Weak selection and the separation of eco-evo time scales using perturbation analysis

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Abstract

We show that under the assumption of weak frequency-dependent selection a wide class of population dynamical models can be analysed using perturbation theory. The inner solution corresponds to the ecological dynamics, where to zeroth order, the genotype frequencies remain constant. The outer solution provides the evolutionary dynamics and corresponds, to zeroth order, to a generalisation of the replicator equation. We apply this method to a model of public goods dynamics and show that the error between the composite solution, which describes the dynamics for all times, and the solution to the full model scales linearly with the strength of selection.

Keywords: eco-evo dynamics, pertubation analysis, time scales

1 Introduction

The processes that affect the size and composition of natural populations occur on a wide range of spatial and temporal scales. For example, speciation can occur due to spatial segregation of subpopulations, which genetically diverge due to adaptions to the local environment [1]. Spatial variation of the environment on smaller scales typically leads to trade-offs such as the growth-mortality trade-off among tropical trees which is caused by variation in light availability [2].

In terms of temporal effects it was previously held that measurable evolutionary change required vast amounts of time, on the order of thousands or millions of generations, to occur, and that therefore there was a clear separation between evolutionary and ecological dynamics. The latter occurs on the order of ten generations or less, but recent field studies and theoretical work

has contradicted this clear cut separation and instead shown that evolution can occur over tens of generations, blurring the difference between evolutionary and ecological dynamics [3]. This rapid change can be driven by a changing environment, e.g. as in the industrial melanism in the peppered moth [4], or as in the case of Darwin's finches by migration into a novel environment with many adaptive peaks [5].

The entanglement of eco-evo time scales raises the question of when it is valid to speak of evolutionary and ecological dynamics as two separate processes. One way to answer this question is to make use of perturbation analysis, which formalises the idea of processes acting on different time scales [6, 7], and makes it possible to quantify the error which the assumption of an absolute separation of time scales introduces. Perturbation analysis is applicable when a model contains a very small (or very large) parameter and aims at expressing the solution as a power series in this small parameter. The first term in this infinite series corresponds to an absolute separation of time scales, and higher order terms provide a correction to the zeroth order approximation. In ecology this method has been used in order to show that the logistic equation can be derived by assuming a separation of time scales between trophic levels, where the resource dynamics occurs on a much faster time scale compared to the population dynamics [8, 9].

Here we apply perturbation analysis to a general population dynamical model where the small parameter corresponds to the difference in frequency-dependent selection between different genotypes. We show that if selection is weak the model can be split up into distinct parts describing the evolutionary and ecological dynamics. We also apply the method to a specific model of public goods dynamics and quantify the error introduced by the zeroth order approximation. Lastly, we discuss the relation between our framework and other methods for deriving approximate models in population dynamics.

2 General model

We consider N interacting subpopulations that represent distinct genotypes (or phenotypes). The population dynamics are assumed to be deterministic and driven exclusively by birth and death and we currently disregard the effects of migration and mutation, although these processes could be added to the model. The dynamics are then governed by the following system of coupled ordinary differential equations:

$$\frac{dx_i}{dt} = F_i(\mathbf{x})x_i - D_i(\mathbf{x})x_i, i = 1, ..., N \tag{1}$$

where $F_i(\mathbf{x})$ is the per capita birth rate and $D_i(\mathbf{x})$ is the per capita birth rate of genotype i, which in this general setting depend on size of all subpopulations population $\mathbf{x} = (x_1, x_2, ..., x_N)$ We now assume that both the birth rate and death rate can be decomposed into the product of a frequency-dependent and

a density-dependent factor, i.e.

$$F_i(\mathbf{x}) = f_i(\mathbf{u})g(s) \tag{2}$$
$$D_i(\mathbf{x}) = d_i(\mathbf{u})h(s) \tag{3}$$

where the frequency-dependent factors f_i and d_i depend on the frequency of all types $\mathbf{u} = (u_1, ..., u_N)$, where $u_i = x_i / \sum_{j=1}^N x_j$ and the density-dependent factor depends on the total population size $s = \sum_{i=1}^N x_i$, and are equal for all genotypes. We thus obtain the following system

$$\frac{dx_i}{dt} = f_i(\mathbf{u})g(s)x_i - d_i(\mathbf{u})h(s)x_i, i = 1, ..., N. \tag{4}$$

