Morphological defense as a nonlinear trigger in an intraguild predation food web

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Abstract

Intraguild predation (IGP) is a type of interaction in which a top predator simultaneously competes and predates an intermediate prey that shares a third prey species with the top predator. While common in nature, most theoretical population dynamics models proposed in the literature predict that this three species interaction usually leads to extinction of the intermediate prey population. Predator-induced defenses are widely seen in these systems and should be incorporated in IGP models to promote coexistence. With this aim, we introduce a nonlinear response to the predation of IG-predator on IG-prey. The phase diagram of species coexistence is obtained as function of the attack efficiency and the degree of nonlinearity of the defense mechanism. Further we show how the nonlinearity affects the equilibrium populations. We unveil that there is an optimal nonlinearity at which the convergence towards the stationary coexistence regime is the fastest.

Keywords: Intraguild predation; Defense mechanism; Nonlinear-induced coexistence.

1. Introduction

Intraguild predation (IGP) is a class of omnivorous food web that combines predation and competition. Two species exploit the same environmental resource and one of them (the IG-predator) predates the other (IG-prey) [1]. Such kinds of food webs are theoretically predicted to decrease the potential of being stable, thus leading to extinction of both species [2]. Notwithstanding, intraguild predation is widespread [3, 4, 5, 6] and this ubiquitous interaction is commonly observed in nature. There are several biological mechanisms to pro-

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mote the persistence of the food web, namely defenses induced by the presence of the IG-predator. Experimental and observational studies showed different dynamical patterns in food webs where inducible defenses are present [7]. Such defenses bring into play changes in morphology [8, 9, 10, 11], life-history [12] and prey behavior [13, 14], to name a few.

Among the systems in which the predator-prey interactions allows for the growth of the intermediate prey, we highlight those on which a morphological defense is induced by the predator presence. In a recent paper, Kratina et al. [7] studied the dynamical properties of a food web consisting of the resource food, a type of unicellular algae, *Rhodomonas minuta*, which is consumed by both the turbellarian flatworm, *Stenostomum virginianum*, and the hypotrich ciliates of genes *Euplotes* spp, while the last is also consumed by the flatworm. In the presence of its predator, the Euplotes changes the morphology increasing substantially the body size, avoiding predation by the flatworm which is a gape-limited predator. Consequently, in the defensive form, the Euplotes are too big to gobble and could promote the species survival and then the persistence of the food web. Simplification on the IGP model to a two-species community with an unlimited resource food proved too simple on account of the low complexity of the system [2, 15, 16]. However, when it is required to take into account the temporal evolution of the resource food, the proper modelling of morphological defenses has been a challenging task [17, 18, 19, 20, 21, 22].

Dealing with two species only, Vos et al. [23] showed, with realistic parameters, how consumer-induced defenses are important to bottom-up control using food chain models. Ramos-Jiliberto et al. [24] explored pre- and post-encounter inducible defenses in predator-prey systems that have similar dynamical effects and show that inducible defenses prevent the paradox of enrichment and should increase the stability. Using dynamic-optimization models, Clark and Harvell [25] studied the cost of defense. Adding of a "delayed" term in reproduction was shown to favor a higher allocation to defense. A model for the predator-induced defense that analyzes the cost-benefit of the defensive morph was introduced in *D. pulex* by modifying the life-time of both induced and normal morphologies

for different predation rates of *Chaoborus*, showing that the inducible defense could be less advantageous in certain cases [26]. Those studies are applied to the complexity of populations dynamics models with up to two species only or with a weak interaction with the resource food [2, 15, 16, 27]. When increasing the complexity of the food webs, with strongly interacting species, the models become more and more unstable and stability requires that the IG-prey be a better competitor than IG-predator [28, 29]. In order to include inducible defenses to obtain the species coexistence in an IGP model, Nakazawa et al. [18] incorporated predator-specific defense adaptation of resource food against both IG- prey and predator, showing clearly that this mechanism favors the coexistence. A key study made by Holt and Huxel [19], focused on the three-species community. The authors introduced other types of community modules as alternate prey. They brought to light the great influence of alternate prey in the persistence of the food web as well as presented a discussion concerning the models with Lotka-Volterra-like functional responses, which are clearly limited. The authors emphasized that it should be necessary to use other nonlinear response models [30, 31] to properly deal with the defense mechanism.

In this work, we introduce morphological defenses in an IGP model, treating the dynamical evolution of the three-specie community. Inserting a nonlinear trigger, we show that it is possible to switch from extinction of the IG-prey (without defenses) to the persistence of the food web (within defenses). We also build a phase diagram in parameter space spanned by the degree of nonlinearity associated to the defense mechanism and attack efficiency of the IG-predator to the IG-prey. Finally, we determine how the rate of convergence to the coexistence regime depends on the degree of nonlinearity introduced into the IG-prey /IG-predator interaction.

2. IG predator-prey model

A basic three-dimensional model of the intraguild predation considers a resource population R (an algae) which is consumed by an herbivorous population E (protozoa), the IG-prey, and by an omnivorous population S (turbellarian

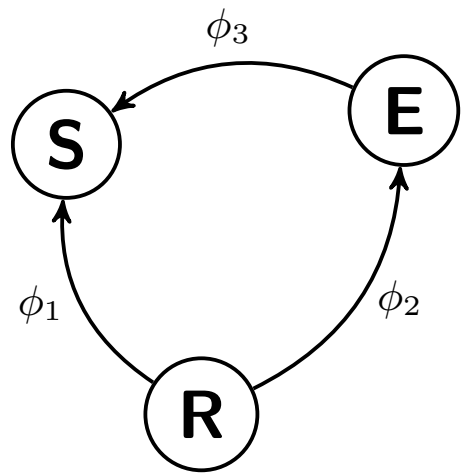

Figure 1: Food web scheme. Arrows indicate that one species (base arrow) is eaten by a second one with a certain functional response ϕ. R stands for the resource, E for the intraguild prey and S for the intraguild predator.

flatworm), the IG-predator. The resource food population R increases logistically and is consumed at rate $-S\phi_1(R)$ by S and $-E\phi_2(R)$ by E, while the IG-prey is consumed by S at a rate $-S\phi_3(E)$, see Fig. 1. Here we add a response function ϕ_3 to the model which includes the morphological defense.

In the presence of the IG-predator, the IG-prey increases in size preventing its consumption and the change in body size brings out negative influences to the prey. As pointed out by Kratina et al. [7], when the S population is high in comparison to E the defense is activated and induces the persistence of the food web. In order to wide up these concepts, one can equivalently consider that the $S \to E$ attack quickly fades away whenever E is low. Conversely it presents a fast increase when the population E is large. The differential equations for this model are:

$$\frac{\mathrm{d}R}{\mathrm{d}t} = rR\left(1 - \frac{R}{K}\right) - E\phi_2(R) - S\phi_1(R), \tag{1}$$

$$\frac{\mathrm{d}E}{\mathrm{d}t} = \varepsilon E\phi_2(R) - S\phi_3(E) - m_E E, \tag{2}$$

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \alpha S\phi_1(R) + \beta S\phi_3(E) - m_S S, \tag{3}$$

