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ORIGINAL ARTICLE

Periodic Oscillations and Transient Dynamics Caused by Saturating Density-Dependent Benefits and Costs in Obligate Mutualisms

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Abstract

It is generally recognized that oscillatory dynamics of mutualism systems arise from external factors such as environmental fluctuations and additional interspecific interactions. However, we here theoretically demonstrate that the saturating density dependence of mutualistic benefits and costs can lead to the periodic oscillations of obligate mutualism systems. This suggests that the dynamic complexity of mutualisms can also arise intrinsically. Our model differentiates benefits in mutualistic interactions from costs and assumes they respectively influence the reproduction rate and mortality of populations. In the symmetric case, where the model structure and parameters are the same for both species, this model shows multiple equilibria and oscillatory dynamics. The difference between benefit and cost may be the primary determinant of these phenomena. The system exhibits damped or periodic oscillations when this difference is intermediate. The two species can stably coexist when benefits significantly outweigh costs, whereas the system faces extinction when costs become relatively high. Asymmetry in benefit and cost between mutualists dramatically changes the system's dynamical regimes. Essentially, these oscillations of mutualism are caused by the transitions of the system between mutualism and antagonism. In addition, our model reveals the transient dynamics of the mutualism system (a phenomenon of regime shift without parameter change), including saddle crawl-bys (moving slowly by saddles) and ghost attractors (slow change in system state near the attractors). Our findings highlight the crucial role of nonlinear benefits and costs in the dynamical complexity of mutualisms.

Keywords Oscillation · Transient dynamics · Mutualism · Density dependence · Nonmonotonic interaction · Complexity

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Extended author information available on the last page of the article

1 Introduction

Understanding the complex dynamics of ecological systems is central in ecology (Elton 1924; May 1974, 2001; Huisman and Weissing 1999; Stenseth 2003). It is widely recognized that complex population dynamics such as oscillations are characteristic of predator–prey, parasite-host, and disease interactions, and can be driven intrinsically by the complex feedbacks of species interactions (May 1972; Gilpin 1975; Morris et al. 2003; Neuhauser and Fargione 2004; Stone et al. 2007; Chaffee and Kuske 2011). However, a body of work shows that mutualism systems can also exhibit oscillatory dynamics in space and time, rather than stable coexistence or extinction as predicted by previous theoretical models (Addicott 1978; Gilpin et al. 1982; Holland 2015; Hale and Valdovinos 2021). In contrast to the endogenous effects of predator–prey systems that lead to oscillations, existing theoretical studies typically attributed oscillatory phenomena in mutualism systems to exogenous effects of other ecological factors, such as environmental fluctuations (Wang and Wang 2022), time delay (Yan and Li 2007), age-structure (Morozov et al. 2016) or additional species interactions (predation, parasitism, competition) (Bronstein et al. 2003; Mougi and Kondoh 2014; Mitani and Mougi 2017; Vazquez and Barradas 2018; Wang 2013; Chen et al. 2020). However, experimental works have found that oscillatory dynamics can take place in purely mutualism systems (Wang et al. 2011; Yurtsev et al. 2016), and Holland and DeAngelis (2010) also theoretically predicted the occurrence of population fluctuations in the absence of external biotic or abiotic factors by the consumer-resource approach. Therefore, understanding how mutualisms trigger dynamic complexity becomes a basic problem in ecology. We here explored the role of the density dependence of mutualistic benefits and costs in leading to the oscillations of mutualism systems, and found transient dynamics in mutualism.

Theoretical studies traditionally focus on the final dynamics around the system attractors, such as steady state, extinction, or more complex limit cycle dynamics or even chaos, while largely disregarding the effect of transient dynamics (Addicott 1981; Stone 2020; Valdovinos et al. 2023). However, unlike the long time scales implied by equilibrium dynamics in mathematical models, experimental observations and management of ecological mutualism systems typically focus on relatively short time scales (Hastings 2004, 2016), and thus we are unable to distinguish whether the oscillatory dynamics observed in natural ecological systems over a finite time course are true limit cycles or unstable transient oscillations. In addition, transient oscillations may persist over very long time periods and are functionally indistinguishable from stable periodic oscillations, but they are not the stable long-term dynamics that would eventually emerge (Morozov et al. 2020). An ecosystem in transient dynamics will suddenly transition to another state or regime at a certain point, even if the environmental conditions (parameters) don't undergo any changes (Hastings et al. 2018). Therefore, focusing solely on the asymptotic behavior of ecological models without considering transients would be misleading for predicting future states and explaining past observations of natural mutualism systems (Hastings 2001; Abbott et al. 2021; Morozov et al. 2023; Pakdaman et al. 1997; Francis et al. 2021).

In this study, we developed a general two-species mutualism model to explore the asymptotic and transient dynamics of mutualism interactions. Specifically, we extended classical Lotka-Volterra dynamics with saturating density-dependent benefits and costs based on the consumer-resource interactions. We analyzed symmetric and asymmetric mutualistic interactions and demonstrated that the saturating density dependence of benefits and costs can lead to periodic oscillations and long transients in obligate mutualism systems. Our results provide an alternative endogenous explanation for the complex dynamics of mutualism systems and have significant implications for maintaining species coexistence and community stability in ecosystems.

The rest of this paper is organized as follows. In Sect. 2, we introduce the biological background of mutualism and formulate a general two-species mutualism model. In Sect. 3, we study the properties of the model. First, we mathematically analyze the existence and local stability of the interior equilibria of the system (Sect. 3.1). Second, we perform an exhaustive study of the steady state and global dynamics of the system for different model parameters through extensive numerical simulations (Sect. 3.2). Finally, in Sect. 4, we discuss our results and present our concluding remarks.

2 Model

Mutualism is an interspecific interaction in which species exchange resources or services (Holland and DeAngelis 2010). It is broadly classified into resource-resource exchange mutualism (e.g., mycorrhizal fungi and their plant hosts provision nutrients to each other) and resource-service exchange mutualism (e.g., pollination and seed dispersal benefit the plants through the provisioning of reproductive services by the animals, while the animals benefit from food resources) (Bronstein 2015; Hammerstein and Noë 2016; Johnson and Bronstein 2019). These exchanges essentially involve energy or time transfer, directly or indirectly affecting the reproduction and survival of mutualists (Heinrich 1972; Flatt and Weisser 2000; Bronstein 2001; Holland 2002; Thompson et al. 2006; Hale and Valdovinos 2021).

Provisioning resources or services (mutualistic costs) reduces the provider's survival and/or reproduction due to the energy and time spent. For example, energy investment in nectar and other food reward production reduces plant reproduction (Harder 1992; Pyke and Ren 2023); energy expended on patrolling and tending fungal gardens increases the mortality rate of leaf-cutter ants (Kang et al. 2011); and the energy consumed by animals in performing pollination services reduces their reproduction or survival (McCallum et al. 2013). On the other hand, acquiring resources or services (mutualistic benefits) increases a species' per-capita birth rate or decreases its per-capita death rate (Holland and DeAngelis 2010; McCallum et al. 2013). Furthermore, the supply of resources and services is constrained by the availability of energy and time, making them depletable (Cushman and Addicott 1989; Cushman and Whitham 1991; Ferriere 2002; Fewell 2016). This limitation imposes additional density-dependent self-limitation on the recipient species via intraspecific competition for these benefits (Palmer et al. 2003; Johnson and Amarasekare 2013).

Both benefits and costs depend on the population densities of the interacting species (Addicott 1979; Cushman and Whitham 1989; Breton and Addicott 1992; Morales 2000; Holland and DeAngelis 2006). These density dependencies are typically modeled as functional responses, taking either linear (Type I) or saturating (Type II) forms

(Holland and DeAngelis 2001; Holland et al. 2002; Hale and Valdovinos 2021). Holland et al. (2002) and Hale and Valdovinos (2021) showed that mutualistic systems with linear benefits and costs can exhibit extinction, stable coexistence, or unbounded growth, but cannot generate complex population dynamics (we also provide proof in "Appendix A"). Indeed, saturating functional responses of benefits and costs are the most widespread in nature, which can cause mutualistic systems to exhibit complex population dynamics. Benefits saturate with increasing partner density due to limitations in the consumer's resource handling time or uptake rate (analogous to consumer-resource foraging interactions; Stephens and Krebs 1986; Wright 1989; Holland et al. 2005; Morris et al. 2010; Zhang and Hui 2014). Costs saturate as providers approach their physiological constraints in energy allocation or time investment (Bronstein 2001; Morris et al. 2010). Thus, it is reasonable to model the benefits and costs to species from mutualistic interactions in the form of Type II functional response (Soberon and Del Rio 1981; Holland et al. 2002; Wang and Wu 2014).