2.1 Change of variables

In order to get a better understanding of the dynamics of this system we make a change of variables to obtain a system of ODEs for the variables $(\mathbf{u}, s)$. Denoting time derivative with a dot, the rate of change of u_i can be written

$$\begin{aligned}
\frac{du_i}{dt} &= \frac{d}{dt}\left(\frac{x_i}{\sum_{j=1}^N x_j}\right) = \frac{\dot{x_i}\sum_{j=1}^N x_j - x_i\left(\sum_{j=1}^N \dot{x_j}\right)}{\left(\sum_{j=1}^N x_j\right)^2} = \\
&= \frac{(f_i(\mathbf{u})g(s)x_i - d_i(\mathbf{u})h(s)x_i)s - x_i\left(\sum_{j=1}^N f_j(\mathbf{u})g(s)x_j - d_j(\mathbf{u})h(s)x_j\right)}{s^2} = \\
&= u_i\left(f_i(\mathbf{u})g(s) - d_i(\mathbf{u})h(s)\right) - u_i\left(\sum_{j=1}^N f_j(\mathbf{u})g(s)u_j - d_j(\mathbf{u})h(s)u_j\right) = \\
&= u_i\left[\left(f_i(\mathbf{u}) - \sum_{j=1}^N u_j f_j(\mathbf{u})\right)g(s) - \left(d_i(\mathbf{u}) - \sum_{j=1}^N u_j d_j(\mathbf{u})\right)h(s)\right].
\end{aligned}$$

In order to simplify this expression we note that sums in the last expression are equal to the average frequency-dependent birth and death rates, which we denote:

$$\bar{f}(\mathbf{u}) = \sum_{j=1}^N u_j f_j(\mathbf{u}) \tag{5}$$

$$\bar{d}(\mathbf{u}) = \sum_{j=1}^N u_j d_j(\mathbf{u}) \tag{6}$$

With these definitions we obtain:

$$\frac{du_i}{dt} = u_i\left[\left(f_i(\mathbf{u}) - \bar{f}(\mathbf{u})\right)g(s) - \left(d_i(\mathbf{u}) - \bar{d}(\mathbf{u})\right)h(s)\right].$$

We now assume that the frequency-dependent birth and death rate for genotype i can be expressed as a baseline birth/death rate (common to all genotypes) plus a genotype-specific term of order ε:

$$\begin{aligned} f_i(\mathbf{u}) &= f_0(\mathbf{u}) + \varepsilon\phi_i(\mathbf{u}) \\ d_i(\mathbf{u}) &= d_0(\mathbf{u}) + \varepsilon\eta_i(\mathbf{u}), \end{aligned} \tag{7}$$

where $\varepsilon \ll 1$ and $\phi_i(\mathbf{u})$, $\eta_i(\mathbf{u})$ are some functions that depend on the frequency of all genotypes. This assumption implies that the difference between the birth rate of genotype i and the mean birth rate $f_i(\mathbf{u}) - \bar{f}(\mathbf{u}) = \varepsilon(\phi_i - \bar{\phi})$, where $\bar{\phi} = \sum_i \phi_i u_i$, i.e. selection is weak.

This results in the following equation for each u_i:

$$\frac{du_i}{dt} = \varepsilon u_i \left[\left(\phi_i(\mathbf{u}) - \bar{\phi}(\mathbf{u})\right) g(s) - \left(\eta_i(\mathbf{u}) - \bar{\eta}(\mathbf{u})\right) h(s) \right].$$

We now proceed to derive an equation for the total population size.