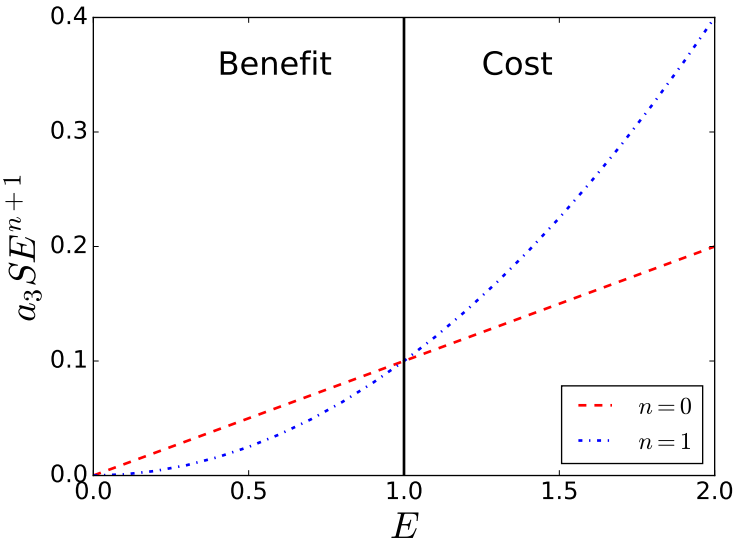

Figure 2: Illustrative plot of the linear and nonlinear IG-prey/IG-predator interaction. Parameters: $a_3 = 0.1$ and $S = 1$. Notice that the nonlinearity strongly suppresses the attack efficiency at low E populations.

where $\phi_{1,2}$ is Lotka-Volterra-like response functions. In ϕ_3 we include the morphological defense of the IG-prey by a nonlinear inducible defense. These functions will be assumed to have the form

$$\phi_{1,2}(R) = a_{1,2}R, \tag{4}$$

$$\phi_3(E) = a_3E^{n+1}, \tag{5}$$

where n is the degree of nonlinearity of the IG-predator/IG-prey interaction.

When the nonlinearity becomes increasingly stronger, the consumption of IG-prey rapidly approaches zero when the IG-prey population E is low. Nevertheless, the nonlinear response turns the IG-predator attack more efficient for higher densities of E. Note that, larger values of n leads to a stronger suppression of the attack efficiency, as shown in Fig. 2. For large E populations, this nonlinear coupling actually favors the consumption of E. This points to a relation between cost and benefit, that plays a key role in the dynamics and is a fundamental element to reach the persistence of the food web. However, as

the population of E is limited by the availability of resources, the regime with very large E population is not reached.

3. Results

3.1. Persistence of the food web

An analysis of the equilibrium points of the above dynamical system shows that the nonlinear defense has the potential to induce a stability switch of the facial fixed point $(R^*, 0, S^*)$. Solving $\mathbf{F}(R^*, E^*, S^*) = 0$, where $\mathbf{F} = (\dot{R}, \dot{E}, \dot{S})^T$, we obtain the equilibrium points of the present dynamical system. The stability is determined by the eigenvalues ω of the Jacobian matrix $J(R^*, E^*, S^*)$, where $\det|J - \omega \boldsymbol{1}| = 0$. The stability is determined by the real part of the eigenvalues, say $\mathrm{Re}\{\omega\}$. Explicitly we have:

$$J = \begin{bmatrix} r - \frac{2r}{K}R - a_2E - a_1S & -a_2R & -a_1R \\ \varepsilon a_2 E & \varepsilon a_2 R - a_3(n+1)SE^n - m_E & -a_3E^{n+1} \\ \alpha a_1 S & \beta a_3(n+1)SE^n & \alpha a_1 R + \beta a_3 E^{n+1} - m_S \end{bmatrix}$$

There are two different Jacobians for $n = 0$ and $n \neq 0$ when $E^* = 0$. For the facial fixed point $(R^*, 0, S^*) = (\frac{m_S}{\alpha a_1}, 0, \frac{r}{a_1}(1 - \frac{m_S}{\alpha a_1 K}))$ we obtain:

$$J_n = \begin{bmatrix} -\frac{rm_S}{\alpha a_1 K} & -\frac{a_2 m_S}{a_1 \alpha} & -\frac{m_S}{\alpha} \\ 0 & \frac{\varepsilon a_2 m_S}{\alpha a_1} - m_E & 0 \\ \alpha r(1 - \frac{m_S}{\alpha a_1 K}) & 0 & 0 \end{bmatrix}, \tag{6}$$

$$J_0 = \begin{bmatrix} -\frac{rm_S}{\alpha a_1 K} & -\frac{a_2 m_S}{a_1 \alpha} & -\frac{m_S}{\alpha} \\ 0 & \frac{\varepsilon a_2 m_S}{\alpha a_1} - m_E - \frac{a_3}{a_1} r(1 - \frac{m_S}{\alpha a_1 K}) & 0 \\ \alpha r(1 - \frac{m_S}{\alpha a_1 K}) & \beta \frac{a_3}{a_1} r(1 - \frac{m_S}{\alpha a_1 K}) & 0 \end{bmatrix}, \tag{7}$$

with the eigenvalues given by:

$$\omega_\pm = \frac{1}{2}\left[-\frac{rm_S}{\alpha a_1 K} \pm \sqrt{\left(\frac{rm_S}{\alpha a_1 K}\right)^2 - 4rm_S\left(1 - \frac{m_S}{\alpha a_1 K}\right)}\right], \tag{8}$$

$$\omega_n = \frac{\varepsilon a_2 m_S}{\alpha a_1} - m_E, \tag{9}$$

$$\omega_0 = \omega_n - \Delta\omega. \tag{10}$$

Here $\Delta\omega = \omega_n - \omega_0 = \frac{a_3}{a_1} r \left(1 - \frac{r m_S}{\alpha a_1 K}\right)$ bring us the difference in stability between the linear and nonlinear response models. $\Delta\omega$ will tell us if it is possible to have a stability switch by introducing the nonlinear inducible defense on the form of Eq. 5. In fact, the fixed point is stable if $\mathrm{Re}\{\omega\} < 0$ for all ω and unstable otherwise.

Table 1: Parameters used in the present study. They were chosen to have the facial fixed point $(R^*, 0, S^*)$ stable in the regime of linear IG-prey/IG-predator interaction.

	Meaning	Value
r	Growth rate	1.5
K	Carrying capacity	5
ε	Attack rate $E \to R$	1.2
α	Attack rate $S \to R$	1
β	Attack rate $S \to E$	0.75
$a_{1,2,3}$	Attack efficiency	0.75,1.5,0.1
m_E	Death rate of E population	0.25
m_S	Death rate of S population	0.15
n	Degree of inducible defense	-

The following numerical analysis was made using the set of parameters shown in Table 1. We find that the $\mathrm{Re}\{\omega_\pm\} < 0$, $\omega_n > 0$ and $\Delta\omega > \omega_n$. Thus in the basic linear model ($n = 0$) the facial point $(R^*, 0, S^*)$ is stable. With the nonlinear trigger, this fixed point becomes unstable for all $n \neq 0$. One reasonable assumption is that the stability switch of the facial fixed point is actually followed by stability switches of other (possibly internal) fixed points. In Fig. 3 we show via numerical solutions of the dynamical equations that the stable point $(R^*, 0, S^*)$ becomes unstable whereas the unstable point (R^*, E^*, S^*) switches to stable when we introduce the nonlinear defense. Another interesting fact is that even if the IG-prey is a better competitor, we still get similar results, reaching the persistence of the food web. We are thus led to conclude that the nonlinear response associated to the defense mechanism is a fundamental tool to preserve the food web.

