

1                   **The Zoolander Effect: Equivalent Models in Ecology and Evolution**

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13   **Abstract**

14   In the 2001 film Zoolander, the lead character, played by Ben Stiller, ditches his old “Blue Steel”  
15   look and develops an exciting new ‘Magnum’ look that the fashion industry enthusiastically  
16   embraces. The evil mastermind, Mr Mugato, played by Will Farrell, exclaims “The man has only  
17   one look, for Christ's sake! ... They're the same face! Doesn't anybody notice this? I feel like I'm  
18   taking crazy pills!” We argue here that eco-evolution is the “Magnum” of biology: it is  
19   fashionable, lots of people love it, but it is not new. We also argue that, like the “Blue Steel” look  
20   in the 2016 sequel, Zoolander 2, eco-evolution is being seen where it does not belong.

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22   **Main Body**

23   To be clear at the outset, there is nothing wrong with eco-evolution's not being new; ongoing  
24   work in eco-evolution leads to a broader appreciation of the links between the ecological and  
25   evolutionary processes that we have long known to exist. However, when old ideas are branded  
26   as new we risk ignoring a significant corpus of previous work. When terms are used cavalierly,

we risk confusing our understanding of the natural world by losing important distinctions among the processes that shape it.

It is probably easiest to start with our second argument about the mis-use of the term “eco-evolution” by defining what it is not. The list captures processes that have been described as eco-evolution in published work. Because our aim is not to embarrass anyone, we have refrained from referencing offending papers. Eco-evolution is not genetic drift – that is non-adaptive evolution. It is also not a change in selection pressure due to an ecological change, leading to a change in allele frequency or the distribution of a heritable phenotypic trait -- that is adaptive evolution. Eco-evolution is also not an ecological change, such as a change in the population growth rate, population size, or a species interaction, that is attributable to phenotypic trait evolution. That is evolutionary-driven ecological change. Indeed, change in the population growth rate due to adaptive evolution is Fisher’s Fundamental Theorem (Fisher 1958). If you call any of these processes eco-evolution, you have fallen for the Zoolander effect.

If you couple adaptive evolution and evolutionary-driven ecological change, you may be able to call it eco-evolution (Pimentel 1961). That is because ecological change has generated evolutionary change, and evolutionary change has generated further ecological change. Why do we say ‘may’? Because the timeframe in which the dynamics unfold matters (Hairston *et al.* 2005).

Models incorporating both ecological and evolutionary dynamics have been around for a long time. But most of these classical models employ weak selection. What this means is the ecological dynamics – for example, the population growing to a (quasi)-carrying capacity – happens much faster than evolution (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.

Eco-evolution requires ecological and evolutionary change to operate on similar time scales (Hairston *et al.* 2005), and this requires strong selection. Why is this distinction important? 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) and create unique dynamic patterns (Hiltunen *et al.* 2014). Thus, knowing when eco-evolution occurs and when it does not 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).

Like “magnum” and “blue steel,” eco-evolution is not new as some advocates like to claim. Laboratory experiments were demonstrating eco-evolution over fifty years ago (Pimentel 1961; Ayala 1965), inspiring hypotheses for its action in nature (Chitty 1967), and inspiring theory that explored its consequences (Levin 1972). The roots of eco-evolution can be traced to the ecological genetics of Ford and laboratory studies attempting to link genetic variation to the outcome of ecological processes (Travis *et al.* 2013). While that work was itself not eco-evolution - the complete feedback loops were not studied - it represented pioneering efforts to integrate ecology and evolution.

Eco-evo has become popular recently because of the demonstrably large magnitude of eco-evo effects and the breadth of systems in which they can be detected (Hairston *et al.* 2005). In particular, demonstrations that phenotypic evolution can alter ecological interactions, generating novel selection pressures, and that these feedbacks could explain significant amounts of observed variation in dynamics led to eco-evolution becoming popular.

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 (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 spreads confusion. More importantly, if everything is called “eco-evo”, then the term loses its ability to define a specific area of parameter space (strong selection, large genotypic 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. We don’t need magnum, we certainly do not need a new magnum sometime hence, and we don’t need to see blue steel where it is not.

#### **Authorship Statement**

All authors contributed equally to this paper.

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