$$\frac{ds}{dt} = \frac{d}{dt}\left(\sum_{i=1}^{N} x_i\right) = \sum_{i=1}^{N} \dot{x}_i = \sum_{i=1}^{N} f_i(\mathbf{u})g(s)x_i - d_i(\mathbf{u})h(s)x_i \tag{8}$$

$$\begin{aligned} &= g(s)\sum_{i=1}^{N} f_i(\mathbf{u})x_i - h(s)\sum_{i=0}^{N} d_i(\mathbf{u})x_i = g(s)s\bar{f}(\mathbf{u}) - h(s)s\bar{d}(\mathbf{u}) \\ &= g(s)s(f_0(\mathbf{u}) + \varepsilon\bar{\phi}(\mathbf{u})) - h(s)s(d_0(\mathbf{u}) + \varepsilon\bar{\eta}(\mathbf{u})) \end{aligned} \tag{9}$$

where in the second to last step we used the fact that $x_i = su_i$. In summary we get the following coupled system of $N+1$ equations:

$$\frac{du_i}{dt} = \varepsilon u_i \left[\left(\phi_i(\mathbf{u}) - \bar{\phi}(\mathbf{u})\right) g(s) - \left(\eta_i(\mathbf{u}) - \bar{\eta}(\mathbf{u})\right) h(s) \right] \tag{10}$$

$$\frac{ds}{dt} = \varepsilon s \left[g(s)\bar{\phi}(\mathbf{u}) - h(s)\bar{\eta}(\mathbf{u}) \right] + s\left(g(s)f_0(\mathbf{u}) - h(s)d_0(\mathbf{u})\right). \tag{11}$$

We thus have $N+1$ equations that describe the dynamics in the $(s, \mathbf{u})$-space. However, note that one equation can be omitted since $u_N = 1 - \sum_{i=1}^{N-1} u_i$.

2.2 Perturbation solution

We would now like to express the solutions $u_i(t)$ and $s(t)$ as a power series in our small parameter ε (i.e. a perturbation solution):

$$\begin{aligned} u_i(t) &= u_{i0}(t) + \varepsilon u_{i1}(t) + \mathcal{O}(\varepsilon^2) \\ s(t) &= s_0(t) + \varepsilon s_1(t) + \mathcal{O}(\varepsilon^2). \end{aligned}$$

The next step is to insert this ansatz into (10), but here care has to be taken with expressions of the form $\phi_i(\mathbf{u})$ and $g(s)$, since we need to evaluate

expressions of the form $\phi_i\left(\mathbf{u}_0(t)+\varepsilon\mathbf{u}_1(t)+\mathcal{O}(\varepsilon^2)\right)$. Now if the functions are multivariate polynomials it is readily seen that

$$\phi_i\left(\mathbf{u}_0+\varepsilon\mathbf{u}_1+\mathcal{O}(\varepsilon^2)\right)=\phi_i(\mathbf{u}_0)+\mathcal{O}(\varepsilon), \tag{12}$$

and similarly

$$g\left(s_0+\varepsilon s_1+\mathcal{O}(\varepsilon^2)\right)=g(s_0)+\mathcal{O}(\varepsilon). \tag{13}$$

If our functions are not polynomials we can invoke the Stone-Weierstrass approximation theorem, which states that any continuous function defined on a compact subset $X\subset\mathbb{R}^N$ can be uniformly approximated by polynomials to any degree of accuracy [10]. If this should be the case we simply replace our original functions with the approximating polynomials and then make use of the property (12) and (13).

We now insert the perturbation ansatz into (10) and comparing terms of order ε^0 we get

$$\begin{aligned}\frac{du_{i0}}{dt}&=0\\ \frac{ds_0}{dt}&=s_0\left(g(s_0)f_0(\mathbf{u}_0)-h(s_0)d_0(\mathbf{u}_0)\right).\end{aligned}$$

This implies that the frequency is unchanged and $u_{i0}(t)=u_{i0}(t=0)$ for all $t\geq 0$, whereas the population size changes according to the difference between the density-dependent per capita growth rate $g(s_0)$ and death rate $h(s_0)$, each with a constant prefactor which depends on the baseline frequency-dependent birth/death rate of the initial frequency of genotypes $\mathbf{u}_0$.

This dynamics occurs on the $\mathcal{O}(1)$ time scale, and exclusively captures changes in population density. Therefore it is natural to define it as the ecological time scale. From the perspective of perturbation analysis this is usually referred to as the inner solution.

