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The evolutionary and behavioral modification of consumer responses to environmental change

Peter A. Abrams

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Harbord St., Toronto, ON, Canada M5S 3G5

HIGHLIGHTS

- Ecologists must often predict population sizes of interacting species, but the models they use to do so often neglect adaptive processes.
- Theory predicting the impacts of adaptive processes can be important in understanding species responses to environmental change.
- Models of consumer–resource systems show that evolution can to reverse, enhance, or offset environmentally-driven change in population sizes.
- This theory should help lay the foundations for a more predictive community ecology.

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ABSTRACT

How will evolution or other forms of adaptive change alter the response of a consumer species' population density to environmentally driven changes in population growth parameters? This question is addressed by analyzing some simple consumer–resource models to separate the ecological and evolutionary components of the population's response. Ecological responses are always decreased population size, but evolution of traits that have effects on both resource uptake rate and another fitness-related parameter may magnify, offset, or reverse this population decrease. Evolution can change ecologically driven decreases in population size to increases; this is likely when: (1) resources are initially below the density that maximizes resource growth, and (2) the evolutionary response decreases the consumer's resource uptake rate. Evolutionary magnification of the ecological decreases in population size can occur when the environmental change is higher trait-independent mortality. Such evolution-driven decreases are most likely when uptake-rate traits increase and the resource is initially below its maximum growth density. It is common for the difference between the new eco–evolutionary equilibrium and the new ecological equilibrium to be larger than that between the original and new ecological equilibrium densities. The relative magnitudes of ecological and evolutionary effects often depend sensitively on the magnitude of the environmental change and the nature of resource growth.

1. Introduction

1.1. Background

Recent empirical work has shown that evolutionary change often modifies the response of population size to environmental changes and species interactions (Strauss et al., 2008; Schoener, 2011). Nevertheless, theory predicting the likely size and direction of evolutionarily driven population change under different scenarios is poorly developed. This article asks how adaptive change in consumption-related traits of a consumer species affects its population density in a consumer–resource system. The analysis concentrates on evolutionary change, but other modalities of adaptive change often have similar effects and are also considered. The traits of interest here determine the per capita resource uptake rate of the consumer. These traits define consumer–resource interactions, and generally have effects on consumer population size (Murdoch et al., 2003). The specific question treated here is how adaptation of consumption traits modifies the 'ecological' response of the consumer species to adverse environmental change. 'Ecological' means the population response that would occur in the absence of any adaptive change in consumer traits. 'Adverse' environmental change means that the initial effect of the alteration is to diminish the consumer's immediate per capita rate of increase.

The analysis does not assume any particular time-scale of evolution, but it separates ecological and evolutionary components of change by using a limiting case where the adaptive (evolutionary) change may be regarded as taking place after the population dynamics have reached a new attractor following an environmental modification. While the time scales of adaptation and ecology are in fact unlikely to be completely separable (Endler, 1986; Thompson, 1998; Hendry and Kinnison, 1999; Fussmann et al., 2007), this modeling exercise is a logical way to separate

E-mail address: peter.abrams@utoronto.ca

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components of change in population density attributable to different processes. Regardless of the speed of adaptation, this approach separates the equilibrium population responses due to adaptive processes (here labeled 'evolutionary') from other ('ecological') processes in the same way they have been separated in much empirical work; i.e., by eliminating one of the two categories of processes. In behavioral ecology, effects due to adaptive behavior can be measured using experiments that eliminate the behavior (by making it impossible for the focal organism to detect cues that induce that behavior) or, more commonly, by eliminating the population response without eliminating the behavior (e.g., by introducing caged organisms which still produce chemical cues of their presence). In evolutionary experiments (e.g. Yoshida et al., 2003), treatments with no genetic variability are used to eliminate the evolutionary component. This method of separating ecological and evolutionary (adaptive) components potentially allows long-term predictions of future population responses when the direction of trait responses is known from experiments with more limited duration. It differs from some previously proposed methods that are only concerned with apportioning population responses within a fixed time frame into those with ecological or evolutionary causes (e.g., Hairston et al., 2005; Ellner et al., 2011).

