Special Issue

Integrating ecology and phylogenetics: the footprint of history in modern-day communities[1]

In the face of rapid changes in Earth's biota, understanding the evolutionary processes that drive patterns of species diversity, differentiation, and coexistence in ecosystems globally has never been more pressing. Advances through computational methods, analytical approaches, long-term observations, and well-designed experiments are essential to sustaining the complex interactions and ecosystem functions of the living world. Early naturalists seamlessly integrated ecology and evolution but lacked the tools to do so in a predictive and quantitative manner. Recent advances in computational tools and in the study of diversity gradients and community assembly have revived historical traditions integrating ecology and evolution. This work increasingly demonstrates that a legacy of evolutionary history persists in ecological patterns and processes we observe today, in concert with growing evidence for rapid adaptive evolution of populations in response to recent environmental change.

The body of work represented in this Special Issue is drawn from scientists working at the interface of ecology and evolution using a range of theoretical and methodological frameworks, and working in a wide range of ecological systems around the globe. The papers are organized around three central themes: (1) methodological advances in the integration of phylogenetics in ecological research; (2) integration of phenotypic and phylogenetic approaches to community assembly, including the role of niche evolution and diversification; and (3) studies that examine the footprint of evolutionary history in trophic interactions and ecosystem function. This collection was catalyzed by a working group sponsored by the Long-Term Ecological Research Network and a subsequent working group supported by the National Center for Ecological Analysis and Synthesis.

Methodological and computational advances have played a key role in the integration of phylogenetics and ecology, as researchers in both fields tackle rapidly growing data sets and apply increasingly sophisticated algorithms to detect processes that drive diversity and assembly of life on Earth. Beaulieu et al. outline a new approach for storing and annotating published phylogenies and then building supertrees for comparative biology. Peres-Neto et al. provide a heuristic and analytical framework for merging metacommunity ecology and community phylogenetics, linking niche properties based on traits and phylogenetics to environmental and spatial variation from a metacommunity perspective. Helmus and Ives develop theoretical expectations for phylogenetic–diversity area (PDA) curves under different ecological and macroevolutionary processes. They test these expectations using simulations and long-term data sets and show that processes that generate and maintain biodiversity at various spatial scales, including extinction, colonization, and within-region speciation, can be distinguished. Davies et al. introduce a new approach to the problem of inferring processes of community assembly from phylogenetic and trait-based studies, without reference to a particular regional species pool. They demonstrate that the observed body size distribution for a desert mammal community exhibits a distinctive signature that is not expected under background models of trait evolution.

Most of the studies in this issue address community assembly, niche evolution, and patterns of diversity. These studies encompass a spectrum of approaches, from community-based studies of co-occurring and potential interacting organisms, to clade-based studies of the evolutionary history of lineages, irrespective of whether taxa currently interact. A common thread in many studies is the effort to bridge temporal dimensions, linking deep evolutionary history with recent community assembly processes. The observation that related species exhibit similarities in form and function

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[1] Reprints of this 234-page Special Issue are available for $25 each, either as a PDF or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1990 M Street, N.W., Suite 700, Washington, D.C., 20036 (esaHQ@esa.org).

that extend to the habitats they select and the niche space they occupy plays a central role in the analysis of community assembly patterns. Yet, opposing views on how the niche evolves leave open the question of when and where phylogenetic niche conservatism is important in ecological processes.

Cavender-Bares and Reich show that traits influencing patterns of phylogenetic beta diversity along a gradient of fire frequency may have originated as long as 80 million years ago, revealing an ancient footprint of history on the ecological assembly and turnover of species. Similarly, Norden et al. find that early successional status is conserved in Neotropical forest trees, leading to consistent shifts in phylogenetic structure in the course of ecological succession. Knapp et al. demonstrate that urbanization causes phylogenetic and functional homogenization in spontaneous yard plant communities due to anthropogenic filters with a strong evolutionary bias that reflects niche conservatism.

Other studies find more mixed evidence in terms of the patterns and consequences of niche conservatism. In Andean hummingbird communities, Graham et al. find that the trait structure of communities cannot be consistently predicted from phylogenetic structure, despite strong phylogenetic signals in functional traits. In six forests spanning tropical and temperate latitudes, Swenson et al. find support for the role of abiotic filtering on the structure of local communities and spatial turnover in community composition, but they do not find strong links between phylogenetic and functional diversity. Using an experimental approach, Burns and Strauss show that trait plasticity can increase the ability of close relatives to coexist but that it also decreases the degree of phylogenetic signal in functional traits. Their study offers an intriguing explanation for why phylogenetic signal among coexisting species may decrease at smaller spatial and temporal scales.

Focusing in on specific clades, Savage and Cavender-Bares found a shift in trait and phylogenetic structure of willow communities across a hydrologic gradient, reflecting changes in community assembly processes and in the phylogenetic structure of the traits involved. In a clade of California annual plants, Emery et al. report that local habitat niches are conserved, while climatic niche axes are not. They argue that ecological specialization may be specific to certain niche axes rather than an overall characteristic of a species. And in the only study in this collection addressing patterns of species richness, Kozak and Wiens ask what determines the total number of coexisting species in local and regional communities of plethodontid salamanders. They argue that variation in the amount of time that different climatic zones have been occupied is the primary factor explaining relationships between climate and diversity, rather than the direct effects of climate on speciation or extinction rates or ecological saturation effects on diversification.

The third group of papers examines trophic interactions, including pollination and herbivory, and the ecosystem consequences of species interactions. Eaton et al. provide evidence that plant–pollinator interactions have repeatedly driven character displacement in floral traits of *Pedicularis* in the Hengduan biodiversity hotspot region of China, and that accelerated floral divergence contributes to the remarkable accumulation of species diversity in the region. In one of several studies that apply an experimental approach, Lamarre et al. examine plant–insect interactions in Amazonian rain forest trees, incorporating shared ancestry to factor out lineage effects on plant chemistry. In contrast to previous studies, they do not find evidence for growth-defense trade-offs but do show that any poorly defended species that suffers high herbivory rates has low abundance. Whitfeld et al. also examine plant–insect interactions in tropical forests, this time in Papua New Guinea. While they find weak evidence of phylogenetic signal in leaf nitrogen content, herbivore abundance is primarily influenced by total leaf biomass, which does not exhibit significant phylogenetic signal. Their study is a reminder of the limitations of phylogenetic methods and the importance of testing the underlying assumptions of phylogenetic signal on a case-by-case basis. Finally, extending the analyses to address ecosystem function, Cadotte et al. show that phylogenetic diversity is a significant predictor of interannual stability in primary productivity in experimental grassland communities. Interestingly, this effect seems to occur because species living with close relatives exhibit greater variability in growth, suggesting that direct effects of competitive interactions may be responsible for the observed patterns.

Collectively, these studies provide synthetic and compelling evidence for the importance of integrating investigations of ecological and evolutionary process to understand the causes, maintenance, and consequences of diversity. They highlight current challenges including the need for a synthesis of phylogenetic knowledge incorporating accurate time calibrations to link to paleoclimate and geologic history. They also underscore the urgency of using phylogenetic information to understand ecosystem processes and services, as well as to predict responses of organisms to global change.

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