Higher-order corrections are obtained by comparing terms of order ε and higher, however this is not possible in this general setting where we have not specified the functions that describe frequency- and density-dependent birth and death rates. In the following section where we treat a specific model for which higher-order terms are obtained.

In order to describe the dynamics for large times on the order of $1/\varepsilon$ (the outer solution) we define a new time scale $\tau=\varepsilon t$ and express the solution as:

$$\begin{aligned}u_i(t)&=U_{i0}(\tau)+\varepsilon U_{i1}(\tau)+\mathcal{O}(\varepsilon^2)\\ s(t)&=S_0(\tau)+\varepsilon S_1(\tau)+\mathcal{O}(\varepsilon^2).\end{aligned}$$

The time derivates on this time scale are given by

$$\frac{dU_{i0}}{d\tau} = \frac{1}{\varepsilon}\frac{dU_{i0}}{dt}$$
$$\frac{dS}{d\tau} = \frac{1}{\varepsilon}\frac{dS}{dt}.$$

Using the power series ansatz yields, to order ε^0

$$\frac{dU_{i0}}{d\tau} = U_{i0}\left[\left(\phi_i(\mathbf{U}_0) - \bar{\phi}(\mathbf{U}_0)\right) g(S_0) - \left(\eta_i(\mathbf{U}_0) - \bar{\eta}(\mathbf{U}_0)\right) h(S_0)\right]$$
$$0 = S_0\left(g(S_0)f_0(\mathbf{U}_0) - h(S_0)d_0(\mathbf{U}_0)\right).$$

In order to eliminate S_0 from the first equation we need to make two of assumptions: firstly, assume that $S_0 \neq 0$ (i.e. the total population size is non-zero) and secondly assume that there exists an $S_0^\star \neq 0$ that solves the second equation $g(S_0)f_0(\mathbf{U}_0) = h(S_0)d_0(\mathbf{U}_0)$. This condition is equivalent to saying that for a fixed distribution of genotypes there exists an equilibrium population size where birth and death rate are equal. If this holds we can write

$$\frac{dU_{i0}}{d\tau} = U_{i0}\left[\left(\phi_i(\mathbf{U}_0) - \bar{\phi}(\mathbf{U}_0)\right) g(S_0^\star) - \left(\eta_i(\mathbf{U}_0) - \bar{\eta}(\mathbf{U}_0)\right) h(S_0^\star)\right], \tag{14}$$

which describes the dynamics on the $1/\varepsilon$ time scale. On this time scale the population size equilibrates instantaneously and we only capture the changes in frequency. It is therefore natural to think of this as the evolutionary time scale.

In summary the perturbation analysis shows that the dynamics of the system (10) has two distinct regimes. For short times $t = \mathcal{O}(1)$ the population size s changes and the frequencies $\mathbf{u}$ are unchanged. This is typically referred to as the ecological time scale. For larger times $t = \mathcal{O}(1/\varepsilon)$ the density is constant whereas the frequency is altered. This is typically referred to as the evolutionary time scale.

3 Application to public goods game under logistic growth

We now apply the above results to a specific model, one that describes the dynamics of public goods production in a population consisting of producers and free-riders [11]. The model assumes that the public good is shared among all individuals and that it has a linear effect on the growth rate. This gives rise to the following frequency-dependent growth rates, where type 1 are the producers and type 2 are the free-riders (see [11] for details):

$$f_1(u) = \alpha(1 + \beta u) - \kappa$$
$$f_2(u) = \alpha(1 + \beta u)$$

where u is the frequency of producers, α is growth rate in the absence of the public good, β describes impact of the public good and κ is the cost of production. In terms of assumption (7) we note that $f_0(u) = \alpha(1+\beta u)$, whereas $\phi_1 = -1$ and $\phi_2 = 0$, and as long as the cost of production is small ($\kappa \ll 1$) selection is weak.