In this paper, we consider a simple two-species mutualism in the closed system (i.e., without immigration or emigration). Following Holland and DeAngelis' (2010) framework of the bi-directional consumer-resource relationship (i.e., the two species are both consumers and resources), we use the Type II functional response to formulate the per-capita benefits of both species, respectively denoted by $B_1(y)$ and $B_2(x)$ for species 1 and 2, which depend on the densities y and x of their partner species (i.e., species 2 and 1):

$$B_1(y) = \frac{b_1 y}{h_1 + y}, \quad B_2(x) = \frac{b_2 x}{h_2 + x}. \tag{1}$$

Here, $y/(h_1 + y)$ and $x/(h_2 + x)$ represent the interacting strength of species 1 and 2 with their partner species, where h_1 and h_2 are the respective half-saturation constants; parameters b_1 and b_2 indicate the benefit levels gained by the two species. Because the costs are paid by the individuals of a species when they bring benefits to their partner species (Bronstein 2001), the total costs respectively paid by the whole populations of species 1 and 2 are $c_1 xy/(h_2 + x)$ and $c_2 xy/(h_1 + y)$, where c_1 and c_2 are the cost levels of the two species. Therefore, the per-capita costs of them are:

$$C_1(x, y) = \frac{c_1 y}{h_2 + x}, \quad C_2(x, y) = \frac{c_2 x}{h_1 + y} \tag{2}$$

We further assume that the benefits gained by a species improve its reproductive efficiency and that the costs paid by it lead to a reduction in survival. This assumption is based on empirical observations, such as Kang et al.'s (2011) study of the leafcutter-fungus mutualism system, in which agricultural services provided by leaf-cutter ants increase the birth rate of the fungi, while consumption by leaf-cutter ants increases the overall mortality rate of the fungi; on the other hand, leaf-cutter ants feeding on fungi increase their birth rate, while the energy spent on patrolling and tending fungal gardens increases the overall mortality rate of the leaf-cutter ants. Therefore, the population dynamics of the two mutualistic species can be described by the following ordinary differential equations:

$$\begin{aligned} \frac{dx}{dt} &= x(r_1 + B_1(y))(1 - a_1x) - C_1(x, y)x - d_1x, \\ \frac{dy}{dt} &= y(r_2 + B_2(x))(1 - a_2y) - C_2(x, y)y - d_2y. \end{aligned} \tag{3}$$

where r_1 and r_2 represent the intrinsic reproductive rates of the two species, and d_1 and d_2 are their death rates independent of population density and mutualistic interactions. Note that $(1 - a_1x)$ and $(1 - a_2y)$ represent the reproductions of the species limited by population densities with a_1 and a_2 being the density-dependent regulation strengths. Thus, r_1a_1x and r_2a_2y give the density-dependent self-limitation via intraspecific competition for background resources; $B_1(y)a_1x$ and $B_2(x)a_2y$ give the density-dependent self-limitation via intraspecific competition for benefits. All parameters in the model are positive. Compared to other popular models of mutualistic interactions, this model separates benefits and costs of the interaction, explicitly links benefits to the growth rate of the population (which can be interpreted as reproductive efficiency), and relates costs to risk of mortality. Moreover, it applies to both obligate and facultative mutualistic interactions, as determined by the relative magnitudes of r_i and d_i $(i = 1, 2)$.

3 Results

In what follows, we focus on obligate, rather than facultative, mutualisms because they represent the 'worst-case scenario', i.e., the two mutualistic species cannot survive alone unless the other provides help (Johnson and Amarasekare 2013), corresponding to $r_i < d_i (i = 1, 2)$ in our model. All our analyses are strictly under this condition. The main objective of our work is to investigate the effects of internal interactions between mutualists on the dynamical behaviors of the obligate mutualism system. Therefore, in order to exclude the influence of asymmetric factors, we first theoretically analyze the existence and stability of equilibria of the symmetric mutualism system (i.e., corresponding parameter values are equal, $b_i = b$, $c_i = c$, $a_i = a$, $h_i = h$, $r_i = r$, $d_i = d$, $i = 1, 2$). Then, we further conduct numerical simulations to study the population dynamics under symmetric interactions between obligate mutualists, as well as the effects of asymmetry in benefits between them on these dynamics.

3.1 Equilibria and their Stability

For the sake of the biological implications, we consider the dynamical behaviors of system (3) in the phase-plane region $R_+^2 = \{(x, y)|x \geq 0, y \geq 0\}$. It is easy to see that system (3) always has the trivial boundary equilibrium (0, 0) but no axial boundary equilibrium. The Jacobian matrix at the trivial boundary equilibrium $E_0(0, 0)$ is given by:

$$J(E_0) = \begin{bmatrix} r_1 - d_1 & 0 \\ 0 & r_2 - d_2 \end{bmatrix}.$$

The eigenvalues of $J(E_0)$ are $r_1 - d_1(< 0)$ and $r_2 - d_2(< 0)$. Therefore, the extinction node $E_0(0, 0)$ is a locally stable equilibrium of the obligate mutualism system. This implies that it is impossible for obligate mutualisms to develop from an initially very low density in the sense of deterministic models.

Our model is highly nonlinear, so it is extremely difficult to derive the analytical expressions for all interior equilibria of system (3). Moreover, to exclude the influence of asymmetric factors, we next theoretically analyze the existence and stability of interior equilibria in the symmetric mutualism (i.e., equal parameters for both species, $b_i = b$, $c_i = c$, $a_i = a$, $h_i = h$, $r_i = r$, $d_i = d$, $i = 1, 2$).

Suppose that $E(x^*, y^*)$ is an interior equilibrium of system (3), then $x^*, y^*(x^* > 0, y^* > 0)$ are positive real roots of the following equations:

$$\begin{aligned} &\left(r + \tfrac{by}{h+y}\right)(1 - ax) - \tfrac{cy}{h+x} - d = 0, \\ &\left(r + \tfrac{bx}{h+x}\right)(1 - ay) - \tfrac{cx}{h+y} - d = 0. \end{aligned} \tag{4}$$

Equation (4) can be transformed into the following system of higher-order binary equations:

$$\begin{aligned} \alpha_0(y)x^2 + \alpha_1(y)x + \alpha_2(y) = 0, \\ \beta_0(y)x^2 + \beta_1(y)x + \beta_2(y) = 0. \end{aligned} \tag{5}$$

where

$$\begin{aligned} \alpha_0(y) &= - a(b + r)y - ahr, \\ \alpha_1(y) &= [b + r - d - ah(b + r)]y + h(r - d - ahr), \\ \alpha_2(y) &= - cy^2 + (b - c + r - d)hy + h^2(r - d), \\ \beta_0(y) &= - c, \\ \beta_1(y) &= - a(b + r)y^2 + [b + r - d - ah(b + r)]y + (b - c + r - d)h, \\ \beta_2(y) &= - ahry^2 + [h(r - d - ahr)]y + h^2(r - d). \end{aligned} \tag{6}$$

Combining the two equations of Eq. (5), we can get:

$$x = -\frac{\alpha_2(y)+\frac{1}{c}\beta_2(y)\alpha_0(y)}{\alpha_1(y)+\frac{1}{c}\beta_1(y)\alpha_0(y)}. \tag{7}$$

