5, g=0.45$, respectively. Right hand column: basins of attractors of y_1 (extinction) and y_3 (persistence) states are shown, depicted by red and dark blue, respectively. The diagrams (d)–(f) are constructed for $g=0.55, g=0.5, g=0.45$, respectively. The other model parameter is $m=4$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The logistic equation, however, predicts only very simple dynamics, such as monotonic convergence to a steady state, and this is clearly at odds with the complexity of the dynamics observed in natural populations where sustained oscillations are much more typical (Ranta et al., 1995; Cushing et al., 2003; Turchin, 2003; Sherratt and Smith, 2008). This is of course hardly surprising, as the logistic equation obviously leaves many things out of focus; in particular, it assumes that offspring start reproducing the moment they are born and are born immediately after

they are conceived. The question arises as to how the logistic equation can be modified in some minimal way to keep the model as simple as possible yet make its properties nontrivial. One way to do this was suggested by Hutchinson in his seminal paper (Hutchinson, 1948) where he showed that taking into account competition during gestation by including a time delay changes the model properties significantly, so that for a sufficiently long delay the population oscillates rather than converges.

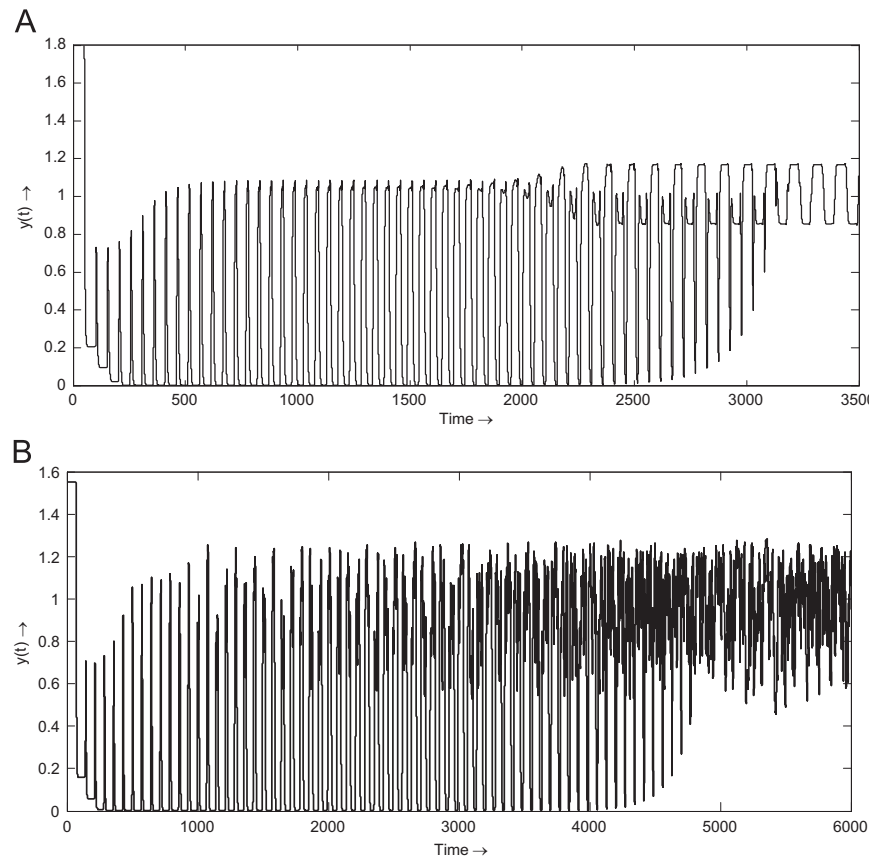


Fig. 6. Long term transient oscillations in the model in the case where the persistence attractor is non-stationary. (a) The final attractor is a limit cycle. The model parameters are $m=6$, $g=0.45$, $\tau=50$, $y_0=1.8$. (b) The final attractor is chaotic. The model parameters are $m=8$, $g=0.44$, $\tau=70$ and $y_0=1.55$.