The two types are assumed to identical except for the public good production and therefore the the density-dependence is identical for both types. It is assumed to follow logistic growth with carrying capacity K, i.e. $g(s) = 1-s/K$, and the per capita death rate is assumed to be constant and equal to μ. This implies that the dynamics of the population are given by:

$$\frac{dx_1}{dt} = f_1(u)x_1\left(1 - \frac{x_1+x_2}{K}\right) - \mu x_1$$
$$\frac{dx_1}{dt} = f_2(u)x_2\left(1 - \frac{x_1+x_2}{K}\right) - \mu x_2.$$

As before we change variables to $s = x_1 + x_2$ and $u = \frac{x_1}{x_1+x_2}$ and obtain the following system

$$\frac{du}{dt} = -\kappa u(1-u)\left(1 - \frac{s}{K}\right) \tag{15}$$
$$\frac{ds}{dt} = -\kappa s u\left(1 - \frac{s}{K}\right) + \alpha(1+\beta u)s\left(1 - \frac{s}{K}\right) - \mu s.$$

We now express the solutions $u(t)$ and $s(t)$ as a power series in κ:

$$u(t) = u_0(t) + \kappa u_1(t) + \mathcal{O}(\kappa^2)$$
$$s(t) = s_0(t) + \kappa s_1(t) + \mathcal{O}(\kappa^2).$$

We insert the power series ansatz into (15) and gather terms with the same power of κ. To zeroth order in κ this yields

$$\frac{du_0}{dt} = 0 \tag{16}$$
$$\frac{ds_0}{dt} = \alpha(1+\beta u_0)s_0\left(1 - \frac{s_0}{K}\right) - \mu s_0, \tag{17}$$

i.e. on the ecological time scale we obtain logistic growth with a growth rate that depends on the initial frequency of producers u_0. With some additional algebra we obtain the following equations to first order in κ:

$$\frac{du_1}{dt} = -\kappa u_0(1-u_0)\left(1 - \frac{s_0}{K}\right)$$
$$\frac{ds_1}{dt} = -s_0 u_0\left(1 - \frac{s_0}{K}\right) + \alpha(1+\beta u_0)s_1\left(1 - \frac{2s_0}{K}\right) + \alpha\beta u_1 s_0\left(1 - \frac{s_0}{K}\right) - \mu s_1.$$

Here things get more complicated. Both the population size and frequency of producers change and the time derivative of u depends s and vice versa. Thus, we no longer have the separation of ecological and evolutionary time scales observed at zeroth order.

By carrying out the change of variables $\tau = \kappa t$ we obtain the system:

$$\begin{aligned} \kappa \frac{du}{d\tau} &= -\kappa u(1-u)\left(1-\frac{s}{K}\right) \\ \kappa \frac{ds}{d\tau} &= -\kappa s u\left(1-\frac{s}{K}\right) + \alpha(1+\beta u)s\left(1-\frac{s}{K}\right) - \mu s. \end{aligned} \tag{18}$$

We now employ the outer power series ansatz

$$\begin{aligned} u(t) &= U_0(\tau) + \kappa U_1(\tau) + \mathcal{O}(\kappa^2) \\ s(t) &= S_0(\tau) + \kappa S_1(\tau) + \mathcal{O}(\kappa^2). \end{aligned}$$

and obtain to zeroth order in κ:

$$\begin{aligned} \frac{dU_0}{d\tau} &= -U_0(1-U_0)\left(1-\frac{S_0}{K}\right) \\ 0 &= \alpha(1+\beta U_0)S_0\left(1-\frac{S_0}{K}\right) - \mu S_0. \end{aligned}$$

The second equation can be solved for S_0 and ignoring the trivial solution $S_0 = 0$ yields $S_0 = K(1 - \frac{\mu}{\alpha(1+\beta U_0)})$. Inserting this into the first equation now gives

$$\frac{dU_0}{d\tau} = -\frac{\mu}{\alpha(1+\beta U_0)} U_0(1-U_0), \tag{19}$$

which provides us with the zeroth order dynamics on the evolutionary $(1/\kappa)$ time scale. Comparing terms of order κ we obtain after some calculations:

$$\begin{aligned} \frac{dU_1}{d\tau} &= U_0(1-U_0)\frac{S_1}{K} + 2U_0U_1\left(1-\frac{S_0}{K}\right) + U_1\left(1-\frac{S_0}{K}\right) \\ \frac{dS_0}{d\tau} &= -S_0U_0\left(1-\frac{S_0}{K}\right) + \alpha(1+\beta U_0)S_1\left(1-\frac{2S_0}{K}\right) + \alpha\beta U_1 S_0\left(1-\frac{S_0}{K}\right) - \mu S_1. \end{aligned}$$

Note here that the equation for S_0 depends on S_1 and if we go to order κ^2 we find that S_1 depends on S_2 etc. Hence there is no way to obtain a closed system of equations for the higher order terms, and we therefore terminate the process at zeroth order.