The population densities in equilibrium (fixed point) depend on the degree of nonlinear defense besides the other usual dynamical parameters. Fig. 4 show us the dependence of the stationary populations in the internal fixed point

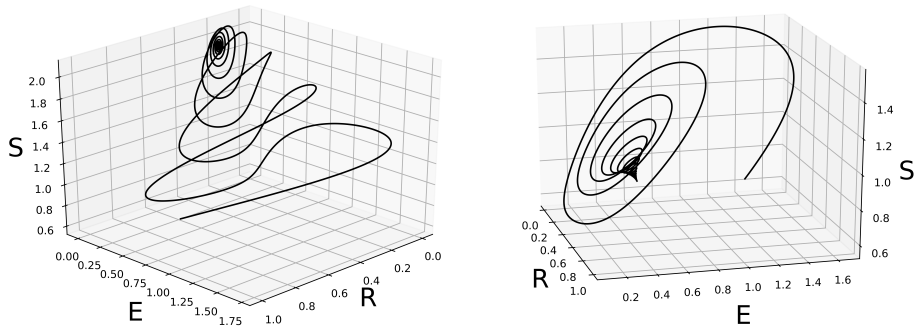

Figure 3: (left) Phase space for $n = 0$ for which we recover the basic model and the E population is extinct. (right) With a nonlinear defense response with $n = 1$ the food web persists. Parameters are given in Table 1.

(coexistence point) against the degree of nonlinearity n. Note that there is a characteristic value of the degree of nonlinear defense above which the equilibrium density of the population of the IG-predator S is zero. Above this value, the defense is so effective that it can lead to the extinction of the population of the IG-predator. This characteristic nonlinearity n^* was determined analytically by analyzing the linear stability of the facial fixed point with only $S^* = 0$ and determining under which condition its stability changes. As a function of the model parameters, it is given by

$$n^* = \ln\left(\frac{m_S - \alpha a_1 R^*}{\beta a_3}\right) / \ln(E^*) - 1, \tag{11}$$

where $R^* = \frac{m_E}{\varepsilon a_2}$ and $E^* = \frac{r}{a_2}\left(1 - \frac{m_E}{\varepsilon a_2 K}\right)$. For the set of parameters used in our numerical work, this characteristic nonlinearity is $n^* \simeq 16.48$.

The attack efficiency of the top predator in the intermediate prey is modulated by two parameters: the linear attack efficiency a_3 and the degree of nonlinear inducible defense n ($n = 0$ means linear). With a fixed n, a_3 controls the attack efficiency while, with a fixed a_3, n controls the defense efficiency (or the attack inefficiency). If we fix all parameters except a_3 and n, we obtain $n^* = A + B\ln(a_3)$ where A and B depend on the system parameters. Based on the above phenomenology, we built a phase diagram by varying these two pa-

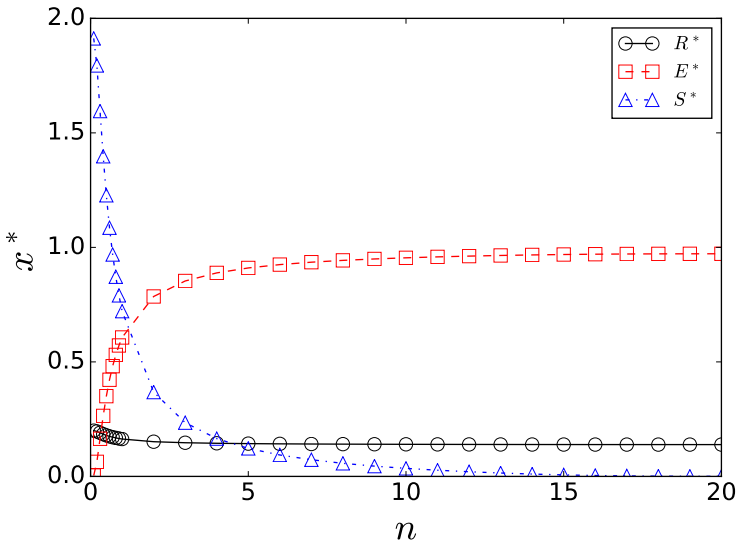

Figure 4: Dependence of the populations at the coexistence equilibrium point on the degree of nonlinear defense. Notice that any degree of nonlinearity leads to the persistence of the IG-prey population. The food web is stable for $n < n^*$. Above this point the IG-predator population becomes extinct. Here x represents either R,E or S. Parameters are given in Table 1.

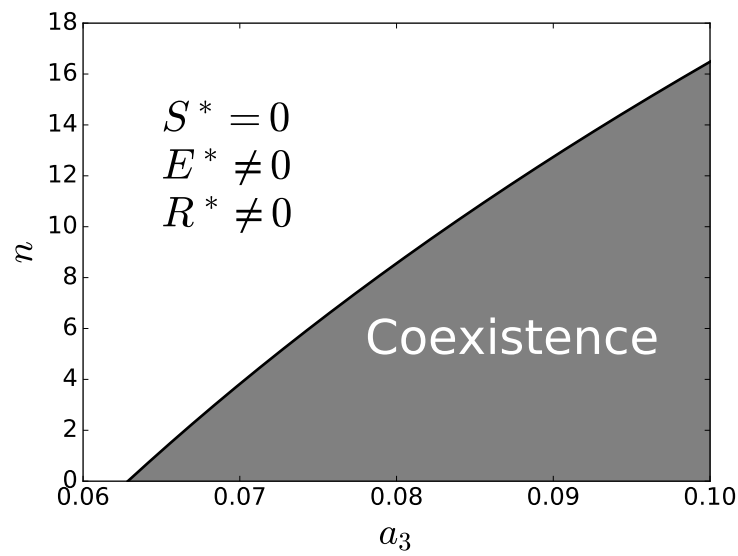

Figure 5: Phase diagram in the parameter space spanned by the attack efficiency a_3 and nonlinearity n. The solid black line shows the characteristic nonlinearity of the defense n^* below which coexistence is stable, although the IG-prey population continuously decreases as $n \to 0$. For $n > n^*$ the IG-predator becomes extinct. Parameters are given in Table 1.

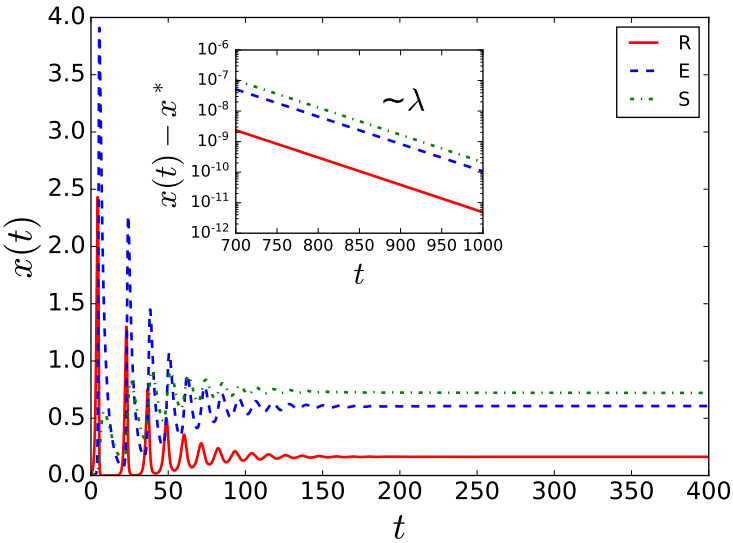

Figure 6: Time evolution of the population densities for $n = 1$. The inset shows the long-time behavior dominated by the lowest Lyapunov exponent λ. Here x represents either R,E or S. Parameters are given in Table 1.

rameters such that below the n^* curve, we obtain the coexistence of all species, see Fig. 5. However, it is important to stress that, the IG-prey population in equilibrium continuously decreases as $n \to 0$ in this regime. For $n > n^*$ the attack is so inefficient that it leads to the extinction of the IG-predator population.

