

Linking evolutionary and ecological theory illuminates non-stationary biodiversity

A. J. Rominger¹, H. Krehenwinkel¹, R. G. Gillespie¹, J. Harte¹, and M. J. Hickerson²

¹Department of Environmental Science, Policy and Management, University of California, Berkeley

²Biology Department, City College of New York

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].

References

- [1] Quental, T.B. and Marshall, C.R. (2013) How the red queen drives terrestrial mammals to extinction. *Science*
- [2] Rabosky, D.L. *et al.* (2015) Species richness at continental scales is dominated by ecological limits. *The American Naturalist* 185, 572–583
- [3] Harmon, L.J. and Harrison, S. (2015) Species diversity is dynamic and unbounded at local and continental scales. *The American Naturalist* 185, 584–593
- [4] Harte, J. and Newman, E.A. (2014) Maximum information entropy: a foundation for ecological theory. *Trends in ecology & evolution* 29, 384–389
- [5] Levin, S.A. (1999) Towards a science of ecological management. *Conservation Ecology* 3, 6
- [6] Barnosky, A.D. *et al.* (2012) Approaching a state shift in earth’s biosphere. *Nature* 486, 52–58
- [7] Nielsen, R. (2005) Molecular signatures of natural selection. *Annu. Rev. Genet.* 39, 197–218
- [8] Nei, M. *et al.* (2010) The neutral theory of molecular evolution in the genomic era. *Annual review of genomics and human genetics* 11, 265–289
- [9] Brown, J.H. (1995) *Macroecology*. Chicago University Press, Chicago
- [10] Quental, T.B. and Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need the fossil record. *Trends in Ecology and Evolution* 25, 434–441

- [11] Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press
- [12] McCormack, J.E. *et al.* (2013) Applications of next-generation sequencing to phylogeography and phylogenetics. *Molecular Phylogenetics and Evolution* 66, 526–538
- [13] Gibson, J. *et al.* (2014) Simultaneous assessment of the macrobiome and microbiome in a bulk sample of tropical arthropods through dna metasystematics. *Proceedings of the National Academy of Sciences* 111, 8007–8012
- [14] Borer, E.T. *et al.* (2014) Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508, 517–520
- [15] Mittelbach, G.G. and Schemske, D.W. (2015) Ecological and evolutionary perspectives on community assembly. *Trends in ecology & evolution* 30, 241–247
- [16] Simberloff, D.S. and Wilson, E.O. (1970) Experimental zoogeography of islands. a two-year record of colonization. *Ecology* , 934–937
- [17] Blois, J.L. *et al.* (2010) Small mammal diversity loss in response to late-pleistocene climatic change. *Nature* 465, 771–774
- [18] Shipley, B. *et al.* (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *science* 314, 812–814
- [19] Rominger, A. *et al.* (2015) Community assembly on isolated islands: macroecology meets evolution. *Global Ecology and Biogeography*
- [20] Harte, J. *et al.* (2015) Integrating macroecological metrics and community taxonomic structure. *Ecology Letters* 18, 1068–1077