Combining Eq. (7) with Eq. (6) and substituting into the second equation of Eq. (5) then yields the following sixth-degree equation with one unknown:

$$\left(A_0y^2 + A_1y + A_2\right)\left(B_0y^4 + B_1y^3 + B_2y^2 + B_3y + B_4\right) = 0. \tag{8}$$

where the coefficients $A_i(i = 0, 1, 2)$, $B_j(j = 0, 1, 2, \ldots, 4)$ are as follows:

$$\begin{aligned} A_0 &= a(b + r), \\ A_1 &= c - b - r + d + ahr, \end{aligned}$$

$$
\begin{aligned}
A_2 &= h(d-r),\\
B_0 &= -a^2c(b+r)^2,\\
B_1 &= a(b+r)\{c(b+c+r-d)+ah[b(b-c+r-d+ahr)-c(b+2r)]\},\\
B_2 &= -a^2h^2[-b(b+2r)(b-c+r-d+ahr)+r(b+c)(b+r)]\\
&\quad +ah\left[-b(b+r)(b-c+r-d)+2cr(b+c+r-d)+bc^2\right]\\
&\quad -c^2(b+c+r-d),\\
B_3 &= -a^2bh^3r(c+r+d-ahr)-abh^2(b+2r)(b-c+r-d)\\
&\quad +ach^2[bd+r(c+r-d)]+ch(b-c)(b+c+r-d),\\
B_4 &= -bh^2[c(d-r)+ahr(b-c+r-d+ahr)]. \qquad (9)
\end{aligned}
$$

It is easy to see that $A_0,\ A_2 > 0,\ B_0 < 0$. By the above analyses, if $x^*,\ y^*(x^* > 0,\ y^* > 0)$ are positive real roots of Eq. (4), then y^* is the positive real root of the following quadratic or quartic equation with one unknown:

$$A_0y^2 + A_1y + A_2 = 0, \qquad (10)$$

$$B_0y^4 + B_1y^3 + B_2y^2 + B_3y + B_4 = 0. \qquad (11)$$

Since the model structure and parameters of the two species are perfectly symmetric and there is always a basin of attraction for system extinction around $E_0(0, 0)$, the interior equilibria and basins of attraction of the system are always symmetric about the line $y = x$. Consequently, if the system persists, there must be at least two interior equilibria on the line $y = x$. These symmetric equilibria, corresponding to the positive real roots of Eq. (10), are either a saddle-node pair (one saddle and one node) or two saddles. The proof, analytical expressions $(E_1(x_1^*,\ y_1^*),\ E_2(x_2^*,\ y_2^*))$, and stability analyses are provided in "Appendix B". On the other hand, since $B_0 < 0$ and $B_4 < 0$ (easily obtained from "Appendix B"), and given the symmetry of interior equilibria about the line $y = x$, Eq. (11) may have zero, two, or four positive real roots, corresponding to the asymmetric interior equilibria of system (3). Although analytical expressions for these asymmetric equilibria can be derived using the quartic formula, they are too complex to readily provide biological insights and render further analysis intractable. Therefore, we omit detailed derivations here and will subsequently perform numerical analyses to reveal the existence and stability of these equilibria.

In summary, if the system persists, in addition to the extinction equilibrium $E_0(0, 0)$, there may be two, four, or six interior equilibria (with at least two symmetric ones). We speculate that the types of steady states in the system are as follows:

1. System (3) exhibits bi-stability. In addition to the extinction attractor $E_0(0, 0)$, there exists only one symmetric attractor of stable coexistence $E_2(x_2^*,\ y_2^*)$. On the separatrix between the two basins of attraction, there exists a symmetric saddle $E_1(x_1^*,\ y_1^*)$.

2. System (3) exhibits quaternary stability. In addition to the extinction attractor E_0 (0, 0), there exists a symmetric attractor of stable coexistence $E_2\left(x_2^*,\ y_2^*\right)$ and two asymmetric coexistence attractors. On the separatrices among the four basins of attraction, there exist a symmetric saddle $E_1\left(x_1^*,\ y_1^*\right)$ and two asymmetric saddles.
3. System (3) exhibits tri-stability. In addition to the extinction attractor $E_0(0,\ 0)$, there exist two asymmetric coexistence attractors. On the separatrices among the three basins of attraction, there exist two symmetric saddles $E_1\left(x_1^*,\ y_1^*\right)$ and $E_2\left(x_2^*,\ y_2^*\right)$.

3.2 Numerical Simulations

Based on the theoretical analyses in the previous section, we next perform numerical simulations to reveal the multi-stability and complex population dynamics of the symmetric obligate mutualism system, and further investigate the effects of asymmetry in benefits between mutualists on these dynamical behaviors.

3.2.1 Asymptotic Dynamics of the Symmetric Obligate Mutualism System

Figure 1 shows the bifurcation portrait of the symmetric obligate mutualism system in the $(b,\ c)$ parameter plane. Different colors and numbers of the domains correspond to different dynamical regimes. The first columns of Figs. 2 and 3 display the equilibria and global population dynamics for each domain in the cross sections of Fig. 1 constructed for $b = 0.5$ (large benefit) and $b = 0.05$ (small benefit), respectively, while the remaining columns illustrate the effects of asymmetry in benefits between mutualists on population dynamics.

Specifically, when mutual facilitation between the species cannot overcome the negative effects, including costs, density-dependent self-limitation via intraspecific competition for benefits and background resources, and the deficit between births and deaths, the system cannot persist; correspondingly, there is no stable interior equilibrium (domains VI, VII of Fig. 1) or even no interior equilibrium (white domain of Fig. 1). Otherwise, when the benefit–cost difference (i.e., the difference between benefits and costs) is extremely large (domain I of Fig. 1), system (3) has two interior equilibria where the smaller one is always a saddle and the larger one is a central stable node, forming bi-stability with the extinction node. In this case, mutualistic species coexist at the central stable node only if their initial densities are above the extinction threshold (e.g., blue basins of attraction in Figs. 2a and 3a).

As the benefit–cost difference decreases into domain II of Fig. 1, two stable foci symmetric about the line $y = x$ appear, forming quaternary stability with the central stable node and the extinction node. For species coexistence in this case, mutualists coexist at the central stable node if the initial densities are approximately equal or strongly unequal (e.g., blue basins of attraction in Figs. 2e and 3e), and coexist in damped oscillations toward the stable foci if the initial densities are weakly unequal (e.g., green basins of attraction in Figs. 2e and 3e).

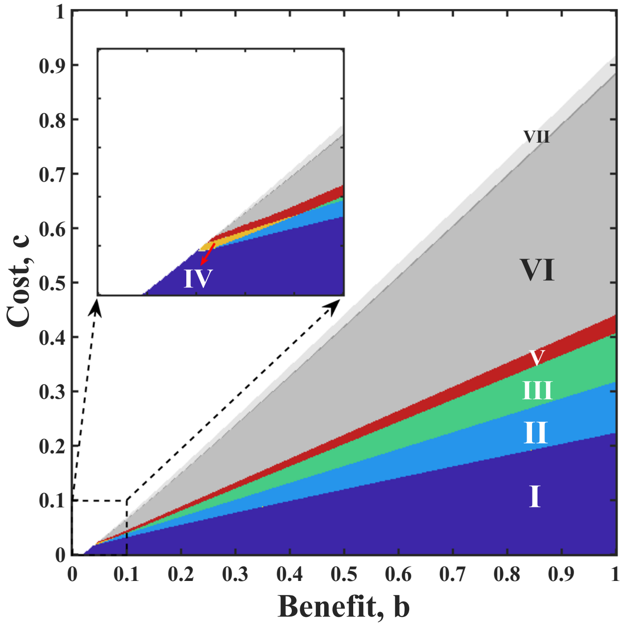

Fig. 1 Bifurcation diagram in the (b, c) plane showing the multiple attractors of the symmetric obligate mutualism system. The domains have the following meaning: domain I-bi-stability with the stable and extinction node; domain II-quaternary stability with the extinction, stable node and two stable foci; domain III-quaternary stability with the extinction, stable node and two stable limit cycles; domain IV-tri-stability with the extinction node and two stable foci; domain V-tri-stability with the extinction node and two stable limit cycles; domains VI, VII-no stable interior equilibrium; white domain-no interior equilibrium. The corresponding global population dynamics of each domain are shown in the first columns of Figs. 2 and 3. Other parameter values remained constant ($a_i = 0.45$, $h_i = 0.5$, $r_i = 0.004$, $d_i = 0.01$, $i = 1, 2$)

The benefit–cost difference further decreases into domain III or IV of Fig. 1 for $b = 0.5$ and $b = 0.05$, respectively. In domain III, the two stable foci destabilize into limit cycle attractors, forming quaternary stability with the central stable node and the extinction node. The population dynamics corresponding to damped oscillations transition into periodic oscillations around the limit cycle attractors (e.g., red basins of attraction in Fig. 2i and m). In domain IV, the central stable node disappears, and the remaining two stable foci form tri-stability with the extinction node. In this case, mutualistic species coexist in damped oscillations toward the stable foci if their initial densities are above the extinction threshold (e.g., green basins of attraction in Fig. 3i).