3.2. Rate of convergence to the coexistence equilibrium

The dynamical behavior of the system can be written in terms of the eigenvectors of the Jacobian matrix $\vec{v}_i$ $(i = 1, 2, 3)$. Near the fixed point (in a linear approximation) we have $v_i(t) \approx v_i(0)e^{\omega_i t}$, where ω_i is the corresponding eigenvalue. In populations dynamics terminology, we say that the eigenvectors are the principal directions to the dynamics of the interacting populations and the eigenvalues are precisely the Lyapunov exponents that will govern the convergence to the possible equilibrium conditions. Then, near the equilibrium point (fixed point), we have

$$x(t) \approx A_x e^{\omega_+ t} + B_x e^{\omega_- t} + C_x e^{\omega_n t} \tag{12}$$

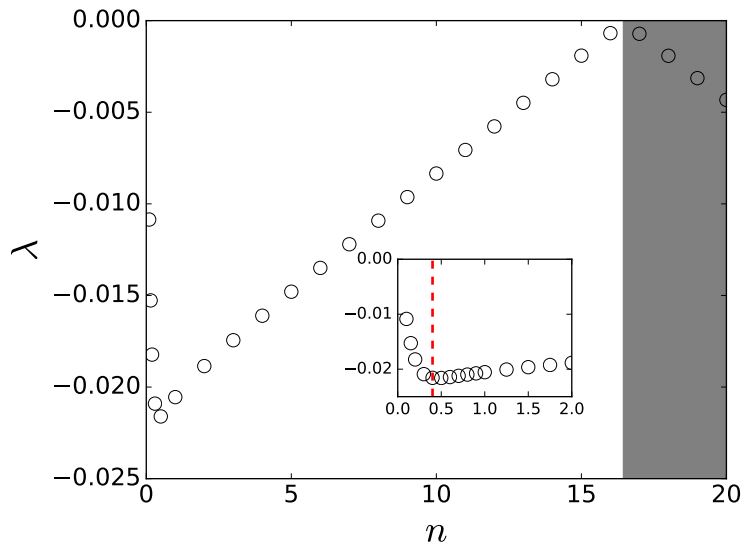

Figure 7: Lyapunov exponent against the degree of nonlinearity. Grey region indicates the deterioration of the food web characterized by the extinction of S population which occur above a critical value n^*. The inset shows that the optimal Lyapunov exponent leading to the fastest convergence to coexistence occurs at $n \simeq 0.45$ (red dashed line). Parameters are given in Table 1.

where x represents either E,R or S.

At an stable equilibrium, all eigenvalues have negative real parts. The asymptotic long-time behavior of the system is governed by the Lyapunov exponent with the smaller real part (in modulus), say λ, i.e. $x(t) - x^* \propto e^{\lambda t}$. Fig. 6 shows the time evolution of all species. In the inset we show the long-time exponential convergence to the equilibrium populations. All of them are governed by a single Lyapunov exponent $\lambda = \omega_n$. The precise value of the lowest Lyapunov exponent was determined from the Jacobian matrix for the internal and facial $(R^*, E^*, 0)$ fixed points.

We calculated the Lyapunov exponents for various values of n, as shown in Fig. 7. With a strong nonlinearity degree $n > n^*$ (grey region) the top predator attack is so inefficient that the IG-prey population overcomes and S is extinct. In this regime the Lyapunov exponent actually governs the rate of convergence towards the facial $(R^*, E^*, 0)$ fixed point. Below n^* the Lyapunov exponent characterizes the rate of convergence towards the coexistence fixed point. It vanishes at n^* as well as at $n = 0$ where the facial $(R^*, 0, S^*)$ becomes stable. Therefore, the rate of convergence to the coexistence equilibrium point depends non monotonically of the nonlinearity degree of the defense mechanism. There is a regime of weak nonlinearities for which the rate of convergence grows with n. On the other hand, it becomes slower as n approaches n^*. The threshold from weak to moderate nonlinearities can be delimited by the condition leading to the fastest convergence to the internal fixed point. For the parameters set used, it occurs roughly at $n = 0.45$.

4. Summary and Conclusions

In summary, we introduced a three species population dynamics model on which a top predator and an intermediate species share the same resource. The dynamic equations only on rare occasions support a stationary coexistence solution of all three populations when the attack of the top predator to the intermediate species is linear. Motivated by the ubiquitous existence of coexistence food webs in nature and of experimental data reporting defense mechanisms of the

intraguild species, we considered a nonlinear attack term to model the defensive response. As the degree of nonlinear defense n increases, the attack becomes more inefficient for low populations of the intraguild species, thus favoring a coexistence regime.

We provided a detailed analysis of the proposed model of a nonlinear interaction between the top predator and the intermediate prey. We demonstrated that the nonlinearity induced by the defense mechanism actually induces the emergence of a wide regime of species coexistence. However, the attack can become so inefficient for very strong nonlinearities that it may lead to the extinction of the top predator population. Coexistence is found to be stable for $0 < n < n^*$, where n^* was shown to grow logarithmically with the linear attack efficiency. We further unveiled that there is an optimal nonlinearity degree for which the rate of convergence towards the coexistence equilibrium is the fastest. This finding can be of evolutionary relevance since natural selection usually drives the interaction between surviving populations to the most adapted condition [29, 32, 33]. The here introduced model can be extended to more complex food web networks. It would be interesting to explore the role played by such nonlinear defense mechanism in other population dynamics models. We hope the present work also motivate experimental works aiming to estimate the degree of nonlinear defense in intraguild predation food webs.

