Invasion exponents in biological networks

Lloyd Demetrius [a,b], Volker Matthias Gundlach [c], Gunter Ochs [d,*]

[a] *Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA*

[b] *Max Planck Institute for Molecular Genetics, 14195 Berlin, Germany*

[c] *FH Braunschweig/Wolfenbüttel, University of Applied Sciences, Fachbereich Wirtschaft, Robert-Koch-Platz 10-14, 38440 Wolfsburg, Germany*

[d] *Hochschule Darmstadt, Haardtring 100, 64295 Darmstadt, Germany*

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ABSTRACT

This article is concerned with the characterization of invasion exponents in biological networks defined by a population of replicating elements: molecules, cells, higher organisms. We show that the outcome of competition between an invader and a resident population is a stochastic process, determined by the rate at which a population returns to its steady state after a random perturbation in the parameters that characterize the replicating elements. This return rate is defined by the macroscopic parameter evolutionary entropy, a measure of the diversity of the interaction between the individuals in the population. We also show that the evolutionary stability of a population, that is the invulnerability of a resident to the introduction of an invader competing for the available resources, are given by extremal states of entropy. These results which pertain to networks of interacting molecules, cells and higher organisms, are generalizations of results established for demographic networks, that is populations of replicating organisms parametrized by the ages at which they reproduce and die.

1. Introduction

Competition between a variant type and a resident population – a mutant allele and the wild type in a population genetics context; an invader and a resident species in an ecological context – is the fundamental process which underlies patterns of diversity in populations and communities.

The efforts to understand the dynamics of this process in structured populations have invariably revolved around some measure of population growth rate, or the long term average growth rate, as the index of invasion success. In discrete population models, population growth rate is described in terms of the dominant eigenvalue of a transition matrix or the Lyapunov exponent of a random matrix product. The studies which have invoked the population growth rate and its analogues, as a predictor of competitive outcome, is extensive — see, for example Charlesworth and Williamson [1], Pollak [2] for population genetic models, Metz et al. [3], Rand et al. [4], Ferriere and Gatto [5] for general population models. In these studies, the invasion exponent can be expressed by the quantity $r = \log \lambda$, where λ denotes, for example, the dominant eigenvalue of a transition matrix. The selective advantage of the invading population is now given by

$$s = \Delta r \tag{1.1}$$

where Δr denotes the difference in the growth rate of invader and resident.

The notion that growth rate characterizes the invasion exponent goes back to Fisher [6], who studied these problems in a population genetics framework, and in honor of Malthus' contribution to population studies, called his invasion exponent the Malthusian parameter. The Malthusian paradigm has, since Fisher's original contribution, driven most studies

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* Corresponding author.
 E-mail address: g.ochs@t-online.de (G. Ochs).

in both population genetics and community ecology — witness, for example, the life-history and ecological studies by Charlesworth [1], Stearn [7] and Roff [8].

Critiques of the Malthusian model have recently emerged from both empirical and theoretical sources. On the empirical side, the works by Williamson [9], Lawton and Brown [10] suggest that population growth rate may not be a good predictor of invasion success. These studies, based on data from a wide class of vertebrates and insects in England, indicate that the intensity of fluctuations in population numbers constitute, in many instances, a more reliable predictor of the outcome of competition between invading and resident species. On the analytic side, Demetrius and Gundlach [11] invoked the theory of diffusion processes to show that, for certain classes of matrix models of population growth, the conditions for invasion involved not only the population growth rate r, but quantities such as the population size N, and the demographic variance σ^2. In age-structured models, this quantity is a measure of the variance in the age at which individuals reproduce and die. The diffusion analysis showed that the selective advantage s, in age-structured models is now given by

$$s = \Delta r - \frac{1}{N} \Delta \sigma^2. \tag{1.2}$$

Here Δr and $\Delta \sigma^2$ denote the difference in growth rate and demographic variance, respectively of invader and resident.

By exploiting the ergodic theory of dynamical systems, it was shown that the selective advantage, as expressed by (1.2), can be described in terms of a unique demographic property, namely the rate at which population returns to its steady state condition after a random perturbation in the individual birth and death rates. This return rate, which can be considered a measure of robustness or population stability, can be characterized by the macroscopic parameter evolutionary entropy, Demetrius, Gundlach and Ochs [12]. In populations structured by age, evolutionary entropy, denoted by H, is given by

$$H = -\frac{\sum p_j \log p_j}{\sum j p_j}. \tag{1.3}$$

Here p_j is the probability that the mother of a randomly chosen newborn belongs to age class j.

The invasion criteria which (1.2) generates can therefore be reformulated in terms of conditions on entropy, contingent on certain resource constraints experienced by the population. The invasion exponent now becomes

$$s = \Delta H,$$

where ΔH denotes the difference in entropy of invader and resident. Our study of the invasion process showed that, whether an increase or decrease in entropy confers a selective advantage, depends on whether the resource abundance is constant or varying.

Now, changes in resource abundance are contingent on the growth rate and the stability of the population. Hence, when the resource abundance and the population numbers are in dynamical equilibrium, the constraints in resource abundance can be described in terms of the demographic parameter, Demetrius and Gundlach [11],

$$\Phi = \frac{\sum p_j \log V_j}{\sum j p_j}. \tag{1.4}$$

Here V_j denotes the net-reproductive function of individuals in age class j.

The quantity Φ is called the reproductive potential. It is related to the population growth rate r and the evolutionary entropy H by the identity

$$r = H + \Phi. \tag{1.5}$$

Consequently, we have the implications

$$\Phi < 0 \Rightarrow r < H; \qquad \Phi > 0 \Rightarrow r > H. \tag{1.6}$$

The population growth rate, r and the demographic stability, as measured by H, will assume a range of values experienced by the resource constraints experienced by the population. Under limited resource conditions, the growth rate will be almost stationary ($r \sim 0$), with small variation in population numbers (H large). When resources vary in abundance, populations will be described by episodes of rapid growth rate (r large) and large fluctuation numbers (H small). In [12], we have exploited these observations and Eq. (1.6) to derive the following relations between resource constraints and the reproductive potential. We have

(a) Resources constant but limited: $\Phi < 0$; (b) Resources varying in abundance: $\Phi > 0$.

This characterization of resource constraints in terms of Φ provides a framework for describing the invasion dynamics of age-structured populations in terms of the reproductive potential and entropy. We derived a set of selection rules which can be qualitatively annotated as follows:

(I) *Constant but limited resource conditions* ($\Phi < 0$)

This condition will result in a relatively constant population size. Mutants with *increased* entropy will almost always invade, mutants with *decreased* entropy will become extinct.

(II) *Resources varying in abundance* ($\Phi > 0$)