As the benefit–cost difference further decreases into domain V of Fig. 1, the central stable node disappears ($b = 0.5$) or the two stable foci destabilize to limit cycle attractors ($b = 0.05$), and the remaining two limit cycle attractors form tri-stability with the extinction node. In this case, mutualistic species coexist in periodic oscillations if their initial densities are above the extinction threshold (e.g., red basins of attraction in Figs. 2q and 3m). Interestingly, if there are basins of attraction of damped or periodic oscillations in the symmetric obligate mutualism system, they always occur in

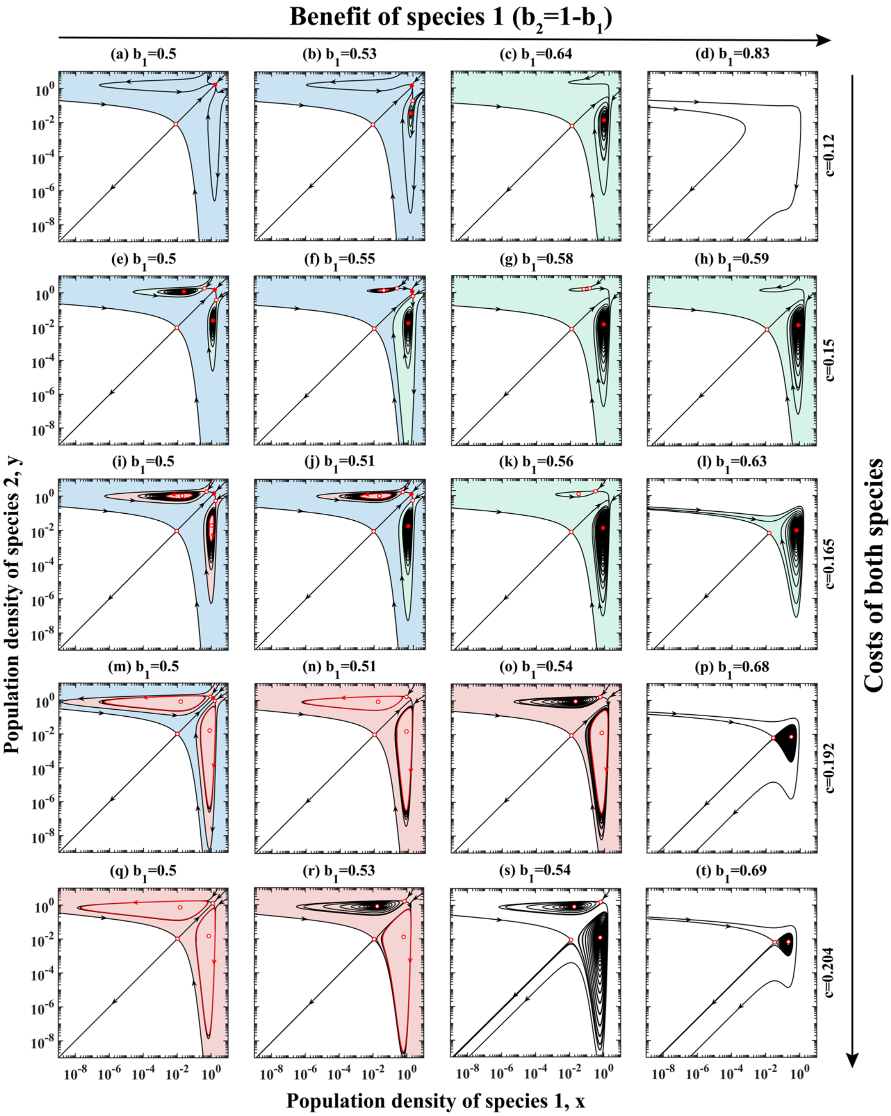

Fig. 2 Phase-plane diagrams of the global population dynamics for symmetric and asymmetric benefits between species 1 and 2 under different costs. The total benefits of the system are fixed at 1 ($b_1 + b_2 = 1$). Column 1: symmetric benefits, corresponding to the domains in the cross section of Fig. 1 constructed for $b = 0.5$; columns 2–4: asymmetric benefits. Solid and open red circles represent stable and unstable equilibrium, respectively. Blue, green, red, and white regions correspond to the attraction basins of stable coexistence, damped oscillations, periodic oscillations, and system extinction, respectively. Black curves with arrows are typical phase trajectories of the system, and red curves with arrows are stable limit cycles of the system. Other fixed parameter values are the same as in Fig. 1 (Color figure online)

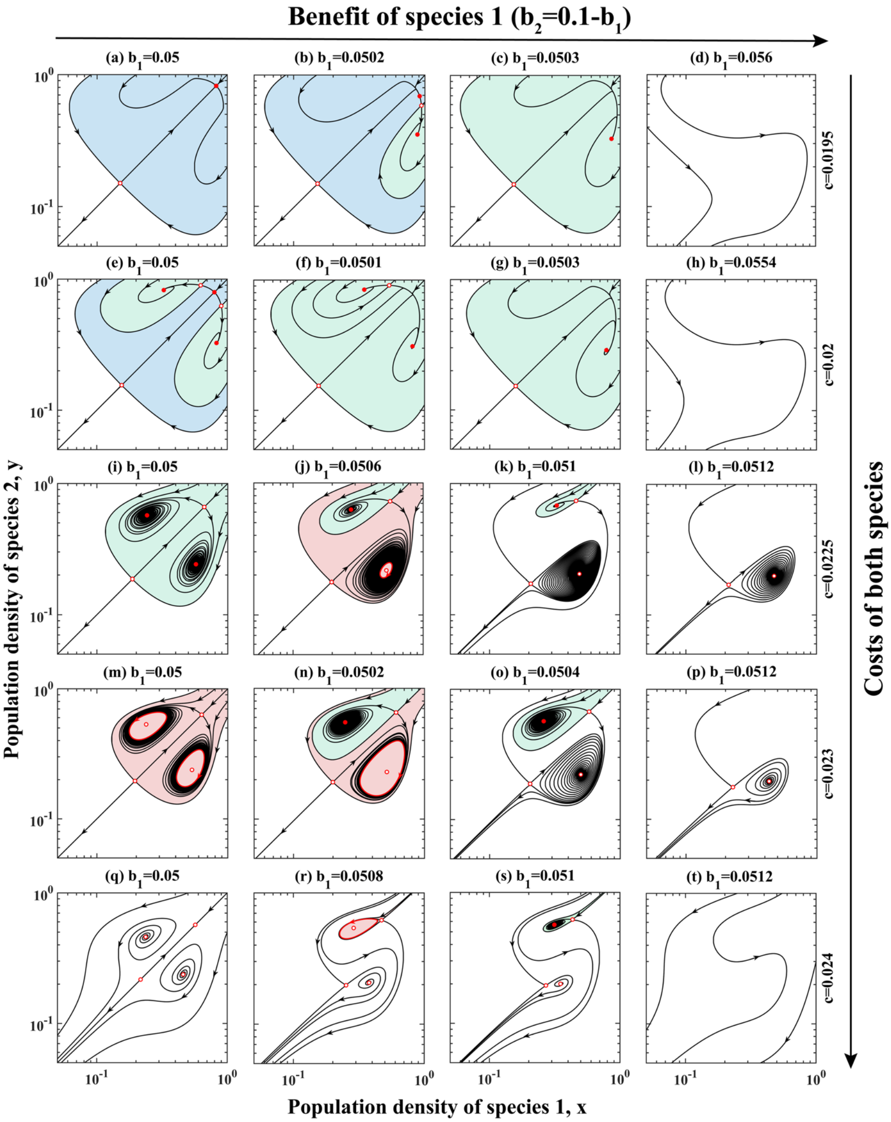

Fig. 3 Same as Fig. 2, but the total benefits of the system take a smaller value: 0.1 ($b_1 + b_2 = 0.1$), and the column 1 corresponds to the domains in the cross section of Fig. 1 constructed for $b = 0.05$

a symmetric pair about the line $y = x$, and the dominant species in the equilibrium state is determined solely by the initial densities.