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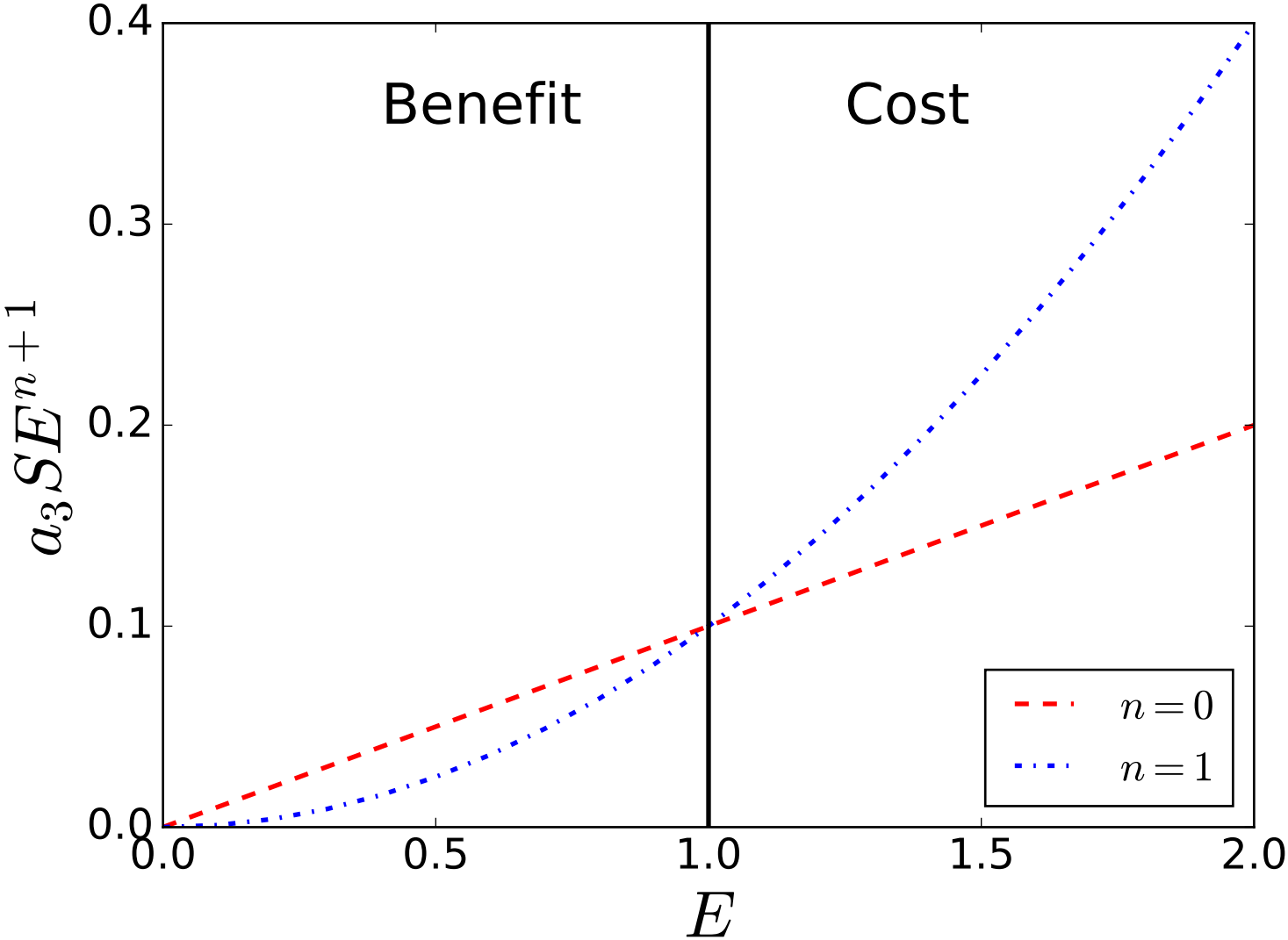
