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Eco-evolutionary dynamics of social dilemmas

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ABSTRACT

Social dilemmas are an integral part of social interactions. Cooperative actions, ranging from secreting extra-cellular products in microbial populations to donating blood in humans, are costly to the actor and hence create an incentive to shirk and avoid the costs. Nevertheless, cooperation is ubiquitous in nature. Both costs and benefits often depend non-linearly on the number and types of individuals involved—as captured by idioms such as 'too many cooks spoil the broth' where additional contributions are discounted, or 'two heads are better than one' where cooperators synergistically enhance the group benefit. Interaction group sizes may depend on the size of the population and hence on ecological processes. This results in feedback mechanisms between ecological and evolutionary processes, which jointly affect and determine the evolutionary trajectory. Only recently combined eco-evolutionary processes became experimentally tractable in microbial social dilemmas. Here we analyse the evolutionary dynamics of non-linear social dilemmas in settings where the population fluctuates in size and the environment changes over time. In particular, cooperation is often supported and maintained at high densities through ecological fluctuations. Moreover, we find that the combination of the two processes routinely reveals highly complex dynamics, which suggests common occurrence in nature.

1. Introduction

The theory of evolution is based on Darwinian selection, mutation and drift. These forces along with neo-Darwinian additions of phenotypic variability, frequency-dependence and, in particular, cooperative interactions within and between species, form the basis for major transitions in evolution (Maynard Smith and Szathmáry, 1995; Nowak and Sigmund, 2004). Ecological effects such as varying population densities or changing environments are typically assumed to be minimal because they often arise on faster timescales such that only ecological averages matter for evolutionary processes. Consequently, evolutionary and ecological dynamics have been studied independently for long. While this assumption is justified in some situations, it does not apply whenever timescales of ecological and evolutionary dynamics are comparable (Day and Gandon, 2007). In such cases, ecological and evolutionary feedback may contribute to the unfolding of the evolutionary process. Empirically, effects of changes in population size are well documented (Dobson and Hudson, 1995; Bohannan and Lenski, 1999; Hudson et al., 1998; Fenner and Fantini, 1999; Bohannan and Lenski, 2000) and has now lead to a burgeoning field in evolutionary theory, which incorporates ecological variation (May and Anderson, 1983; Frank, 1991; Heesterbeek and Roberts, 1995; Roberts et al., 1995; Kirby and Burdon, 1997; Gandon and Nuismer, 2009; Salathé et al., 2005; Quigley et al., 2012; Gokhale et al., 2013; Song et al., 2015).

In particular, the independent study of ecological and evolutionary processes may not be able to capture the complex dynamics that often emerge in the combined system. Such potentially rich eco-evolutionary dynamics has been explored theoretically and, more recently, empirically confirmed (Post and Palkovacs, 2009; Hanski, 2011; Sanchez and Gore, 2013). Population genetics and adaptive dynamics readily embrace ecological scenarios (see e.g. Pagie and Hogeweg, 1999; Aviles, 1999; Yoshida et al., 2003; Day, 2005; Hauert et al., 2006b; Day and Gandon, 2006, 2007; Lion and Gandon, 2009; Jones et al., 2009; Gandon and Day, 2009; Wakano et al., 2009; Cremer et al., 2011) whereas the traditional focus of evolutionary game theory lies on trait frequencies

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or constant population sizes (Taylor and Jonker, 1978; Hofbauer and Sigmund, 1998; Nowak et al., 2004). Here we propose ways to incorporate intricacies of ecological dynamics along with environmental variation in evolutionary games.

1.1. Ecological setting

Evolutionary game dynamics is typically assumed to take place in a population of individuals with fixed types or ‘strategies’, which determine their behaviour in interactions with other members of the population (Maynard Smith and Price, 1973; Zeeman, 1981). Payoffs determine the success of each strategy. Strategies that perform better than the average increase in abundance. This is the essence of the replicator equation (Hofbauer and Sigmund, 1998) but neglects that evolutionary changes may alter the population dynamics or vice versa. Traditionally the population consists of two strategies whose frequencies are given by x and $y = 1 - x$. In order to incorporate ecological dynamics we assume that x and y are (normalized) densities of the two strategies with $x + y \leq 1$ (Hauert et al., 2006a). Consequently, $z = 1 - x - y$ provides a measure for reproductive opportunities, e.g. available space. Ecological dynamics is reflected in the change of the population density, $x + y$. The evolutionary dynamics of the strategies is affected by intrinsic changes in population density as well as extrinsic sources such as seasonal fluctuations in the interaction parameters and hence the payoffs. For example, in epidemiology the coevolutionary dynamics of virulence and transmission rate of pathogens depends on ecological parameters of the host population. More specifically, changes in the mortality rate of hosts evokes a direct response in the transmission rate of pathogens while virulence covaries with transmission (Day and Gandon, 2006). Another approach to implement eco-evolutionary feedback is, for example, to explicitly model spatial structure and the resulting reproductive constraints (Lion and Gandon, 2009; Alizon and Taylor, 2008; Le Gaillard et al., 2003; Van Baalen and Rand, 1998), which then requires approximations in terms of weak selection or moment closures to derive an analytically tractable framework. In contrast, while our model neglects spatial correlations, it enables a more detailed look at evolutionary consequences arising from intrinsically and extrinsically driven ecological changes.