3.2.2 Asymptotic Dynamics of the Asymmetric Obligate Mutualism System

In natural ecosystems, resource allocation between mutualistic partners is often asymmetric (Wang et al. 2011, 2024; van der Kooi et al. 2021). Therefore, we further explored the effects of asymmetry in benefits between mutualists on population dynamics. Based on previous analyses, we can fix the total benefits of the system at 1 and 0.1, respectively, and then increase species 1's benefits and decrease species 2's benefits. In this way, the degree of asymmetry in benefits between mutualists gradually increases, leading to shifts in the dynamical regimes (columns 2–4 of Figs. 2 and 3).

The extremely high degree of asymmetry in benefits between mutualists results in the extinction of species 2 first and its partner species 1 subsequently (e.g., Figs. 2d and 3d). On the premise that the system can persist, the asymmetry in benefits gradually shifts system (3) from multi-stability to bi-stability. For the large total system benefits ($b_1 + b_2 = 1$), when the cost is relatively small (rows 1–3 of Fig. 2), the stable dynamics dominate the symmetric system. In this case, the asymmetry in benefits shifts system (3) into a new bi-stability with species 1-dominated damped oscillations and extinction. When the cost is relatively large (rows 4–5 of Fig. 2), the oscillatory dynamics dominate the symmetric system. In this case, the asymmetry in benefits shifts system (3) into a new bi-stability with species 1-dominated periodic oscillations and extinction.

For the small total system benefits with relatively large costs (rows 3–5 of Fig. 3, $b_1 + b_2 = 0.1$), the asymmetry in benefits causes system (3) to undergo different and counterintuitive shifts relative to those in large total system benefits. Specifically, the species 2-dominated basin of attraction gradually diminishes but stabilizes, while the species 1-dominated basin of attraction gradually expands but destabilizes and eventually disappears before the former. In particular, the asymmetry in benefits can drive the system to transition from extinction to periodic or even damped oscillations dominated by species 2.

3.2.3 Transient Dynamics of the Obligate Mutualism System

In previous sections, we focused on the asymptotic behavior of the obligate mutualism system and explored how environmental conditions (i.e., model parameters) shift its dynamical regimes. In this section, we observe that the system can persist in a certain dynamical regime for thousands of generations but later suddenly transition to another state or regime in the absence of any underlying changes in environmental conditions. This preceding regime therefore appears to be 'quasi-stable' rather than actually stable and is referred to as a long transient (Hastings et al. 2018; Morozov et al. 2020).

We identify five scenarios of long transients due to saddle crawl-bys and ghost attractors in the obligate mutualism system (as in Fig. 4). Specifically, the long transient caused by a saddle crawl-by occurs when the system's state is close to a saddle point (Fig. 4a). In this case, the two mutualistic species persist at an almost constant low density for approximately 1500 generations before suddenly transitioning to a high-density stable steady state. A similar long transient behavior caused by the ghost of a saddle-node occurs when the system is just beyond the saddle-node bifurcation (Fig. 4b). After a fast decay from the initial state, the two mutualistic species persist at an almost constant density (i.e., the ghost steady state value, comparable to that of the stable steady state before the saddle-node bifurcation) for approximately 6000 generations, followed by a sudden transition to periodic oscillations. With parameters moving further away from the Hopf bifurcation point, the limit cycle grows in size

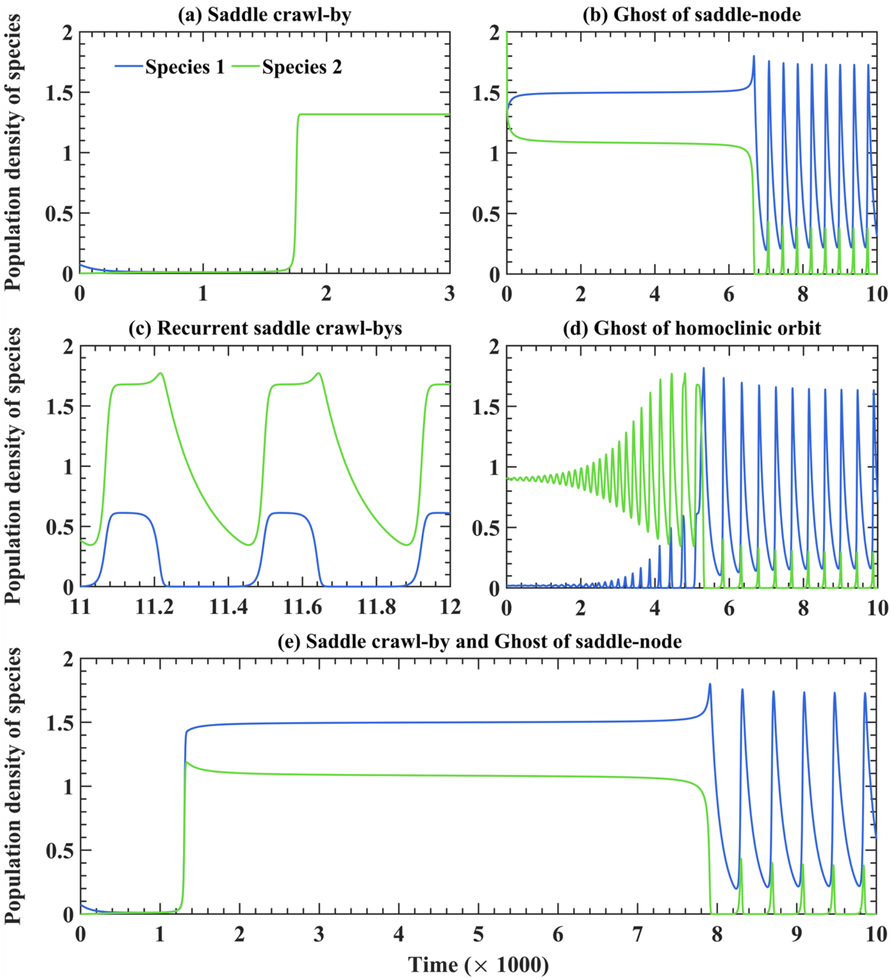

Fig. 4 Five scenarios of long transients due to saddle crawl-bys and ghost attractors in the obligate mutualism system. Blue and green lines represent the population densities of species 1 and 2, respectively. **a** The long transient caused by a saddle crawl-by; an almost constant low-density regime transitions to a high-density stable steady state. The parameters and initial conditions are $b_1 = 0.5$, $x_0 = 0.0724$, $y_0 = 0.0001$. **b** The long transient caused by a ghost of a saddle-node; an almost constant high-density regime transitions to periodic oscillations. The parameters and initial conditions are $b_1 = 0.50634$, $x_0 = 2$, $y_0 = 2$. **c** The long transient caused by recurrent saddle crawl-bys on the limit cycle before homoclinic bifurcation. The parameters and initial conditions are $b_1 = 0.53187$, $x_0 = 0.02$, $y_0 = 0.9$. **d** Transient oscillations caused by a ghost of a homoclinic orbit after homoclinic bifurcation. The parameters and initial conditions are $b_1 = 0.53188$, $x_0 = 0.02$, $y_0 = 0.9$. **e** Two consecutive long transients: first caused by a saddle crawl-by, then followed by a ghost of a saddle-node. The parameters and initial conditions are $b_1 = 0.50634$, $x_0 = 0.074$, $y_0 = 0.0001$. For all panels, $b_2 = 1 - b_1$, $c_1 = c_2 = 0.192$, and other fixed parameter values are the same as in Fig. 1 (Color figure online)

and closely approaches the saddle point. Figure 4c illustrates the long transient caused by recurrent saddle crawl-bys on this limit cycle near the saddle point before the homoclinic bifurcation. When parameters are just beyond the homoclinic bifurcation point, the ghost of a homoclinic orbit can induce transient oscillations. As shown in Fig. 4d, the two mutualistic species first approach the ghost of a homoclinic orbit with damped oscillations (for approximately 4,000 generations), then linger in the region of this ghost orbit for about 1,200 generations, and eventually transition suddenly to periodic oscillations, accompanied by a shift in the dominant species. Additionally, Fig. 4e displays two consecutive long transients caused by a saddle crawl-by followed by a ghost of a saddle-node. In this process, the two mutualistic species first persist at an almost constant low density for approximately 1000 generations (the saddle crawl-by phase), then rapidly transition to an almost constant high density and persist for about 6000 generations (the ghost of a saddle-node phase), and eventually transition suddenly to periodic oscillations.