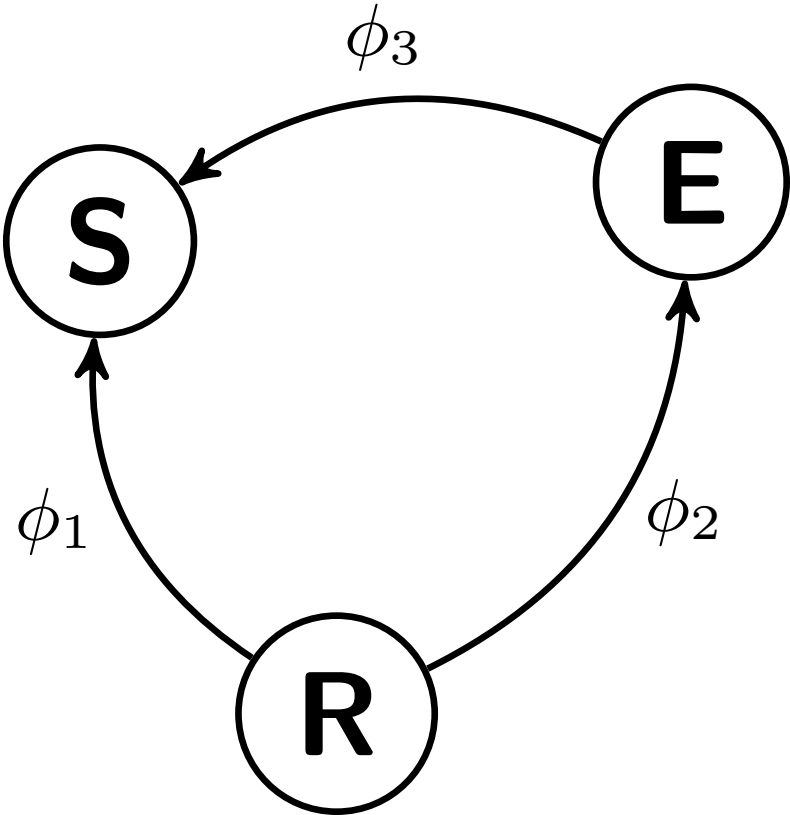
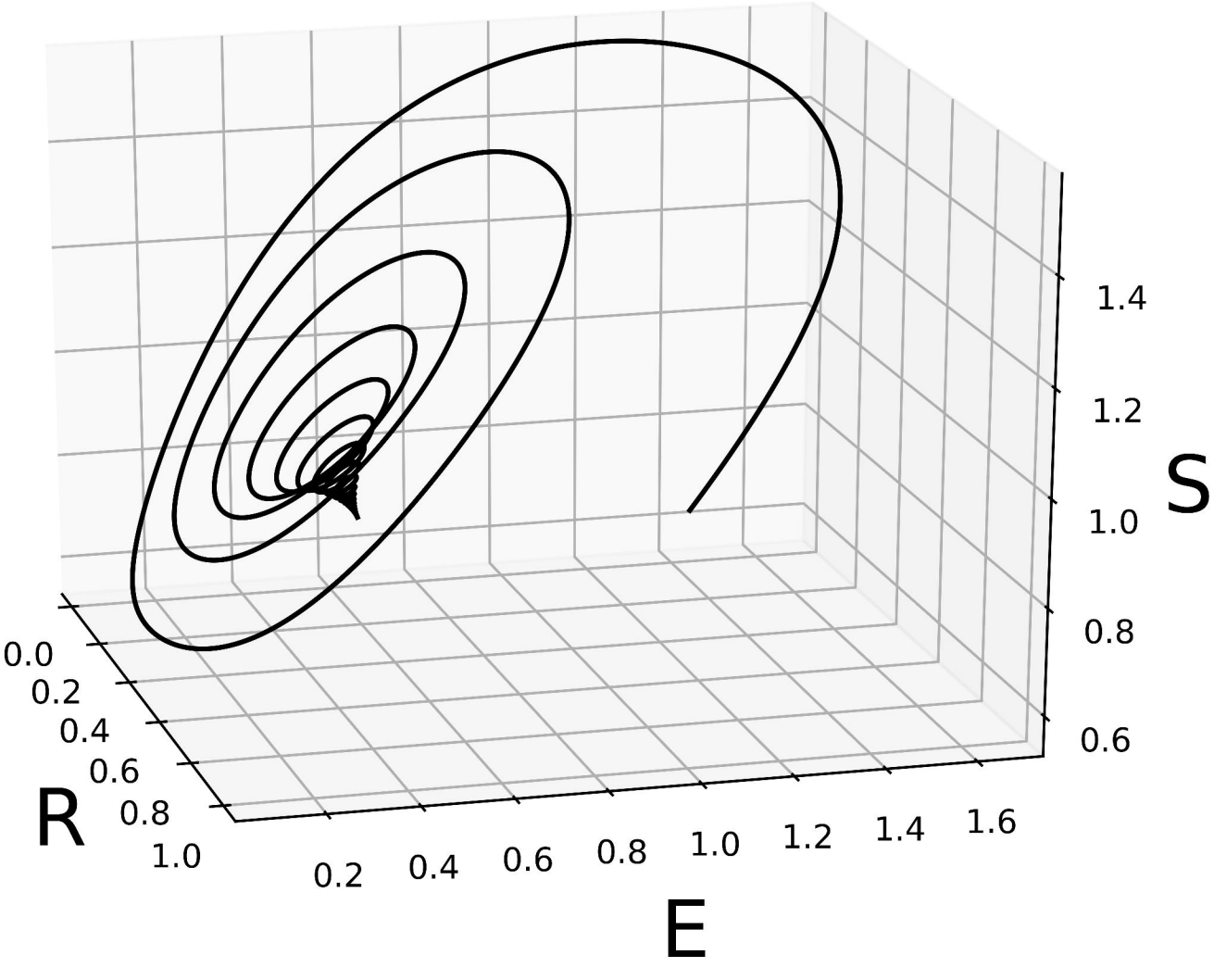
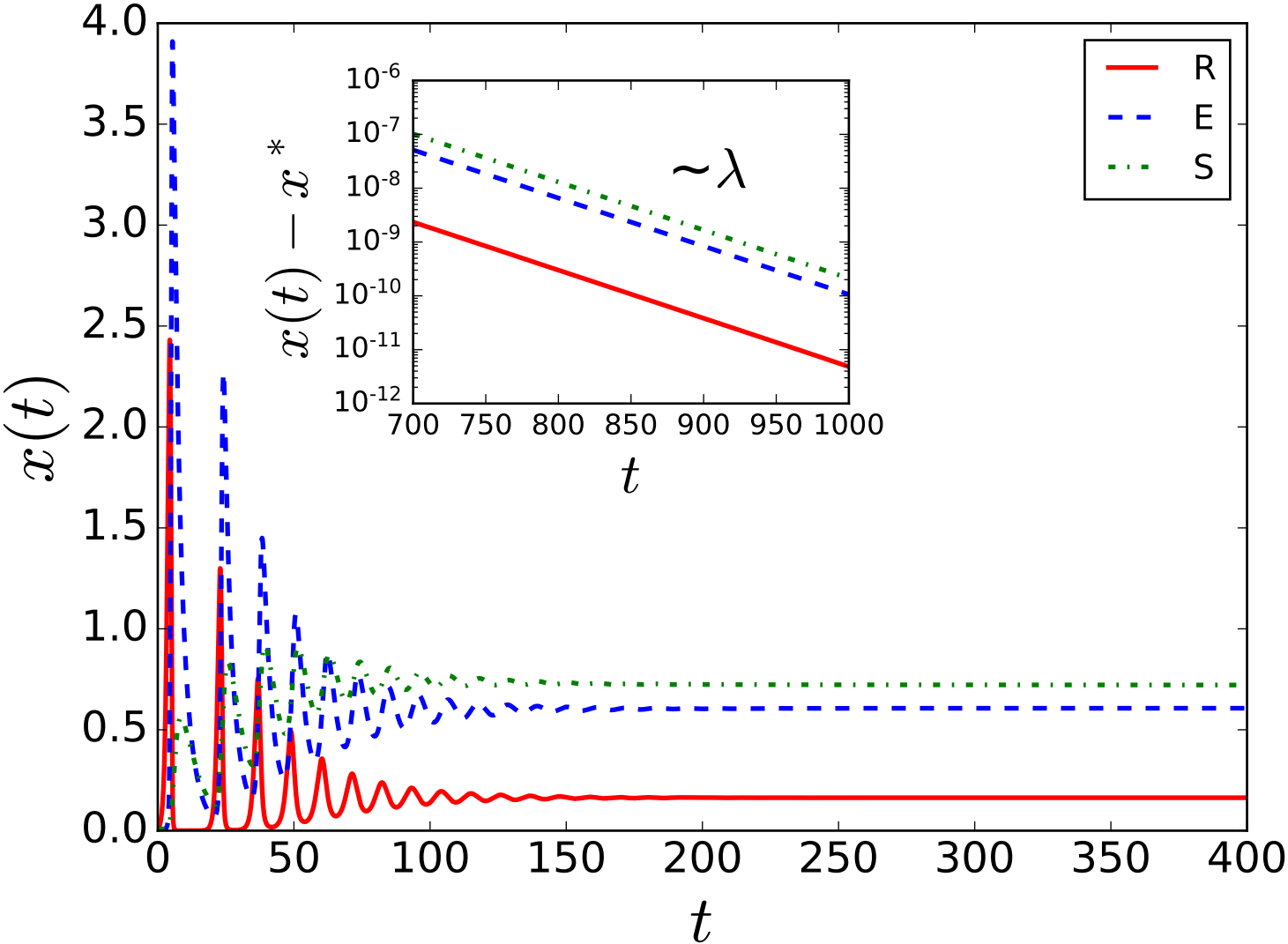
