Original Research Article

Evolutionary stability under limited population growth: Eco-evolutionary feedbacks and replicator dynamics

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A B S T R A C T

This paper further develops a new way of modelling evolutionary game models with an emphasis on ecological realism, concerned with how ecological factors determine payoffs in evolutionary games. Our paper is focused on the impact of strategically neutral growth limiting factors and background fitness components on game dynamics and the form of the stability conditions for the rest points constituted by the intersections of the frequency and density nullclines. It is shown that for the density dependent case, that at the stationary state, the turnover coefficients (numbers of newborns per single dead adult) are equal for all strategies. In addition, the paper contains a derivation of the EESS (eco-evolutionarily stable states) conditions, describing evolutionary stability under limited population growth. We show that evolutionary stability depends on the local geometry (slopes) of the intersecting nullclines. The paper contains examples showing that density dependence induces behaviour which is not compatible with purely frequency dependent static game theoretic ESS stability conditions. We show that with the addition of density dependence, stable states can become unstable and unstable states can be stabilised. The stability or instability of the rest points can be explained by a mechanism of eco-evolutionary feedback.

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1. Introduction

Current developments in evolutionary biology emphasize the role of relationships between selection mechanisms and ecological factors (Schoener, 2011; Morris, 2011; Pelletier et al., 2009). This perspective is very interesting from the point of view of formal modelling, which can contribute to this research program not only by quantitative predictions, but also by rigorous conceptualization of the analyzed mechanisms. Thus, this direction should also be considered in the development of modelling approaches such as evolutionary game theory. Recent developments in this field, focused on the realistic modelling of the turnover of individuals (i.e. the dynamics of the replacement of the dying adult individuals by newly introduced juveniles), can be useful in pursuing this goal. In this study we will analyze the interplay between selection dynamics of strategy frequencies and the ecological dynamics shaping the population size. In addition we will investigate the relationships between game theoretic equilibrium conditions and nullclines of the selection and ecological dynamics.

In the classical approach to evolutionary game theory (Maynard Smith, 1982; Hofbauer and Sigmund, 1988, 1998), a well-mixed population with clonal reproduction and no mutation evolves under natural selection. The strategies are heritable phenotypic traits or different behavioral patterns and payoff functions describing their fitness. The merits and limitations of such an approach are discussed in Maynard Smith (1982) (for interesting general work based upon similar principles but with an infinite strategy set, see for example Gorban, 2007; Meszena et al., 2006; Oechssler and Riedel, 2001). An abstract "fitness" is expressed as an infinitesimal growth rate r and described in undefined "units", which are the currency in which evolutionary "costs" and "benefits" are counted. The basic model of the game dynamics of k competing strategies are replicator dynamics, defined on the $k-1$ dimensional simplex. Table 1 contains the list of important symbols. Then $q_i = n_i / \sum_j n_j$ (n_i is the number of carriers of the ith strategy) is the frequency of the ith strategy and $r_i(q)$ is its payoff function:

$$\dot{q}_i = q_i \left(r_i(q) - \sum_j r_j(q) \right) \quad \text{for } i = 1, \ldots, k-1. \tag{1}$$

In the classical approach to evolutionary game modelling there is no explicit analysis of the impact of limitations of the population

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Table 1
Important symbols.

n	Population size
q_i	Frequency of the ith strategy
K	Carrying capacity (maximal environmental load)
$W_i(q)$	Fertility payoff of the ith strategy
$s_i(q)$	Prereproductive survival payoff function of the ith strategy
$V_i = \sum_j q_j s_i(e_j) W_i(e_j)$	Mortality–fertility trade-off function (example of fertility payoff)
τ_1	Rate of occurrence (intensity) of the game event
τ_2	Rate of occurrence of the background event
W_B	Average background event fertility
$m_B = 1 - b_B$	Average background event mortality
$\theta = \tau_2/\tau_1$	Average number of background events between two focal events
$\Phi = \theta W_B$	Rate of the average background fertility
$\Psi = \theta m_B$	Rate of background mortality
$g(n, q)$	Function describing the right hand side of the frequency equation
$f(n, q)$	Function describing the right hand side of the population size equation
$V_1(q)$	General fertility payoff of the first strategy related to the focal game
$s_1(q)$	General survival payoff of the first strategy related to the focal game
$B_1(q) = V_1 + \Phi$	General fertility factor of all events of the first strategy
$M_1(q) = 1 - s_1 + \Psi$	General mortality factor of all events of the first strategy
$\overline{B}(q) = q_1 B_1 + (1-q_1)B_2$	Average fertility factor
$\overline{M}(q) = q_1 M_1 + (1-q_1)M_2$	Average mortality factor
$r^u(q) = \overline{B}(q) - \overline{M}(q)$	Rate of the unsuppressed growth
S	Hawk-Dove example survival payoff matrix
$F = WP$	Hawk-Dove example fertility payoff matrix
$d = 1 - s$	Probability of death during a contest in a Hawk-Dove game
$\tilde{q}(n)$	Frequency nullcline
$\tilde{n}(q)$	Density nullcline