Apart from the long transient caused by recurrent saddle crawl-bys (Fig. 4c) and two consecutive long transients (Fig. 4e), the asymptotic dynamics following the other three scenarios of long transients (Fig. 4a, b and d) are diverse in the obligate mutualism system. Specifically, the system exhibits four types of asymptotic dynamics, including the extinction state, the stable steady state, the stable steady state via damped oscillations, and periodic oscillations. The long transient caused by a saddle crawl-by can transition to all four types of asymptotic dynamics (Fig. 4a, Fig. 5a–c); the long transient caused by a ghost of a saddle-node can transition to periodic oscillations (Fig. 4b) or the stable steady state via damped oscillations (Fig. 5d); the transient oscillations caused by a ghost of a homoclinic orbit can transition to periodic oscillations (Fig. 4d), the stable steady state via damped oscillations (Fig. 5e), or the extinction state (Fig. 5f).

4 Discussion and Conclusion

In this study, we developed a general population dynamic model for the mutualism of two species to explore whether just the internal interactions between mutualists can lead to complex dynamics. Compared to other popular models of mutualistic interactions (Gause and Witt 1935; Dean 1983; Zhang 2003; Thompson et al. 2006; Holland and DeAngelis 2010; Cropp and Norbury 2019), our model separates benefits and costs of the interaction, explicitly links benefits to the growth rate of the population (which can be interpreted as reproductive efficiency), and relates costs to risk of mortality. Furthermore, we assume that the mutualistic benefits and costs are regulated by population densities in the form of Type II functional response (i.e., saturating density-dependent benefits and costs). These mechanisms may be key factors influencing the population dynamics of obligate mutualism systems.

Previous theoretical studies have shown that the dynamical behaviors of purely mutualism systems are embodied as simple states of either stable coexistence or extinction (Vandermeer and Boucher 1978; Wolin and Lawlor 1984; Fishman and Hadany 2010; García-Algarra et al. 2014; Wang and Wu 2014; Hale et al. 2022). However, real ecosystems do not persist at such steady-state values (Gilpin et al. 1982). Experimental works have found that population oscillations can take place in purely mutualism systems (Yurtsev et al. 2016), and theoretically, Holland and DeAngelis (2001) and McGill (2005) also claimed that periodic oscillations are possible in their early studies on mutualism systems. In this study, our model demonstrates that the saturating density dependence of benefits and costs can lead to oscillatory dynamics in obligate mutualism systems under intermediate benefit–cost differences, validating Holland and DeAngelis' (2010) predictions about population fluctuations.

In obligate mutualism systems, the interaction outcome between species is determined by the sign of the net effects (i.e., the balance between positive and negative effects) on each species' population growth rate (Bronstein 1994). In our model, positive effects derive from mutualistic benefits that increase per-capita birth rate, while negative effects include mutualistic costs that increase per-capita death rate, density-dependent self-limitation via intraspecific competition for benefits and background resources, and the deficit between births and deaths. Mutualism persists when positive effects exceed negative effects (positive net effects), resulting in positive net population growth rates for both species ($dx/dt > 0$ and $dy/dt > 0$). Conversely, when negative effects outweigh positive effects (negative net effects), leading to negative net population growth rates for one or both species ($dx/dt < 0$ or $dy/dt < 0$), the interaction transitions to antagonism (e.g., exploitation or competition) (Holland and DeAngelis 2002, 2009; Hernandez and Barradas 2003; Labouche and Bernasconi 2013). In our system, differences in how benefits and costs for each species vary with population density can alter the sign of the net effects under intermediate benefit–cost differences, causing the interaction to transition between mutualism and antagonism (Holland et al. 2002; Morris et al. 2010; Wang et al. 2011; Zhang et al. 2021). Such nonmonotonic interactions tend to intrinsically drive population oscillations in mutualism systems (Yule et al. 2020).

Specifically, when both partners are rare, intraspecific competition for benefits and background resources is weak. In this case, their positive effects (Fig. 6b and c, black dotted lines) are sufficient to overcome negative effects (Fig. 6b and c, black solid lines), resulting in mutualism between species 1 and 2 with positive population growth (Fig. 6, $T_1 - T_2$). As the population densities of both species increase, the benefits of species 1 (the small population, the black dotted line in Fig. 6b) gradually saturate, but its costs continue to increase with the population density of its partner species 2 (the large population). Once the positive effects of species 1 cannot counteract its negative effects, its population density declines; consequently, the benefits gained by species 2 decrease but still temporarily exceed its negative effects (Fig. 6, $T_2 - T_3$). At this point, mutualism disappears, and the interaction between species 1 and 2 transitions to antagonism. As the population density of species 1 declines continuously, the population density of species 2 begins to decline due to insufficient benefits. The costs of species 1 subsequently decrease until its negative effects no longer outweigh its positive effects (Fig. 6, $T_3 - T_4$); then, the population density of species 1 resumes positive growth (Fig. 6, $T_4 - T_5$). Accordingly, the benefits gained by species 2 increase until they are sufficient to overcome its negative effects, and the population density of species 2 also resumes positive growth (Fig. 6, T_5). The system thus recovers mutualism between the two interacting species, and both partners coexist in periodic oscillations. In the process of population oscillations, when both species are abundant, the intraspecific competition for benefits significantly increases their density-dependent self-limitation (Fig. 6b and c, magenta dashed lines); when one species is abundant but the other is rare, the density-dependent self-limitation via intraspecific competition for background resources limits the unbounded growth of the large population, avoiding the collapse of the system (Fig. 6b and c, cyan dashed lines).

In addition, our results reveal the long transients of the obligate mutualism system—a phenomenon of regime shift without parameter change (Figs. 4 and 5). Two of the key mechanisms driving long transients are saddle crawl-bys and ghost attractors (Hastings et al. 2018, 2021; Morozov et al. 2024). The saddle crawl-by occurs in the vicinity of a saddle point, where the system spends considerable time, thereby generating a long transient (Morozov et al. 2020; Rubin et al. 2023). The ghost attractor refers to a region in the phase space, i.e., the vicinity of the location where a stable attractor (e.g., a stable node or limit cycle) was before a bifurcation (Hastings et al. 2018; Morozov et al. 2024). When parameters are just beyond the bifurcation point,