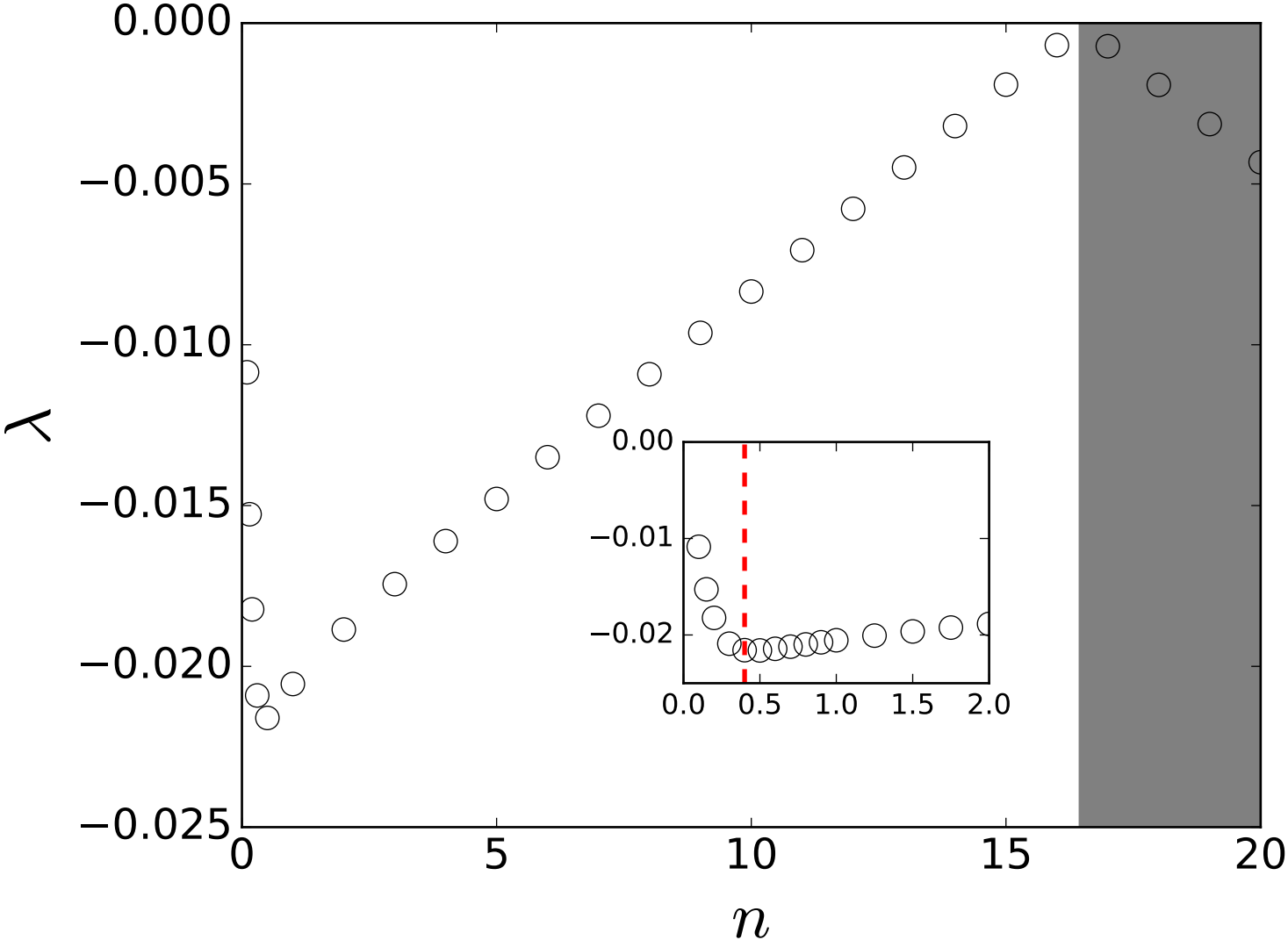
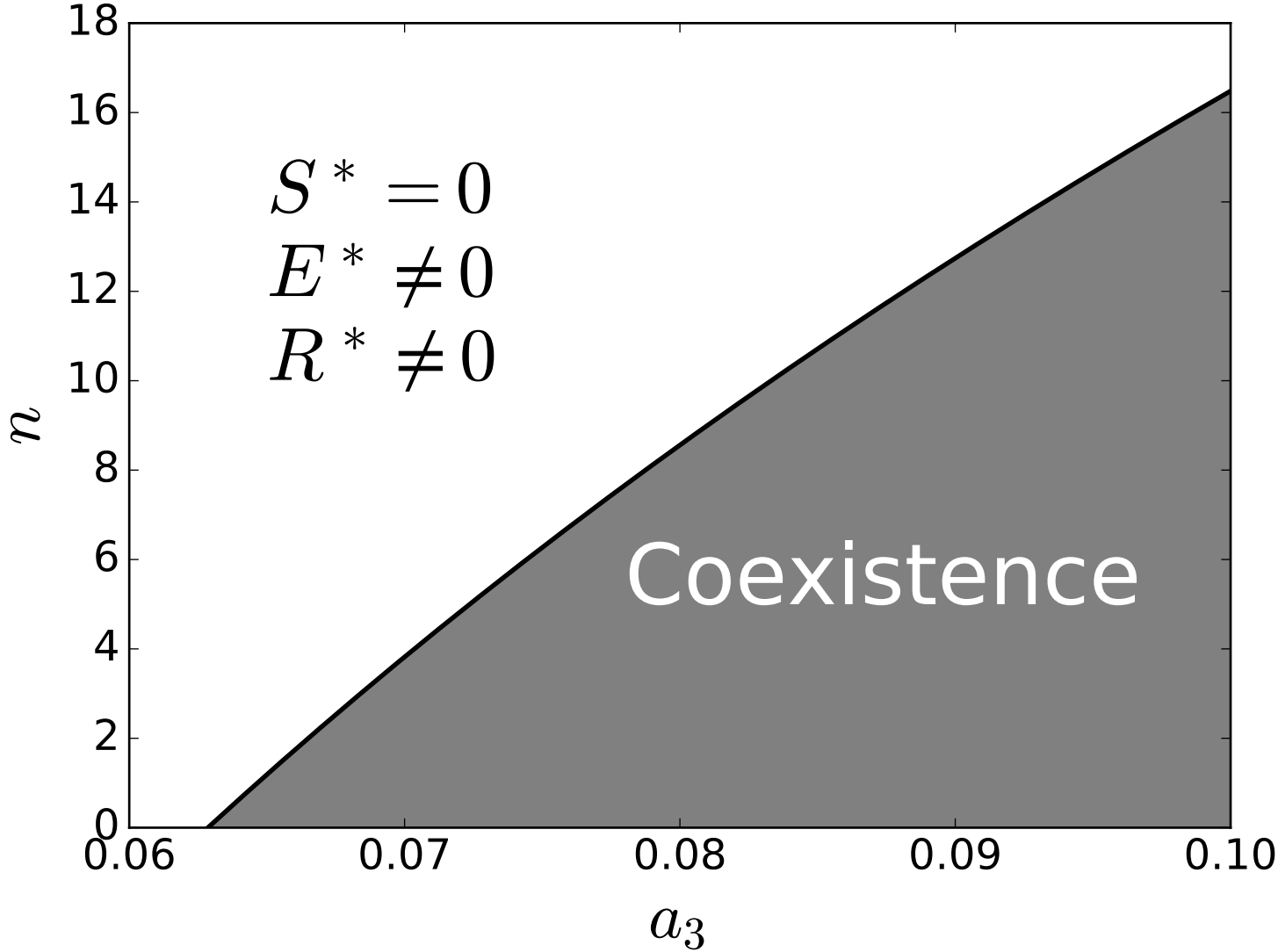