Adaptation of any kind is often assumed to be beneficial to populations as well as to individuals. This is reflected, for example, in the idea of 'evolutionary rescue' of declining populations (e.g. Gonzalez et al., 2013; Reznick, 2013). It is also the prediction of the theory of r–K selection in stable environments (e.g., Roughgarden, 1971, 1979). Nevertheless, it has long been known that evolution need not maximize population size (Haldane, 1932), as individually advantageous traits can be disadvantageous to the population. There have been a number of analyses predicting that adaptive evolution can even lead to extinction of the evolving species (Rosenzweig, 1971; Matsuda and Abrams, 1994; Webb, 2003; Parvinen, 2005; Ferriere and Legendre, 2013; but see Abrams and Matsuda, 1994). A less extreme form of nonmaximization occurs when an evolutionary response simply reduces population size. An example is provided by evolution of resource use in a resident consumer species caused by an introduced competitor; Abrams (2012) shows that this response usually decreases the population density of the evolving resident consumer, and this adaptively-caused decrease is often much larger than the original ecological decrease. The fact that most populations do not have population-maximizing trait values leads to the possibility that environmental change that adversely affects individuals can lead to an evolutionary or behavioral response that results in the population ultimately increasing above its original level (examples in Abrams, 2002; Abrams and Vos, 2003).

Nevertheless, the ecological circumstances under which evolution is most likely to increase or decrease population size following an environmental change have not been explored systematically. A logical starting point for exploring evolution's role in this scenario is a simple 1-consumer-1-resource system, and this exploration is pursued here. The resource uptake trait is described by a fitness gradient model of evolutionary change. Most of the analysis assumes that a tradeoff exists, such that increases in the uptake rate have adverse effects on another fitness related parameter of the consumer. Environmental changes cause the evolutionarily stable value of the resource uptake rate to shift, and this shift has its own effects on population size. These effects are detailed below.

1.2. The model and general approach

The models assume that the dynamics of a consumer with population size (here measured by density) N are given by the following equation:

$$\frac{dN}{dt} = N[Bb(CR) - d_0 - d_1(C)] \tag{1a}$$

The per capita resource uptake rate, C, is a key parameter in any consumer–resource model, and the evolving trait is assumed to affect C. In the rest of the article, the parameter C itself is referred to as the trait. Consumed resource (density R) is converted into new consumer individuals according to the conversion function, b, which increases with the resource intake rate (CR), and has a maximum of one. The per capita birth rate is the given by a maximum birth rate, B, multiplied by the conversion function. The environment is a major determinant of B. Per capita losses always include a component that is independent of both uptake rate and traits (the constant, d_0), but may also include a component that increases with uptake rate (d_1). The function d_1 represents a cost of greater uptake abilities; acquisition of resources almost invariably entails some expenditure of energy or risk of injury/mortality or both (Abrams, 1982, 1984; Lima and Dill, 1990; Lima, 1998). Evolution of body size represents a scenario where both conversion efficiency and loss are linked to uptake rate (Yodzis and Innes, 1992). The parameters B and d_0 as well as any parameters in the cost function, d_1, may be modified by environmental change.

Eq. (1a) is combined with the following description of resource dynamics:

$$\frac{dR}{dt} = R[f(R) - CN] \tag{1b}$$

where the per capita resource growth in the absence of the consumer is given by the decreasing function $f(R)$. (Allee Effects are ignored here.) It is possible for environmental change to affect parameters in the resource growth, f. The evolutionary model assumes that the consumer's trait changes at a rate proportional to the rate of increase in individual fitness with a unit increase in the trait:

$$\frac{dC}{dt} = v(C)(BRb' - d'_1) + \gamma(C) \tag{1c}$$

where primes note derivatives with respect to the argument of the function. The first term on the right hand side of the evolutionary Eq. (1c), is the product of the genetic variance, v, and the fitness gradient with respect to C (i.e., $BRb - d_1'$). The gradient dynamics embodied in Eq. (1c) represents a commonly used simplified description of evolutionary dynamics (Abrams et al., 1993; Michod, 1999; Abrams, 2001). Genetic variance, v, may decline as the trait approaches minimum or maximum values. Additional factors such as biased mutation may also influence dynamics independently of the fitness gradient. These additional factors are embodied in γ, which is a function of C that forces the trait value away from its minimum and maximum values (when such values exist), but has virtually no effect at intermediate trait values (see e.g. Abrams and Matsuda, 2004). The function γ may also be regarded simply as a mathematical method of avoiding adaptive change into biologically meaningless ranges of the parameter C.

The environmental change that affects the above system is assumed to have an immediate negative effect on consumer or resource growth. (Positive effects are not treated explicitly, as they have the opposite consequences for population sizes.) Such adverse environmental change may increase the loss rates d_0 or d_1, decrease the uptake parameter, C, or decrease the maximum birth rate, B. Adverse change could also decrease the resource per capita resource growth, f. However, changes in f are not considered further, because they do not alter the evolutionary equilibrium C, which is determined by Eqs. (1a) and (1c). The joint equilibrium of these two equations is not affected by f, provided the consumer persists. Direct environmental effects on C have the same consequences as increases in the function d_1, so they are not given a separate treatment here. The analysis begins by asking how