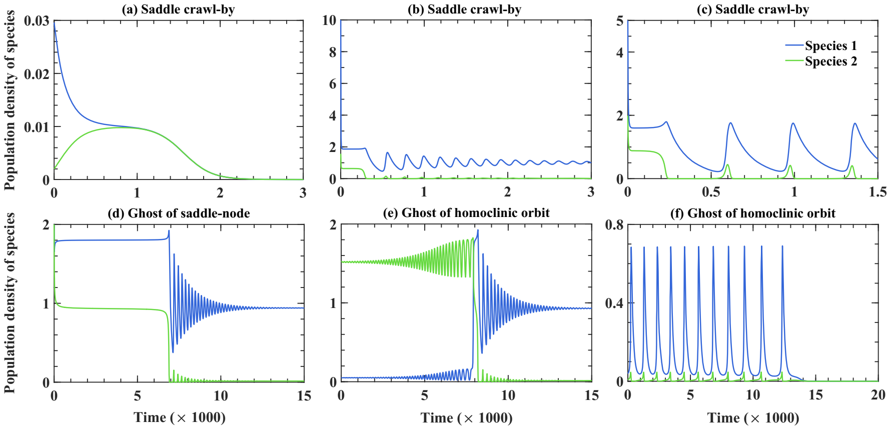

Fig. 5 Diversity of asymptotic dynamics following long transients in the obligate mutualism system. Blue and green lines represent the population densities of species 1 and 2, respectively. **a** The long transient caused by a saddle crawl-by; an almost constant density regime transitions to an extinction state. The parameters and initial conditions are $b_1 = 0.5$, $c_1 = 0.192$, $x_0 = 0.0296$, $y_0 = 0.002$. **b** The long transient caused by a saddle crawl-by; an almost constant density regime transitions to a stable steady state via damped oscillations. The parameters and initial conditions are $b_1 = 0.55$, $c_1 = 0.15$, $x_0 = 10$, $y_0 = 1.56643$. **c** The long transient caused by a saddle crawl-by; an almost constant density regime transitions to periodic oscillations. The parameters and initial conditions are $b_1 = 0.5$, $c_1 = 0.192$, $x_0 = 5$, $y_0 = 1.99$. **d** The long transient caused by a ghost of a saddle-node; an almost constant density regime transitions to a stable steady state via damped oscillations. The parameters and initial conditions are $b_1 = 0.5679$, $c_1 = 0.15$, $x_0 = 2$, $y_0 = 2$. **e** Transient oscillations caused by a ghost of a homoclinic orbit after homoclinic bifurcation; transient oscillations transition to a stable steady state via damped oscillations. The parameters and initial conditions are $b_1 = 0.5708$, $c_1 = 0.15$, $x_0 = 0.0515$, $y_0 = 1.5185$. **f** Transient oscillations caused by a ghost of a homoclinic orbit after homoclinic bifurcation; apparently sustainable periodic oscillations transition to an extinction state. The parameters and initial conditions are $b_1 = 0.67$, $c_1 = 0.192$, $x_0 = 0.04$, $y_0 = 0.008$. For all panels, $b_2 = 1 - b_1$, $c_2 = c_1$, and other fixed parameter values are the same as in Fig. 1 (Color figure online)

the stable attractor vanishes; however, the system's dynamics can mimic this attractor's behavior over considerable time in this vicinity, thus generating a long transient (Medeiros et al. 2017).

Specifically, we identify five scenarios of long transients due to saddle crawl-bys and ghost attractors: the saddle crawl-by, the ghost of a saddle-node, recurrent saddle crawl-bys before homoclinic bifurcation, the ghost of a homoclinic orbit after homoclinic bifurcation, and two consecutive long transients caused by the saddle crawl-by followed by the ghost of a saddle-node (Fig. 4). Moreover, the asymptotic dynamics following a long transient are diverse, depending on the final attractor corresponding to the system's initial state (Fig. 5). The inherent impermanence of transients means that mutualistic systems exhibiting an apparently stable dynamical regime (e.g., stable steady states or sustainable oscillations) over years of observation can suddenly transition to another regime (transient or asymptotic dynamics), even without any underlying changes in environmental conditions (Hastings et al. 2018; Morozov et al. 2024). Therefore, as with asymptotic dynamics, transient dynamics are equally essential for predicting future states and explaining past observations in natural mutualism systems (Pakdaman et al. 1997; Hastings 2004, 2016; Francis et al. 2021).

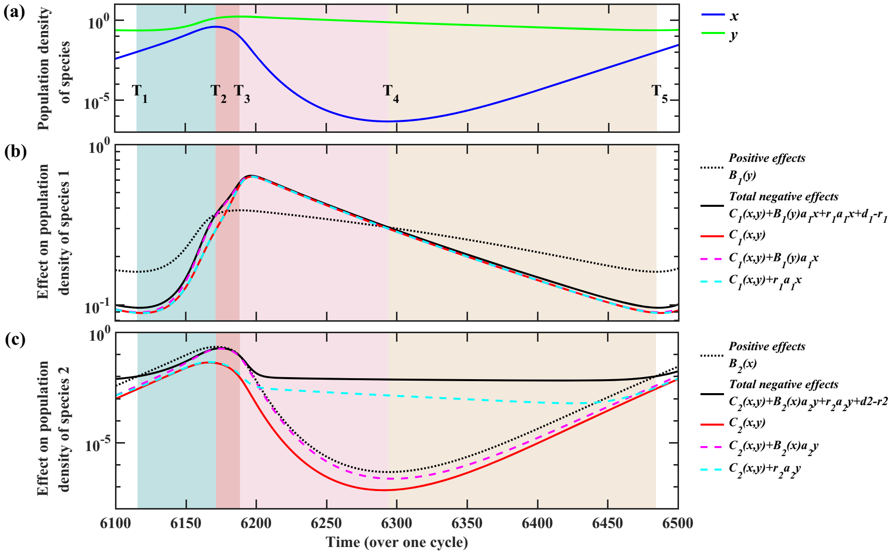

Fig. 6 Time series of **a** population densities, (**b, c**) the positive and negative effects on population density of species 1 and 2 in periodic oscillations over one cycle. Blue solid, green solid lines in (**a**) represent the population densities x, y of species 1 and 2, respectively. Black dotted lines in (**b, c**) represent the positive effects of species 1 and 2 arising from mutualistic benefits (i.e., $B_1(y)$, $B_2(x)$). Black solid lines in (**b, c**) represent the total negative effects of species 1 and 2 arising from mutualistic costs (i.e., $C_1(x, y)$, $C_2(x, y)$), density-dependent self-limitation via intraspecific competition for benefits (i.e., $B_1(y)a_1x$, $B_2(x)a_2y$) and background resources (i.e., r_1a_1x, r_2a_2y), and the deficit between births and deaths (i.e., $d_1 - r_1$, $d_2 - r_2$). Red solid, magenta (cyan) dashed lines in (**b, c**) represent the mutualistic costs, the sum of mutualistic costs and dependent self-limitation via intraspecific competition for benefits (background resources), respectively. Initial conditions and model parameters are $x_0 = 0.1$, $y_0 = 0.5$, $c = 0.192$, $b_1 = b_2 = 0.5$. Other fixed parameter values are the same as in Fig. 1 (Color figure online)

In conclusion, this study explored the complex population dynamics of obligate mutualism systems in the absence of exogenous effects from biotic or abiotic factors by considering the differential impacts of saturating density-dependent mutualistic benefits and costs on demographic rates such as reproduction and mortality. Our results suggested that just the internal interactions between mutualists can result in periodic oscillations and long transients in obligate mutualism systems. We concluded that nonmonotonic interactions (i.e., cyclic transitions between mutualism at low densities and antagonism at high densities) caused by saturating density-dependent feedbacks of mutualistic benefits and costs essentially regulate the population dynamics, which limit the unbounded growth trend while preventing the extinction of populations, thus sustaining the oscillatory coexistence of mutualistic species. Our study revealed the existence and maintenance mechanisms of complex dynamics in obligate mutualism systems. Our findings have potential implications for the conservation and management of real-world mutualistic communities.

Appendix A

Theorem 1 *The obligate mutualism system with benefits and costs in the form of Type I functional response cannot exhibit periodic oscillations.*

Proof In the form of Type I functional response, the per-capita benefits and costs for both species are given by:

$$\begin{aligned} B_1(y) = b_1 y,\ B_2(x) = b_2 x; \\ C_1(y) = c_1 y,\ C_2(x) = c_2 x. \end{aligned}$$

Consequently, the population dynamics of the obligate mutualism system can be described by the following ordinary differential equations:

$$\begin{aligned} \tfrac{dx}{dt} &= x(r_1 + b_1 y)(1 - a_1 x) - c_1 xy - d_1 x, \\ \tfrac{dy}{dt} &= y(r_2 + b_2 x)(1 - a_2 y) - c_2 xy - d_2 y. \end{aligned} \tag{A1}$$

Parameters are all the same as in system (3) in the main text, with $r_i < d_i (i = 1, 2)$. Evidently, system (A1) has a stable extinction equilibrium $E(0, 0)$ but no axial boundary equilibrium. Given an interior equilibrium is $E(x^*, y^*)$ $(x^* > 0, y^* > 0)$, the Jacobian matrix at it is expressed as:

$$J(E) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix},$$

where

$$\begin{aligned} a_{11} &= -a_1 x^*(r_1 + b_1 y^*) < 0, \\ a_{12} &= x^*\big[b_1 - c_1 - a_1 b_1 x^*\big], \\ a_{21} &= y^*\big[b_2 - c_2 - a_2 b_2 y^*\big], \\ a_{22} &= -a_2 y^*(r_2 + b_2 x^*) < 0. \end{aligned}$$

The characteristic equation of the matrix $J(E)$ is:

$$\lambda^2 - Tr\lambda + \Delta = 0,$$

where $Tr = a_{11} + a_{22}$ and $\Delta = a_{11}a_{22} - a_{12}a_{21}$.