Benefit
Cost
$n = 0$
$n = 1$
$a_3 S E^{n+1}$
E
0.0
0.1
0.2
0.3
0.4
0.0
0.5
1.0
1.5
2.0

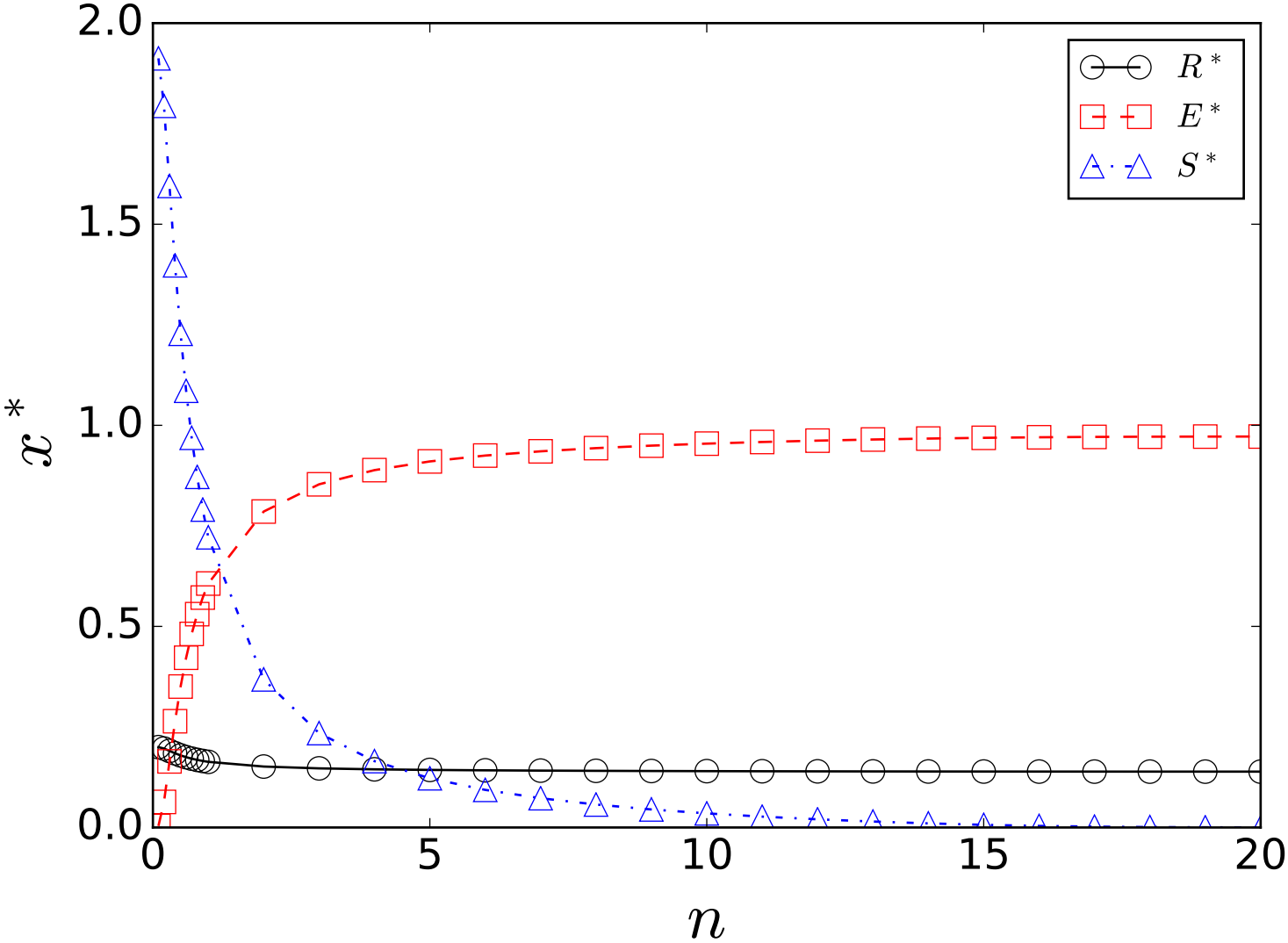

ϕ_3
S
E
ϕ_1
ϕ_2
R

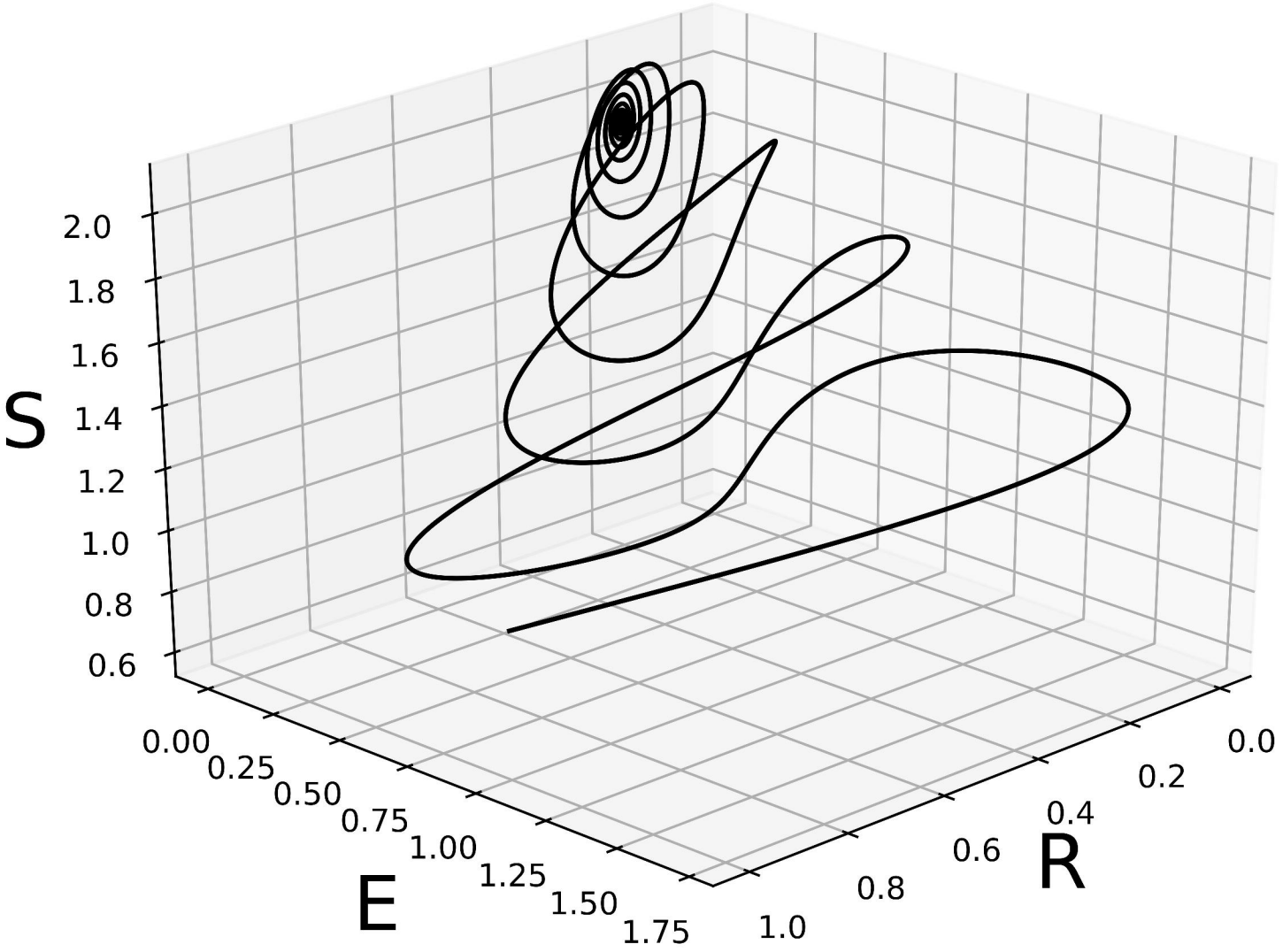

0.0
0.2
0.4
0.6
0.8
1.0
R
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
E
0.6
0.8
1.0
1.2
1.4
S


R
E
S
$x(t)$
t
$x(t) - x^*$
$\sim\lambda$
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
50
100
150
200
250
300
350
400
10^{-6}
10^{-7}
10^{-8}
10^{-9}
10^{-10}
10^{-11}
10^{-12}
700
750
800
850
900
950
1000


0.000
−0.005
−0.010
−0.015
−0.020
−0.025
0
5
10
15
20
λ
n
0.00
−0.01
−0.02
0.0
0.5
1.0
1.5
2.0


$S^* = 0$
$E^* \neq 0$
$R^* \neq 0$
Coexistence
n
a_3
0
2
4
6
8
10
12
14
16
18
0.06
0.07
0.08
0.09
0.10


2.0
1.5
1.0
0.5
0.0
0
5
10
15
20
x^*
n
R^*
E^*
S^*


S
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
E
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
R
0.0
0.2
0.4
0.6
0.8
1.0