size. In more complex approaches (Cressman, 1992; Cressman et al., 2001; Cressman and Garay, 2003a,b; Argasinski, 2006) density dependence has been taken into consideration. The specific case of selectively neutral density dependence, which means that the growth suppression acts on all strategies in the same way, was analyzed in Argasinski and Kozłowski (2008). It was shown there that the classical approach (1) can be problematic, when growth limitation, related to the logistic equation, is implemented. The dynamics stop when the carrying capacity is reached. This is caused by the fact that both birth and death rates are suppressed, leading to a population of immortal individuals. This problem can be solved by using the assumption that only the birth rate is suppressed by juvenile recruitment survival, which leads to a generalization of the replicator dynamics completed by the equation for the population size (Argasinski and Broom, 2012). In this approach payoffs are described explicitly as demographic vital rates (mortality and fertility), not as an abstract fitness. Thus assume that $W_i(q)$ is the fertility function, suppressed by the density dependent juvenile recruitment function $(1 - n/K)$ (where $n = \sum_j n_j$ and K is the carrying capacity describing the maximal population load, Hui, 2006), and $d_i(q) = 1 - s_i(q)$ is the adult mortality. This leads to the following:

$$\dot{q}_i = q_i \left[\left(W_i(q) - \sum_j W_j(q) \right) \left(1 - \frac{n}{K} \right) - \left(d_i(q) - \sum_j d_j(q) \right) \right] \quad (2)$$

for $i = 1, \ldots, k-1$,

$$\dot{n} = n \left(\left(1 - \frac{n}{K} \right) \sum_j W_j(q) - \sum_j d_j(q) \right), \quad (3)$$

where the bracketed term from (1) splits into two brackets describing differences in fertilities and mortalities. The replicator system (2) is completed by Eq. (3) describing the changes of the population size caused by selection of the strategies. A similar method was applied in a number of papers (Hauert et al., 2006, 2008; Argasinski and Kozłowski, 2008; Zhang and Hui, 2011; Argasinski and Broom, 2012; Huang et al., 2015; Gokhale and Hauert, 2016). In this approach population size does not converge to an arbitrary carrying capacity as in many models (for example Cressman and Křivan, 2010; Křivan, 2014) but to a dynamic equilibrium between mortality and fertility (this is often called an emergent carrying capacity, Bowers et al., 2003; Sieber et al., 2014). The general selective properties of this approach were presented in Argasinski and Broom (2013), where the simplified version of (2) and (3) with payoffs as constants was analyzed. It was shown there that when the population reaches the close neighbourhood of the population size equilibrium (nullcline of the equations for n), then newborns form the pool of candidates from which individuals replacing the dead adults in their nest sites will be drawn. This mechanism was termed the "nest site lottery". This process promotes the strategies that maximize the number of newborns replacing each single dying adult (termed the "turnover coefficient"), however among strategies maximizing this quantity it is profitable to maximize the mortality (the number of dead adults) and thus also the number of newborns replacing them. Therefore, we have a two stage fitness measure.

The previous paper, Argasinski and Broom (2012), was focused on the description of the above approach using demographic parameters, mortality as the probability of death (or equivalently survival) and fertility as per capita number of offspring. This allows for a description of the abstract and unclear parameters such as "fitness" or "growth rate" by clear and measurable parameters. In addition, the new approach is focused on the detailed description of the structure of cause-effect chains underlying the particular interactions. For example, the modelled interaction described by the game theoretic structure can be composed of several mortality and fertility stages following each other. This aspect can be illustrated by the simplest case of a single pre-reproductive mortality stage preceding the fertility stage. Then only survivors of the interaction can reproduce, which should be incorporated into the payoff functions. Thus the fertility payoffs $W_i(q)$ will be replaced by the mortality–fertility trade-off function $V_i(q) = \sum_j q_j s_i(e_j) W_i(e_j)$ (where e_j is the vector describing the jth pure strategy) describing the reproductive success of the survivors. The new conceptual framework was applied to the classical Hawk-Dove game to illustrate the advantages over the classical approach.

The general framework was clarified in a second paper (Argasinski and Broom, submitted for publication) focused on the derivation of the game theoretic model from the general population dynamics model also describing factors other than the modelled type of interaction. For example individuals playing the Hawk-Dove game during the mating conflict (the modelled focal interaction) can also be killed by predators (background interactions without relation to the strategies in the focal game). This leads to a model of a population of individuals playing different types of games describing different interactions occurring at different rates (see Appendix 1 for more details). Thus, by analogy with chemical kinetics (Upadhyay, 2006), the game theoretic structure is equivalent to stoichiometric coefficients describing the outcomes of a single reaction between particles (in our case, interactions between individuals) and the rate of occurrence is equivalent to the reaction rate. The new framework focuses on births and deaths (described by separate payoff functions) as the aggregated outcomes of the physical interactions between individuals and the elements of the environment. This is why it