

Linking evolutionary and ecological theory illuminates non-stationary biodiversity

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Whether or not biodiversity dynamics are governed by stable equilibria remains an unsolved question in ecology and evolution [1, 2, 3]. An ecological steady state exists if changes in biodiversity occur slowly and in sync with environmental changes [4]. The existence (or non-existence) of such steady states has wide ranging implications, for example, whether conservation should focus on conventional preservationist paradigms or adaptive management [5]. Whether biodiversity rapidly and consistently tends toward a steady state also determines how species and communities will respond to global environmental change [6]. Evolutionary genetics [7, 8] and macroecology [9] represent two primary lenses through which we view biodiversity dynamics. Population genetics and phylogenetics provide an integrated view of changes in population demography and lineage origination over scales of generations to geological epochs but cannot be used to directly infer the ecological composition of any given time period [10]. Conversely, macroecology, and its constituent theories, provides a static description of the commonness and rarity of species co-occurring in the same landscape [11, 4]. With advances in molecular methods [12] allowing genetic data to be gathered across entire communities [13], the field is ready to not only combine the theoretical insights of genetics and ecology, but also test predictions with real data.

Neutral or null models in both population genetics/phylogenetics and ecology seek to provide idealized descriptions of systems free of additional complicating mechanisms [8, 11, 4]. Departures from these idealizations can be seen as evidence for violations of the core theoretical assumptions of the model, such as selective neutrality and constant population size in the case of population genetics [7, 8], or biotic interactions and habitat filtering in the case of ecology [14, 15]. As such, departures from mechanistically idealized theories can be more informative than conformation to those theories. Combining the insights from both theoretical perspectives can shed light on the mechanistic reasons for departures from steady state.

We posit that two primary classes of non-steady state exist that can be better understood by combining ecological theory with comparative population and phylogenetic insights. The first occurs when a biological assemblage is undergoing succession following disturbance

or formation of new habitat; in this case populations of most species in the community and species composition itself will be in flux due to the stochasticity of immigration and small population sizes. In such a situation the assemblage may be expected to eventually converge on a steady state [16]. Recovery from disturbance [16], range expansion following climate change [17] and primary succession [18] are all potential examples of such non-steady state. The second case occurs when novel mechanisms actively drive an assemblage away from steady state; such mechanisms could include escalatory species interactions or rapid diversification and adaptation in the face of newfound selective pressures [19]. In both cases idealized ecological theory should fail to predict the static biodiversity patterns of the system and departures from population genetic theory should indicate what demographic dynamics are associated with the failure of ecological theory.

In our manuscript for *Trends in Ecology and Evolution* we will explore the specific hypotheses that can be tested by combining ecological and population genetic theory. We will use simulated results to demonstrate how unique evolutionary/demographic scenarios leave distinct signatures in both genetic and ecological data, detectable by analyzing departures from theory. We will also discuss the methodological advances, both in mathematics and the wet lab, that have been achieved and will be required to achieve the most insight from this approach [13, 20].

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