3.1 Numerical comparison

In order to compare the accuracy of the zero order approximation of the original system (15) we calculate a composite solution using the method of matched asymptotic expansions [12]. The composite solution is obtained by adding the inner and outer solutions and subtracting the overlap, which is given by the the outer limit of the inner solution, and the inner limit of the outer solution. If we assume that the initial conditions is given by $(u(t=0), s(t=0)) = (a, b)$, and since u remains unchanged for the inner solution, this implies that

$$\lim_{t\to\infty} u(t) = \lim_{\tau\to 0} U(\tau) = a$$
$$\lim_{t\to\infty} s(t) = \lim_{\tau\to 0} S(\tau) = K(1 - \frac{\mu}{\alpha(1+\beta a)})$$

where the equality for s comes from the fact that s is completely determined in terms of u in the inner solution. The composite solution can now be written

$$u_c(t) = u_0(t) + U_0(\kappa t) - a \tag{20}$$
$$s_c(t) = s_0(t) + S_0(\kappa t) - K(1 - \frac{\mu}{\alpha(1+\beta a)}).$$

A numerical solution to (15) is shown in Figure 1 for different values of the small parameter κ together with the zero order composite solution (20). As expected a small value of κ leads to solution which shows clearer separation in ecological and evolutionary dynamics where the population first grows to carrying capacity without changes in frequency and then a subsequent change in frequency.

In order to quantify the error introduced by the zero order approximation we calculate the total squared error

$$E(\kappa) = \int_0^{T_{max}} (u(t) - u_c(t))^2 + (s(t) - s_c(t))^2 \, dt \tag{21}$$

where all solutions are calculated numerically using the `lsoda`-solver as implemented in SciPy's `odeint`. Figure 2 shows that as expected the error $E(\kappa)$ scales as κ as long as $\kappa \ll 1$.

4 Discussion

We have shown how perturbation analysis together with the assumption of weak selection provides a formal way of expressing the dynamics of a population on ecological and evolutionary time scales. The approximate solution is expressed as a power series in a parameter that quantifies the deviation between the frequency-dependent birth and death rates of each genotype and

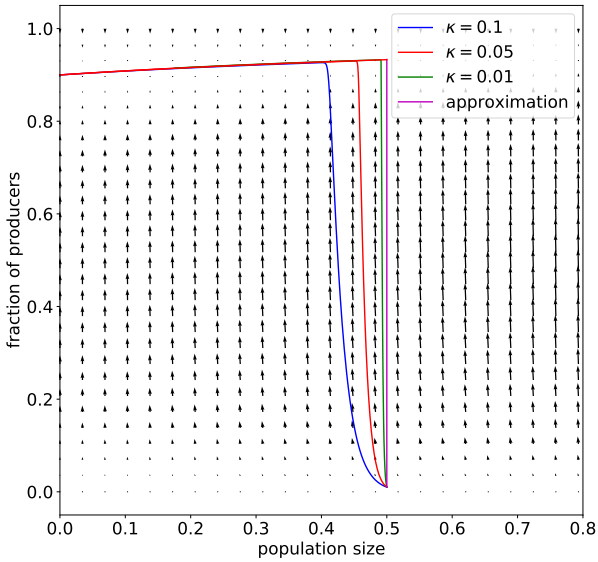

Fig. 1 Solution of (15) for different values of κ with the initial condition $(u, s) = (0.5, 0.01)$. The other parameters are set to $\alpha = \beta = 1$ and $K = 1$. The magenta curve shows the zeroth order composite solution (20). The underlying vector field corresponds to $\kappa = 0.1$

the average. We have applied the method to a specific model of a two strategy public goods game and showed that the error introduced by a zero order approximation scales as the cost of public goods production.

