Toward A More Precise - and Accurate - View of Eco-Evolution

Ronald D. Bassar[1†], Tim Coulson[2], Joseph Travis[3], David N. Reznick[4]

1 Department of Biology, Williams College, MA, USA; rdb4@williams.edu

2 Department of Zoology, University of Oxford, Oxford, UK; tim.coulson@zoo.ox.ac.uk

3 Department of Biological Science, Florida State University, Tallahassee, FL, USA; travis@bio.fsu.edu

4 Department of Biology, University of California, Riverside, California, USA; david.reznick@ucr.edu

† To whom correspondence should be addressed.

Thompson Biology Lab

59 Lab Campus Drive

Williamstown, MA 01267, USA

Email: rdb4@williams.edu

Phone 413-597-2119

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Abstract

Over the past fifteen years, the number of papers focused on “eco-evo dynamics” has increased exponentially (Figure 1). This pattern suggests the rapid growth of a new, integrative discipline. We argue that this overstates the case. First, the terms “eco-evo dynamics” and “eco-evo interactions” are used too imprecisely. As a result, many studies that claim to describe eco-evo dynamics are actually describing basic ecological or evolutionary processes. Second, these terms are often used as if the study of how ecological and evolutionary processes are intertwined is novel when, in fact, it is not. The result is confusion over what the term “eco-evolution” and its derivatives describe. We advocate a more precise definition of eco-evolution that is more useful in our effort to understand and characterize the diversity of ecological and evolutionary processes and that focuses attention on the subset of those processes that offer novel results.

Main Body

To be clear at the outset, there is nothing wrong with the current enthusiasm for eco-evolutionary studies. While the basic ideas behind them are not brand new, they continue to uncover novel theoretical and empirical results that change how we think about nature. However, if the term “eco-evolutionary dynamics” is co-opted by a definition that is too broad, the importance of those results becomes harder to appreciate and the distinctive signature of genuine eco-evolutionary dynamics harder to distinguish.

The problem begins with verbal definitions of eco-evo dynamics that are very broad - any situation in which an ecological process leads to an evolutionary outcome or vice-versa (e.g. Hendry’s (2017), cases 1 and 2 [p. 23]). We do not claim that all such situations are not interesting; we claim that many of them are merely basic ecological or evolutionary processes.

Consider some simple examples. When a population decline (ecological process) leads to a loss of genetic variation in the absence of selection (an evolutionary outcome), this is classic genetic drift. When a novel pathogen invades a community (an ecological process) and creates a novel selective pressure to which its new host responds (an evolutionary outcome), that is classic adaptive evolution. Conversely, when changes in the mean value of a heritable phenotypic trait (an evolutionary process) causes a change in the population growth rate (an ecological outcome), that is a reflection of Fisher's Fundamental Theorem of Natural Selection (Fisher 1958).

One could describe these scenarios as eco-evo dynamics but that would merely give a new name to long-established processes. More importantly, and to our point, describing them as such blurs the distinction between these processes and others that are qualitatively quite different.

A more pointed definition of eco-evolutionary dynamics might be situations in which both ecological and evolutionary dynamics are coupled to each other through reciprocal feedbacks (Pimentel 1961). In Pimentel's original definition, the coupling of ecology and evolution was viewed through density-dependent regulation and evolution: "Density influences selection; selection influences genetic make-up; and in turn, genetic make-up influences density" (p. 65). Of course, population density is not the only possible ecological parameter involved (Lion 2018); it is merely the simplest to study. This definition corresponds to the verbal definitions offered by Hendry (2017, p. 23, cases 3-5) and Kokko and Lopez-Sepulcre (2007) and the mathematical definition offered by Lion (2018).

We advocate taking this definition a step further and restricting the term "eco-evolutionary dynamics" to cases in which there is no separation in time between the ecological and evolutionary dynamics (Hairston *et al.* 2005). This is similar in spirit to Hendry's (2017) general definition that requires the dynamics to unfold in "contemporary time."

Why impose a further restriction on the definition? Models incorporating both ecological and evolutionary dynamics have been around for a long time. But most of these classical models employ weak selection and low levels of phenotypic variance (Lion 2018). This means that the ecological dynamics – for example, the population growing to a (quasi)-carrying capacity – happens much faster than the evolutionary ones (change in allele frequencies or the mean of a heritable phenotypic trait) (Lande 1982). The very slow subsequent evolution may increase carrying capacity, and the very slow subsequent change in carrying capacity may alter selection pressures. Models of weak selection combine ecological and evolutionary dynamics, but the assumption of weak selection places the dynamics on different timeframes, which allows them to be analyzed independently.

