Special Feature

Evolutionary Biology and Community Ecology[1]

Ecological communities are collections of species that co-occur in space and time and that potentially interact with one another. Community ecologists study both the patterns within and among these collections of species and the processes that generate those patterns. Many metrics have been used to search for patterns in community "structure," including the number of species, absolute and relative abundances, the types of species present (e.g., guilds, trophic levels), and their phenotypic properties (e.g., body size, morphological attributes, physiological tolerances, behavioral responses). Many processes can shape patterns in these metrics of community structure, including the supply of energy and materials, environmental tolerances (e.g., abiotic limits, disturbance), direct interactions among species (e.g., interference competition, predation, mutualism, disease, parasitism), indirect effects of direct interactions transmitted through intermediate species (e.g., exploitative competition), migration and dispersal, and historical contingencies.

Natural communities are the result of not only present ecological processes, but also past and continuing evolutionary processes. These evolutionary processes create new species, shape and constrain their phenotypes and thus their abilities to engage in ecological interactions, and finally extirpate species. While most ecologists are mindful that evolution is important in shaping community structure, the general role of evolution is often ignored when considering the ecology of specific communities. Specific types of evolved species differences resulting from community-level processes were once actively investigated (e.g., evolved niche differences among species), but such concepts and approaches are now frequently avoided. However, ignoring evolution leaves many fundamental questions about community structure unanswered. For example, where did the collection of species we see coexisting today come from in the first place, why do these species have the phenotypic properties they possess, and why are other types of species not present? Understanding the structure of communities requires explicit integration of microevolutionary and macroevolutionary concepts and methodologies into community ecology.

We feel that now is an appropriate time to reconsider how to integrate evolutionary biology into our understanding of community ecology. Past debates on the role of niche theory and theories that assume stability of communities have clarified questions and problems in community ecology. Meanwhile investigations into evolutionary processes at all levels have become increasingly sophisticated. The development of quantitative genetic methods has allowed investigators to study mechanisms causing evolutionary change in natural populations. The introduction of molecular methods to systematics studies has generated new interest in exploring the evolutionary relationships among species and the mechanisms leading to the diversification of taxa. Also, these technical advances have sparked a tremendous amount of new theoretical work on both microevolutionary and macroevolutionary processes. We are at the point where we can begin to assemble theoretical constructs that incorporate both ecological and evolutionary processes to address the development and maintenance of community structure, and use empirical tools to address the simultaneous operation of ecological and evolutionary processes in natural communities.

The integration of evolutionary principles into community ecology is also important for the development of biologically sound conservation practices. Understanding the processes that lead to species' extinctions is critical for slowing the loss of biological diversity. Deciding which species and communities to protect and which to leave to their own fates must be made with an understanding of their evolutionary potentials. Being able to predict if and how species will evolutionarily respond to perturbations such as global climate change, species introductions, and habitat alterations will allow us to better predict the likelihood of persistence of individual species

[1] Reprints of this 60-page Special Feature are available for $9.00 each. Order reprints from the Office of the Executive Director, Ecological Society of America, 2010 Massachusetts Ave., NW, Washington, DC 20036.

and changes in overall community structure in the face of these perturbations. Also, the sound design of preserves, refuges, and management and harvesting strategies must be made in light of the past environmental conditions to which species are adapted, must anticipate the potential evolutionary trajectories on which species may be cast, and must foster the continued creation of new species in the long term. Finally, the coevolution of species within a community is also likely to affect the stability of the whole assembly: understanding such emergent properties will help in determining the community-level effects of species loss. This predictive power is not possible without the integration of evolutionary thinking into community ecology.

The collection of papers in this Special Feature was assembled with these issues in mind. Species interactions are themselves agents of natural selection acting on the taxa involved in the interaction, and evolutionary responses in interacting species can change not only the strength of the interaction but also overall community structure. Abrams reviews empirical and theoretical studies exploring how evolutionary responses can alter community structure for two well-studied interactions: competition leading to character displacement, and species introductions into simple food webs. He highlights the abundance of possible alterations to community structure that may result from evolutionary responses in these two types of interactions.

While the relative importance of indirect and direct effects is still controversial, it is clear that in specific communities indirect effects can play an important role in determining species abundances and species diversity. Miller and Travis attempt to take our understanding one step further by discussing how indirect effects may affect the evolution of species in communities. In particular, they discuss the potential role of indirect effects in determining whether traits that determine the response to or effect on other species are more likely to evolve when different types of direct and indirect effects exist. They then discuss the importance of evolution and indirect effects for coevolution, community compartmentalization, and stability.

The phenotypic properties of species can either constrain or enhance their abilities to engage in ecological interactions. Using sunfishes as an example, Wainwright demonstrates how functional relationships among phenotypic characters influence the performance of a species to engage in ecological interactions, and how knowledge of these functional relationships provides predictive power for understanding the outcomes of species interactions. He also discusses how evolution of functional relationships may bias species interactions into particular forms.

In his paper on phylogenetic perspectives, Losos addresses how past macroevolutionary events (i.e., speciation, extinction, and migration) and historical contingencies can shape present-day community structure. Drawing on results from many systems and particularly on the well-studied *Anolis* assemblages of the Caribbean islands, he illustrates how phylogenetic methods can be used to test hypotheses about the relative importance of various factors to the development of overall community structure.

Community ecologists are also beginning to examine how present-day species diversity is influenced by macroevolutionary and biogeographic processes. The ways in which ecological interactions influence extinction is already an integral part of community ecologists' thinking, but the effects of interactions on speciation rates are rarely considered. McPeek examines an unexplored way in which local species interactions in a community context could influence the potential for allopatric speciation and thereby the generation of species diversity.

We can develop valuable insights into whether communities represent stable associations of species and how species associations may respond to environmental changes by examining patterns of species associations in the fossil record. Jablonski and Sepkoski examine the contribution of paleontological data over a variety of time scales for exploring whether communities respond to environmental change as cohesive units or as individual species and the degree to which species associations are stable. They also discuss patterns in the fossil record that relate to how species interactions may have shaped biotas on long time scales.

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Key words: character displacement; community; competition; evolution; functional morphology; indirect effects; macroevolution; paleontology; speciation.