Linking evolutionary genetics and ecological theory to understand non-stationary biodiversity

Whether or not biodiversity dynamics are governed by stable equilibria remains an unsolved question in ecology and evolution (Rabosky 2009; Quental and Marshall 2013; Rabosky et al. 2015; Harmon and Harrison 2015). An ecological steady state exists if changes in biodiversity occur slowly and in sync with environmental changes (J. Harte 2011). The existence (or non-existence) of such steady states has wide ranging implications. For example, whether conservation should focus on conventional preservationalist paradigms or adaptive management (Levin 1999) depends on whether biodiversity is largely in steady state or not. Whether biodiversity rapidly and consistently tends towards a steady state determines how species and the communities they form will respond to global environmental change (Barnosky et al. 2012). Evolutionary genetics and macroecology 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. Conversely, macroecology, and its constituent theories, provides a static description of the commonness and rarity of species co-occurring in the same landscape. With advances in molecular methods allowing for genetic data to be gathered across large numbers of taxa, representing entire communities of co-occurring species, the time is ripe to not only combine the theoretical insights of genetics and ecology, but also test predictions with real data.

Theory development in both molecular evolution and macroecology are based on the mathematics of long-term stationarity, thus assuming that the systems they describe are in steady state. This feature of all theories derives both from the mathematical simplicity of stationarity and the unusual, albeit short-term, global stability observed during the formative period of the study of ecology. As a result the study of biodiversity as non-stationary phenomenon has been limited by a lack of conceptual tools for describing alternate, non-steady states and a lack of hypotheses to test for the causes and consequences of non-stationarity.

Theoretical advances in both population genetics/phylogenetics and ecology share a common mathematical core and neutral or null models in both fields seek to provide idealized descriptions of systems free of additional complicating mechanisms. In the case of population genetics theory departures from these idealizations can be seen as evidence for violations of the core theoretical assumptions of the model, such as selective neutrality, constant population size, etc. In the case of mechanistically simplified and idealized ecological theories, departures from theoretical predications again represent a violation of the simplifying assumptions of the theory, indicating the importance of potential mechanisms such as biotic interactions and habitat filtering (J. Harte 2011). As such, departures from mechanistically idealized population genetic and ecological 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 and can be better understood by combining comparative population and phylogenetic insights across multiple species and ecological theory. The first class of non-steady state 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. Recovery from disturbance, range expansion following climate change and primary succession 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. 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. This perspective immediately begs the question of how many species must have population-level dynamics out of molecular steady state for there to be a detectable signal of the entire community deviating from ecological steady state. We will explore this question using simulation to not only evaluate how many species deviating from molecular steady state are needed, but also whether the population dynamics of common or rare species are more influential to deviation from ecological theory.

Understanding the ecological basis for different evolutionary outcomes could prove more challenging because the ecological conditions of the present do not necessarily represent the conditions of the past (when selection, divergence or diversification began). However, combining ecological and molecular genetic theory with time perspectives provided by the fossil record or chronosequences may provide a solution. These study systems can provide snap shots of both ecological patterns (species composition and interactions) as well as their evolution through phylogenetic, landscape genetics on chronosequences and ancient DNA analysis.

In our manuscript for Trends in Ecology and Evolution we will explore the specific hypotheses that can be tested by a combined study of ecological and population genetic theory, using 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 that have been achieved and will be required to achieve the most insight from this approach and a preliminary analysis of ecological data from an oceanic island chronosequence that highlights the need for combining perspectives from ecological and population genetic theories. These methodological advances, many of which are underway, include both the wet lab and bioinformatic challenges of assembling and analyzing genetic data from many species simultaneously and the mathematical challenge of uniting two related but separate theories of diversity that operate at different scales, one molecular and one ecosystem-wide. We will also put forward two means of incorporating the time perspective explicitly as both molecular and ecological approaches are time implicit. The fossil record provides a time-averaged view with deep extent but coarse resolution. Chronosequences provide fine resolution snap shots of ecological communities in varying stages of assembly but their use is contingent on the assumption that similar processes have occurred throughout the evolution of the chronosequence.

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