1.2. Non-linear social dilemmas

Social dilemmas occur whenever groups of cooperators perform better than groups of defectors but in mixed groups defectors outcompete cooperators (Dawes, 1980). This creates conflicts of interest between the individual and the group. In traditional (linear) public goods (PG) interactions cooperators contribute a fixed amount $c > 0$ to a common pool, while defectors contribute nothing. In a group of size N with m cooperators the payoff for defectors is $P_D(m) = r\,m\,c/N$ where $r > 1$ denotes the multiplication factor of cooperative investments and reflects that the public good is a valuable resource. Similarly, cooperators receive $P_C(m) = P_D(m) - c = P_D(m-1) + rc/N - c$, where the second equality highlights that cooperators ‘see’ one less cooperator among their co-players and illustrates that the net costs of cooperation are $-rc/N + c$ because a share of the benefits produced by a cooperator returns to itself. Therefore, it becomes beneficial to switch to cooperation for large multiplication factors, $r > N$, but defectors nevertheless keep outperforming cooperators in mixed groups. The total investment in the PG is based on the number of cooperators in the group but the benefits returned by the common resource may depend non-linearly on the total investments. For example, the marginal benefits provided additional cooperators may decrease, which is often termed diminishing returns. Conversely, adding more cooperators could synergistically increase the benefits produced as in economies of scale. While well studied in economics (Taylor and Ward, 1982; Kollock, 1998; Schelling, 2006) such ideas were touched upon earlier in biology (Eshel and Motro, 1988) but only recently have they garnered renewed attention (Bach et al., 2006; Hauert et al., 2006b; Wakano et al., 2009; Pacheco et al., 2009; Wakano and Hauert, 2011; Archetti et al., 2011; Purcell et al., 2012; Peña et al., 2014, 2015).

The nonlinearity in PG can be captured by introducing a parameter ω, which rescales the effective value of contributions by cooperators based on the number of cooperators present (Hauert et al., 2006b). Hence, the payoff for defectors, $P_D(m)$, and cooperators, $P_C(m)$, respectively, is given by,

$$P_D(m) = \frac{rc}{N}(1 + \omega + \omega^2 + \cdots + \omega^{m-1}) = \frac{rc}{N}\frac{1 - \omega^m}{1 - \omega} \tag{1a}$$

$$P_C(m) = P_D(m) - c = \frac{rc}{N}\omega(1 + \omega + \cdots + \omega^{m-2}) + \frac{rc}{N} - c, \tag{1b}$$

such that the benefits provided by each additional cooperator are either discounted, $\omega < 1$, or synergistically enhanced, $\omega > 1$. The classic, linear PG is recovered for $\omega = 1$. This parametrization provides a general framework for the study of cooperation and recovers all traditional scenarios of social dilemmas as special cases (Nowak and Sigmund, 2004; Hauert et al., 2006b).

2. Eco-evolutionary dynamics

The overall population density, $x + y$, can grow or shrink from 0 (extinction) to an absolute maximum of 1 (normalization). The average payoffs of cooperators and defectors, f_C and f_D, determine their respective birth rates but individuals can successfully reproduce if reproductive opportunities, $z > 0$, are available. All individuals are assumed to die at equal and constant rate, d. Formally, changes in frequencies of cooperators and defectors over time are governed by the following extension of the replicator dynamics (Hauert et al., 2006a),

$$\dot{x} = x(zf_C - d) \tag{2a}$$

$$\dot{y} = y(zf_D - d) \tag{2b}$$

$$\dot{z} = -\dot{x} - \dot{y} = (x + y)d - z(xf_C + yf_D). \tag{2c}$$

The average payoffs are calculated following Eq. (1), where the interaction group size depends on the population density (see Appendix A). This extends the eco-evolutionary dynamics for the linear PG (Hauert et al., 2006a) to account for discounted or synergistically enhanced accumulation of benefits (Hauert et al., 2006b). The difference in the average fitness between defectors and cooperators, $F(x, z) = f_D - f_C$ is now given by

$$F(x, z) = 1 + (r - 1)z^{N-1} - \frac{r}{N}\frac{(1 - x(1 - \omega))^N - z^N}{1 - z - x(1 - \omega)} \tag{3}$$

and provides a gradient of selection. Note that in the special case of the linear PG, $\omega = 1$, Eq. (3) reduces to a function of z alone.

2.1. Intrinsic fluctuations

Homogeneous defector populations go extinct but pure cooperator populations can persist and withstand larger death rates d under synergy than discounting (see Appendix A.1, Fig. A.8). In order to analyse the dynamics in heterogeneous populations it is useful to rewrite Eq. (2) in terms of z and the fraction of cooperators, $f = x/(1 - z)$:

$$\dot{f} = \frac{\dot{x}y - \dot{y}x}{(1 - z)^2} = -zf(1 - f)F(f, z) \tag{4a}$$

$$\dot{z} = -(1 - z)(fz(r - 1)(1 - z^{N-1}) - d). \tag{4b}$$