Hutchinson's paper (1948) was hugely influential, eventually resulting in a vast number of publications exploring the effects of time delays in population dynamics, e.g. see Cushing (1977), Gopalsamy and Ladas (1990); Kuang (1993), Smith (2011) and the references therein. Yet despite this it can hardly be regarded as a sensible model – even as a conceptual model – for the following two reasons. First, like the logistic equation it still assumes that offspring start reproducing immediately after their birth. And second, the inclusion of the time delay into Hutchinson's equation is purely heuristic. Whilst it does not result in much ambiguity in the case of logistic-type growth, it immediately leads to a problem if the Allee effect is present. In this case, it is not clear where the time delay should be included, and its inclusion into different parts of the equation can have a very different effect (Jankovic and Petrovskii, 2014). Correspondingly, our goal in this paper is to derive the simplest sensible model accounting for maturation time. This was done in Section 2. We should mention that an equation similar to our Eq. (12) but without the Allee effect, was first considered (but not derived) in the context of medical applications and is often referred to as the Mackey–Glass model (Mackey and Glass, 1977). The Mackey–Glass model is known to have rich dynamics including periodic, multi-periodic and chaotic oscillations (Mackey and Glass 1977). In this paper, we have shown that the modification of the Mackey–Glass model that includes the strong Allee effect preserves the dynamical complexity of the original model but, additionally, is also capable of producing long-living transients (see Figs. 4 and 6) and intermittent dynamics.

Note that in nonlinear models the evidence for regime shifts as a result of long living transients can be demonstrated mainly by numerical simulations. Thus, searching for long living transients in various specific systems is currently the main methodology to explore this complex phenomenon, with the goal to collect

evidence of how widespread such dynamics are in population models. This is especially important taken into account the well-known property of structural sensitivity of biological models, where very close mathematical models using different parameterizations of functions can predict completely different patterns of population dynamics (Fussmann and Blasius, 2005; Cordoleani et al., 2011; Adamson and Morozov, 2014). Interestingly, long-term transients were obtained in another delay model using a different parameterization of the Allee effect (i.e. based on an exponential decay of the growth rate at large density y ; see Liz and Ruiz-Herrera, 2015). Therefore, the existence of long living transients seems to be a robust property of this class of models. We mention here that, for an exhaustive comparison between the two models using different parameterizations, one should also investigate the dependence of the trajectories' final destination on the initial conditions and the maturation delay. Unfortunately, such dependence was not investigated by Liz and Ruiz-Herrera (2015). However, it has been done in this paper for our model (12) where the complex structure in (y_0, τ) parameter plane has been demonstrated (see Fig. 5). Another interesting feature which we found in model (12) and, which needs to be verified in other similar models, is that long term transients occur even in the case where the final attractor is complex, for instance when it is chaotic (Fig. 6B).

Based on the rich behavior of our model, and taking also into account the clear and arguably ecologically sensible assumptions behind its derivation, we conclude that Eq. (11) (or simplified Eq. (12) in dimensionless variables) would make a good candidate to replace the logistic equation and the Hutchinson equation as the "minimum conceptual model" of population dynamics. In particular, the existence of long-living transients (including chaotic transients) is one of the main properties that makes Eq. (12) interesting and relevant. Long-

living transients are increasingly recognized as an important property of ecological dynamics (Hastings, 2001, 2004) but the mechanisms resulting in them largely remain obscure. It is not even clear whether transients are a common property of natural ecosystems or whether it is an exotic phenomenon. In this paper, we have shown that long-living transients can arise from the interplay between the strong Allee effect (as determined by the sigmoidal shape of the per capita growth rate $r(y)$, see Eq. (10)) and the time delay. The presence of the time delay in the growth term in our model is not an assumption but a well-established fact: as is shown by the model derivation, it takes into account maturation which is a basic property of all biological species. We therefore conclude that, somewhat counter-intuitively, the existence of long-living transients is an inherent property of any species whose population growth rate is affected by a strong Allee effect.

Appendices A, B and C. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2016.02.016>.

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