The "separation of time" approximation fails when, in purely genetic models, selection is strong or, in phenotypic models, when the variance in the critical traits is large (Lion 2018). Why emphasize this situation? Because it is the one in which wholly novel results emerge. When ecological and evolutionary changes operate on similar time scales, the joint dynamics can stabilize ecological interactions that would be otherwise unstable (Abrams & Matsuda 1997), create unique dynamic patterns (Hiltunen *et al.* 2014), and qualitatively change the outcome of many types of species interactions (Ashby *et al.* 2019). Thus, knowing when eco-evolution occurs and when it does not, under our definition, is a key diagnosis in ecology.

How do these models of strong selection fit into the taxonomy of models that are structured by phenotypic traits or alleles? An ecological model is one that contains no heritable genetic variation (Tuljapurkar & Caswell 2012). It does not contain explicit rules of genetic inheritance. Models can be structured by non-heritable phenotypic traits, and in these models, selection, and the population dynamics, are emergent features of the model (Ellner *et al.* 2016). An evolutionary model is one that is structured by heritable genetic variation (Charlesworth 1994), but in which weak selection is (often) a fixed quantity that is defined rather than an emergent result of the ecology of the system (Crow & Kimura 1970).

Broadly speaking, two classes of eco-evolutionary model have been constructed. First, there are coupled models of the dynamics of population size and of the mean of heritable phenotypic trait values (Yoshida *et al.* 2003). In these models, one equation describes how the dynamics of the mean of a heritable phenotype or frequency of a genotype in a species is determined by a function through which population size determines the strength of selection. The second equation describes how the dynamics of population size (also mean fitness) is determined by the mean value of the heritable phenotypic trait or genotype frequency. These models are typically continuous time coupled ordinary differential equations.

The second approach models the dynamics of entire distributions of heritable traits (Barfield *et al.* 2011; Childs *et al.* 2016). These distributions determine distributions of vital rates, from which fitness is an emergent property (Easterling *et al.* 2000). The vital rates also determine numerical dynamics, which can, in turn, alter the ways in which trait distributions affect vital rates (Coulson *et al.* 2017). This feedback loop is combined with development and inheritance functions to drive joint multi-generational dynamics of traits, demography, population density, and selection (Simmonds *et al.* 2020). When entire distributions of traits and fitness must be studied, then ecological and evolutionary time cannot be separated (Lion 2018).

How do we know that eco-evolutionary dynamics, as we have defined it, are of more than theoretical interest? When ecological and evolutionary time scales cannot be separated, evolutionary change can be as rapid as ecological change and there is ample evidence that rapid evolutionary change occurs often enough to be important, not merely interesting (Reznick *et al.* 2019b). Moreover, the recent enthusiasm for eco-evolutionary studies has begun to generate empirical demonstrations of eco-evolutionary dynamics in nature (Hairston *et al.* 2005; Reznick *et al.* 2019a).

Why do we emphasize the lack of novelty of genuine eco-evolutionary dynamics? Laboratory experiments were demonstrating these dynamics over fifty years ago (Pimentel 1961; Ayala 1965). These pioneering studies ought not to be forgotten. They inspired hypotheses for explaining striking natural phenomena like the cycling of rodent populations (Chitty 1967) and motivated the earliest theoretical work that explored the consequences of eco-evolutionary dynamics for predator-prey systems (Levin 1972) and character displacement (Slatkin 1980). The roots of eco-evolution can be traced to the ecological genetics of E. B. Ford, A. D. Bradshaw, and others, along with laboratory studies attempting to link genetic variation to the outcome of ecological processes (Travis *et al.* 2013). While that work might be called eco-evolution under some definitions (e.g. Hendry's 2017 cases 1 and 2), we argue that much of it was not because it did not include reciprocal feedbacks. It did, however, represent pioneering efforts to integrate ecology and evolution.

Eco-evolution has become popular recently because it has been shown that the evolution of one organism can have large effects on the structure and function of its ecosystem (Hairston *et al.* 2005; Bassar *et al.* 2010) and the significant amount of evidence that evolutionary change can occur rapidly (Hendry & Kinnison 1999; Carroll *et al.* 2007). As such, eco-evolution offers great promise to help unify ecological and evolutionary theory, and to help explain how systems respond to all sorts of environmental change (Coulson *et al.* 2011; Childs *et al.* 2016). In that light, it is important to recognize eco-evolution for what it is, when and where it occurs, and when and where it does not. Calling any process involving ecological dynamics and trait or genetic variation eco-evolution obscures the novelty associated with the consequences of reciprocal feedbacks between ecology and evolution on the same time scale. More importantly, if everything is called "eco-evo", then the term loses its ability to define a specific area of parameter space (strong selection, non-negligible phenotypic variances, large genetic effects on ecological variables) and we lose the ability to ask how often nature occupies this region of parameter space. We also risk future generations forgetting the corpus of work on genuine eco-evolution being conducted now.

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Figure 1. Number of papers returned, by year, by a search in Web of Science with the term "eco-evolutionary dynamics" as accessed on January 7, 2021.