

# Special Issue

## Integrating Phylogenies into Community Ecology<sup>1</sup>

The organisms that live together in a community do so both because they are present in the larger regional pool and because they have characteristics that permit their existence at that locality and their coexistence with other species in the community. Neither a species' regional presence nor its characters can be fully understood without taking the species' history into account. That history is contingent on chance events and on deterministic interactions with other species in historical communities. As this historical approach gains favor in ecology, and as our understanding of the tree of life expands, ecologists and systematists are increasingly working together. However, this new partnership often requires synthesizing ideas across disciplines. Our goal with this Special Issue is to explore the practical interchange of concepts between evolutionary biology and community ecology, highlighting studies that both use phylogenetic information and consider the community context of individual organisms, and that represent a range of disciplines, from microbiology and parasitology to ornithology.

Several common threads weave through the papers. The first concerns the importance and definition of the local community itself. As one steps back and takes a historical and biogeographic view of a species, averaging over variation in local community composition across its range, local interspecific interactions appear less influential for the species' evolution. Ricklefs, in considering the causes of variation in the emergent property of community species richness, goes so far as to say that "ecologists [must] abandon the idea of the local community." At the same time, however, there is abundant evidence that inter-individual interactions do influence which particular taxa co-occur (e.g., Webb et al.), alter their ranges, and under certain circumstances, lead to evolutionary adaptation that reduces negative interspecific interaction. Separating the effects of local processes on regional patterns and regional processes on local patterns will always be hard. However, with large and numerous samples we can come to understand variation in community structure over wide areas. Lovette and Hochachka draw on the vast Breeding Bird Survey data set to examine both local and regional composition in warbler communities, and Kembel and Hubbell examine phylogenetic community structure of trees at varying scales within the 50-ha BCI Forest Dynamics Plot.

As well as drawing spatial boundaries around communities, we are forced to define their taxonomic bounds. Cavender-Bares et al. demonstrate how increasing the "phylogenetic scale" of communities influences our understanding of their phylogenetic structure. Brooks et al. and Weiblen et al. address the complex question of the phylogenetic structure of compound communities, with platyhelminth parasites of anurans, and insect herbivores of plants, respectively.

The second key thread dealt with by many authors is, "what exactly are ecological characters, and how do they evolve?" For ecologists, it is obvious to ask how an organism's niche has evolved and to treat it as a character to be reconstructed on a phylogeny. However, systematists often argue that because the habitats and realized niches that we can observe are influenced by interspecific interactions and community composition, they are not actually evolvable entities. Instead we should decompose overall niches into directly heritable, morphological, and physiological characters. For example, Agrawal and Fishbein show how defensive syndromes involve combinations of numerous characters of plants, and Fine et al. show that defensive traits evolve in a trade-off with growth. Different components of the overall niche may also be subject to different ecological interactions: an organism might occupy a habitat that conforms to a niche on one environmental axis, while competition within a habitat might lead to resource partitioning on another axis. Silvertown et al.

<sup>1</sup> Reprints of this 166-page Special Issue are available for \$20.00 each. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006. Costs for this Special Issue were defrayed by NSF grant DEB-0408432 to C. O. Webb and J. B. Losos. NCEAS funded a workshop on "Phylogenies and Community Ecology" in 2002, which a number of authors in this Special Issue attended.

and Ackerly et al. attempt to detect which characters diverged earlier during the course of plant diversification. Knouft et al. use the new methods of GIS-based niche modeling to examine the evolution of multidimensional niches in a clade of lizards, by associating specimens' collection locations with layers of environmental variation in space.

Inferring evolutionary process from the pattern of character evolution we observe requires models of character change under known mechanisms. Unbounded continuous characters evolving under Brownian drift (slow relative to speciation rate) will tend to show conservatism (closely related species tend to be similar). Stabilizing selection will tend to increase that conservatism, while, conversely, a reduced number of potential character states, a long time between speciation events, and divergent selection will tend to increase convergence. Using various methods, the authors found generally more conservatism in ecological characters (e.g., Ackerly et al., Silvertown et al.) than convergence (e.g., Knouft et al.), with some studies finding no clear relationship of traits with relatedness (e.g., Agrawal and Fishbein). Overall, the results are consistent with the action of divergent selection in some systems, overlaid on a null expectation of some level of phylogenetic conservatism in all systems.

The third major thread in these papers is closely linked to the second: "what is the phylogenetic relatedness of co-occurring taxa in communities, and what does this tell us about community assembly?" Authors used a number of methods to combine community lists with phylogenies to answer this question. Cavender-Bares et al. and Lovette and Hochachka correlated taxon co-occurrence rates (across many samples) with phylogenetic distance (e.g., with Mantel tests). Horner-Devine and Bohannan, Kembel and Hubbell, Weiblen et al., Silvertown et al., and Webb et al. tested the observed distribution of intra-sample, inter-taxon phylogenetic distances against null models of community assembly (so raising many of the perennial questions of community null models). Several authors pointed out that methods using inter-taxon phylogenetic distance rather than ancestral state reconstruction are less prone to bias introduced by the sampling of taxa that are very widely distributed on the tree of life. Several authors found that taxa in their communities were more closely related than expected, indicating a common role of habitat choice and evolutionarily conserved characters (e.g., Horner-Devine and Bohannan, Weiblen et al.). Cavender-Bares et al. and Kembel and Hubbell found cases where taxa were less closely related than expected. Taking the results of trait evolution and community phylogenetic structure together, the importance of community interactions does appear to be diminished, and a long-term regional view of taxa more justified. However, Lovette and Hochachka found both conservatism of habitat specialization in warblers at regional scales and evidence for competitive "repulsion" among close relatives at local sites. Because different combinations of trait evolution pattern and ecological interaction (competition vs. habitat choice) can give similar community phylogenetic structure, trait data, community data, and phylogenies are all needed for a full understanding of the evolution and assembly of communities.

The discussion of the nature of communities and niche evolution is decades old; note that a similarly titled Special Feature appeared in this journal ten years ago. However, the vast number of species that have been sequenced, and for which phylogenies have been generated, means that ecologists can now often infer the phylogenetic relationships of their taxa from publications and databases without further systematics work. We hope that this Special Issue will inspire readers to take advantage of these opportunities, to phrase their questions in a more evolutionary way, and as Westoby anticipates, to participate in the new Natural History.

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