The implications of time scale separation in population dynamics has been approached previously by Lion [13]. In his extensive synthesis he shows how separation of time scales is assumed in many theoretical constructs such as evolutionary game theory and adaptive dynamics, and also how population dynamics relate to population genetics in terms of the Price equation and Fisher's fundamental theorem on natural selection. Our focus here is more narrow and our main contribution is to relate ecological and evolutionary time scales to inner and outer perturbations solutions and to show that this is possible for a wide class of models that assume density- and frequency-dependence on birth and death rates.

An important results is the derivation of the equation for the outer/evolutionary dynamics (14), which can be viewed as a generalisation of the replicator equation

$$\frac{du_i}{dt} = u_i \left(f_i(\mathbf{u}) - \bar{f}(\mathbf{u}) \right),$$

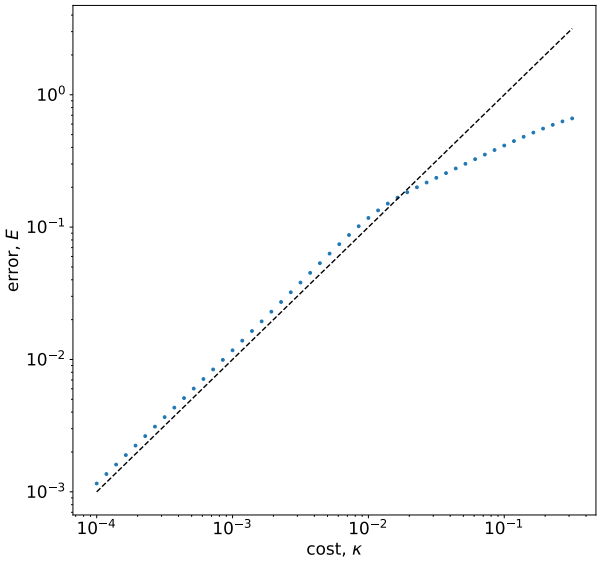

Fig. 2 The total error between the numerical solution of the original system (15) and the composite solution (20) as defined by (21) with $T_{max} = 2000$. The initial condition was set to $(u, s) = (0.5, 0.01)$ and the parameters are set to $\alpha = \beta = 1$ and $K = 1$. The dashed line corresponds to $E(\kappa) \sim \kappa$.

with the addition of density-dependent rates that modulate the intensity of selection. Our equation also captures the effects of frequency-dependence on both birth and death rates. The replicator equation has been derived for constant [14] and exponentially growing [15] populations, whereas (14) holds (to zeroth order in ε) for any type of density- and frequency-dependent growth.

The model of the public goods game has been analysed previously in order to obtain an approximate equation of the change in producer frequency [11]. In that case an equation for the invariant manifold was derived and solved in terms of a power series in the death rate μ. The resulting differential equation for the change in producer frequency was given by

$$\frac{du}{dt} = -\frac{\mu\kappa}{\alpha(1+\beta u) - u\kappa} u(1-u),$$

which at a first glance differs from (19). However, a Taylor expansion of the prefactor to first order in κ is given by $\frac{-\mu\kappa}{\alpha(1+\beta u)}$ and if time is rescaled according to $\tau = \kappa t$ (as was done to obtain (19)) we see that an equation identical to (19) is obtained. The two approaches thus yield identical equations for the evolution of the producer frequency.

The framework we have introduced is applicable to a large class of population dynamical models with density- and frequency-dependence, and makes it possible to derive approximate solutions in the case of weak selection. The use of composite solutions in addition makes it possible to obtain solutions valid for all times. If selection is not weak it is possible to include higher-order terms in the power series expansion and still obtain distinct models for the ecological and evolutionary time scales. As was seen for the public goods model these higher order corrections typically involve changes in both density and frequency.

The method presented here also makes it possible to test if, for a given model, separation of time scales is a sensible approximation. This could for example be used to investigate if evolutionary game theory, which only describes changes in frequency, is a reasonable description of a certain system, or if changes in density have to be accounted for.

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