Since $a_{11} < 0$ and $a_{22} < 0$, $Tr < 0$. A stable limit cycle (surrounding an unstable equilibrium) requires $Tr > 0$, but $Tr < 0$ holds for all interior equilibria of the system. Therefore, it is impossible for the system (A1) to have a stable limit cycle attractor, and thus there are no periodic oscillations.

Appendix B

Theorem 2 *The symmetric interior equilibria of system (3) are either a saddle-node pair (one saddle and one node) or two saddles.*

Proof Assume that $x = y$, and substitute it into any equation in Eq. (4), then it can yield Eq. (10). Hence, the roots of Eq. (10) correspond to two symmetric interior equilibria of system (3). Using the quadratic formula, we can get the symmetric interior equilibrium $E_i\left(x_i^*, y_i^*\right)$, $i = 1, 2$, $x_1^* = y_1^* < x_2^* = y_2^*$:

$$\begin{aligned} x_{1,2}^* =& y_{1,2}^* = \frac{-A_1 \pm \sqrt{A_1^2 - 4A_0A_2}}{2A_0} \\ =& \frac{-(c-b-r+d+ahr) \pm \sqrt{(c-b-r+d+ahr)^2 - 4a(b+r)h(d-r)}}{2a(b+r)} \end{aligned}$$

From Eq. (9), A_0, $A_2 > 0$, then $A_1 < 0$, $A_1^2 - 4A_0A_2 > 0$, i.e., $c - b - r + d + ahr < 0$, $(c - b - r + d + ahr)^2 - 4a(b + r)h(d - r) > 0$.

The Jacobian matrix of system (3) about interior equilibrium point $E(x^*, y^*)$ can be simplified as:

$$J(E) = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix},$$

where

$$\begin{aligned} a_{11} &= \frac{cx^*y^*}{(h+x^*)^2} - \left(r + \frac{by^*}{h+y^*}\right)ax^*, \\ a_{12} &= \frac{bhx^*(1-ax^*)}{(h+y^*)^2} - \frac{cx^*}{h+x^*}, \\ a_{21} &= \frac{bhy^*(1-ay^*)}{(h+x^*)^2} - \frac{cy^*}{h+y^*}, \\ a_{22} &= \frac{cx^*y^*}{(h+y^*)^2} - \left(r + \frac{bx^*}{h+x^*}\right)ay^*. \end{aligned}$$

The characteristic equation of the matrix $J(E)$ is given by:

$$\lambda^2 - Tr\lambda + \Delta = 0,$$

where $Tr = a_{11} + a_{22}$ and $\Delta = a_{11}a_{22} - a_{12}a_{21}$.

Since $y^* = x^*$ for the symmetric interior equilibrium, $a_{11} = a_{22} = \frac{x^* f_1}{(h+x^*)^2}$, $a_{12} = a_{21} = \frac{x^* f_2}{(h+x^*)^2}$, in which $f_1 = -a(b+r)x^{*2} + [c - ah(b+2r)]x^* - arh^2$, $f_2 = -(abh + c)x^* + h(b - c)$. Then, $Tr = 2a_{11}$, $\Delta = (a_{11} + a_{12})(a_{11} - a_{12})$, $Tr^2 - 4\Delta = 4a_{12}^2 > 0$. Therefore, Tr has the same sign as f_1, Δ has the same sign as $(f_1 + f_2)(f_1 - f_2)$, and the eigenvalues of $J(E)$ for the symmetric interior equilibrium are all real, no oscillations exist. We have:

$$f_1 + f_2 = -a(b+r)x^{*2} - 2ah(b+r)x^* + h(b - c - arh),$$

$$f_1 - f_2 = -a(b+r)x^{*2} + 2(c - ahr)x^* - h(b - c + arh).$$

Let $f = a(r+b)x^{*2} + (c - b - r + d + ahr)x^* + h(d - r)$, it is easy to verify that f intersects with $f_1 + f_2$ on their axis of symmetry (one positive and one negative). $E_i\left(x_i^*, y_i^*\right)$ correspond to the positive real roots of Eq. (10), i.e., $f_{E_i} = 0$, $i = 1, 2$. According to the opening directions and the convexity and concavity of f and $f_1 + f_2$, we can conclude that $(f_1 + f_2)_{E_1} > f_{E_1} = 0$, $(f_1 + f_2)_{E_2} < f_{E_2} = 0$, $(f_1 - f_2)_{E_i} = (3c - b + d - r - ahr)x_i^* - h(b - c - d + r + arh)$, $i = 1, 2$.

Let $(f_1 - f_2)^* = (3c - b + d - r - ahr)x^* - h(b - c - d + r + arh)$, it intersects the x-axis at $x_0 = \frac{h(b-c-d+r+arh)}{3c-b+d-r-ahr}$, and has the same sign as $f_1 - f_2$ at $E_i\left(x_i^*, y_i^*\right)$, $i = 1, 2$. Since $c - b - r + d + ahr < 0$, $h(b - c - d + r + arh) > 0$.

Then, we can obtain the types of symmetric interior equilibria which are determined by the sign of $(f_1 - f_2)^*$ at $E_i\left(x_i^*, y_i^*\right)(i = 1, 2)$ for the following cases:

1. Case $3c - b + d - r - ahr < 0$, then the slope and intercept of $(f_1 - f_2)^*$ are negative, i.e., $(f_1 - f_2)_{E_1} < 0$, $(f_1 - f_2)_{E_2} < 0$. Since $(f_1 + f_2)_{E_1} > 0$ and $(f_1 + f_2)_{E_2} < 0$, $\Delta_{E_1} < 0$, $E_1\left(x_1^*, y_1^*\right)$ is a saddle; $f_{1_{E_2}} < 0$, $Tr_{E_2} < 0$, $\Delta_{E_2} > 0$, $E_2\left(x_2^*, y_2^*\right)$ is a stable node.
2. Case $3c - b + d - r - ahr > 0$,

(i) If $x_0 > x_2^*$, then $(f_1 - f_2)_{E_1} < 0$, $(f_1 - f_2)_{E_2} < 0$, and the types of symmetric interior equilibria are the same as in the first case.

(ii) If $x_1^* < x_0 < x_2^*$, then $(f_1 - f_2)_{E_1} < 0$, $(f_1 - f_2)_{E_2} > 0$. Since $(f_1 + f_2)_{E_1} > 0$ and $(f_1 + f_2)_{E_2} < 0$, $\Delta_{E_1} < 0$, $\Delta_{E_2} < 0$, $E_1\left(x_1^*, y_1^*\right)$, $E_2\left(x_2^*, y_2^*\right)$ are both saddles.

(iii) If $x_0 < x_1^*$, then $(f_1 - f_2)_{E_1} > 0$, $(f_1 - f_2)_{E_2} > 0$, Since $(f_1 + f_2)_{E_1} > 0$ and $(f_1 + f_2)_{E_2} < 0$, $f_{1_{E_1}} > 0$, $Tr_{E_1} > 0$, $\Delta_{E_1} > 0$, $E_1\left(x_1^*, y_1^*\right)$ is an unstable node; $\Delta_{E_2} < 0$, $E_2\left(x_2^*, y_2^*\right)$ is a saddle.

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Author Contributions All authors contributed to the study conception and design. Xue-meng Song, Yan-Ping Liu and Feng Zhang formulated the original approach and built the model. Xue-meng Song, Feng Zhang and Ming-Rui Song wrote codes and ran the analyses. Xue-meng Song wrote the first draft. All authors reviewed and edited the writing at all stages of revision. All authors read and approved the final manuscript.

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Declarations

Conflict of interest The authors declare that they have no Conflict of interest regarding the publication of this paper.

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