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Introduction to Niche Theory and Speciation

This special collection, which is split between the May and July issues, originated from the workshop 'Niche Theory and Speciation' (http://nichews.elte.hu). The meeting took place at Keszthely (Lake Balaton) in Hungary in August 2011, and was organized by Géza Meszéna, Åke Brännström, Ulf Dieckmann, Gabriella Magyar, Liz Pásztor, and András Szilágyi. Funding was provided by the European Science Foundation in the framework of the Research Networking Programme 'Frontiers of Speciation Research', and also by the International Institute for Applied Systems Analysis (Laxenburg, Austria).

The word 'niche' notoriously lacks a broadly accepted definition; and we did not attempt to enforce any particular definition for this special collection. Instead, the non-specific title 'Niche Theory and Speciation' encouraged contributors to interpret and study niches in the manner they felt most useful and informative for their study system of question. Although the various papers yielded a diversity of interpretations and applications, all authors clearly subscribe to the idea that niches involve adaptation to different conditions (environments, habitats, resources), and that this adaptation can drive speciation – although not inevitably. This special collection represents a celebration and exploration of this process in its various guises.

As editors, our goal was to attract the best possible set of papers. We therefore expressly left it open to authors to decide the papers they wished to contribute. Some of the papers are written summaries of work presented at the 2011 meeting, whereas others grew out of discussions during and after the event. We also solicited some additional papers from investigators who had been invited to the original meeting but who were unable to attend. We also strove for a lively mix of empirical and theoretical papers given that progress in the field will undoubtedly require effort from both sides. In the end, all papers emphasized the connection between ecology and evolution, but these links emerged naturally rather than being forced by the editors.

Empirical insights

The empirical papers, published here, tended to focus on specific niche axes driving divergence, as well as factors constraining that divergence. These papers examined situations arrayed across the continuum of progress towards speciation, from polymorphism within populations through comparisons of conspecific populations to analyses of well-defined species.

Studies at the earliest stages of divergence are valuable for informing the selective forces that start everything in motion. In this special collection, De Leon *et al.* show how individual niche specialization (diets) within a population of Darwin's finches might form the initial seeds of their adaptive radiation into different species. In addition, Magalhaes *et al.* demonstrate how habitat segregation of cichlid fishes along a depth gradient can lead to the beginnings of morphological and genetic divergence. However, divergence was not always strong along this depth axis, which implies constraints on divergence even when different niches are present. Revealing one such constraint, Falk *et al*. found that *Tribolium* beetles selected in different environments in the laboratory did not evolve reproductive isolation – probably because selection was so strong as to cause population bottlenecks that led to genetic drift that hampered adaptive divergence.

Studies further along the speciation continuum, such as comparisons of conspecific populations, can reveal selective forces that are reasonably effective at causing some divergence but that are perhaps not enough to finish the job. For example, Sapir and Mazzucco examine a latitudinal gradient in *Iris* plants and show that reproductive isolation among populations depends on a complex interplay of inbreeding and outbreeding depression manifest at different spatial scales. Then, Foote summarizes suggestive – but as yet inconclusive – evidence that different killer whale populations are reproductively isolated by diet, although geographical separation may be more important. Finally, Nosil and Hohenlohe show that sexual isolation between populations of *Timema* walking sticks is likely the result of only a few axes of sexual selection, and that these axes are more strongly shaped by the geographical context (parapatry vs. allopatry) than by the specific host-plant species.

Studies near the end of the speciation continuum, such as those comparing separate – but still closely related – species, can hopefully reveal selective forces that finish the job. In this respect, Ingram *et al.* show that genetic divergence among sympatric whitefish species is greater in lakes that have a greater potential for depth segregation but is not strongly related to divergence in diet. Similarly, Soberón and Martínez-Gordillo analyse a phylogeny of *Neotoma* rodents and find contrasting patterns of divergence resulting from adaptation to different habitats versus adaptation to different food sources.

A striking theme to emerge from these empirical papers is that divergence in resources – a frequently considered niche axis – can certainly contribute to speciation, but that other factors can be more important. In particular, diet divergence seems to be often overwhelmed or trumped by divergence in water depth, spatial distance, genetic drift, or geographic context (parapatry vs. allopatry). This realization highlights the critical need for studies to continue their shift away from emphasizing a single niche axis based on resources towards a more comprehensive consideration of multiple axes that can be influenced by various spatial and demographic factors.

Theoretical insights

In contrast to the empirical work, with its strong focus on identifying key niche axes, the theoretical papers consider abstract niche axes that can represent any kind of niche segregation. These studies, which run the gamut from pure ecology to classic issues in evolutionary ecology, are published in the July issue (Vol. 14(5)).

From a purely ecological point of view, Barabás *et al.* review current theoretical developments on partitioning a niche axis. They study why we don't see a continuum of ecological types, or species, occupying a niche continuum. Ito and Dieckmann add evolution, but not diploid genetics, to the picture. They use adaptive dynamics to demonstrate that evolutionary branching (ecology-driven asexual speciation) becomes easier if one takes into account the finiteness of the elementary evolutionary steps. Going further, Fazalova and Dieckmann investigate a full-fledged genetic model of speciation. They show that even partial spatial segregation caused by random grouping of individuals can help drive the emergence of sexual isolation. Brännström *et al.* go beyond the single event of speciation when they review the 'large community evolution models'. They ask two key questions: How do invasions and adaptation influence community formation, and which mechanisms promote diverse and stable communities? Finally, Mallet argues that the *r*/*K* controversy was one of the underlying, historical reasons that ecological and evolutionary thinking diverged – and now we have the painful job of unifying them again. In the context of speciation, he explains that transition from polymorphism to distinct species cannot properly be discussed if the notions of selection and competition are considered unrelated.

The picture emerging from the theoretical papers in some respects echoes the empirical findings. In particular, environmental gradients that we think of as niche axes promote evolutionary divergence – but this connection is not trivial and not automatic. The way evolution partitions the niche space is not predetermined simply by the structure of that space.

Two solitudes or sister cities?

The empirical and theoretical contributions to this special collection focused on different sets of questions. Whereas the former focused mainly on documenting the specific niche axes driving divergence and the effectiveness of those axes, the latter generally assumed a generic niche axis and explored the details of its effects on divergence. Perhaps this difference means that empirical work lags behind theory, and that once we figure out the key niche axes in nature we will become more concerned with the questions currently explored by theory. Or, perhaps it means that theory should spend more time considering the basic question of what types of niche axes are likely to be most important in driving diversification.

Of course, the theories presented here are pretty far from the details of any biological situation because the specifics of differentiation are often indifferent from a theoretical point of view. But perhaps this is not a shortcoming given that theory obviously never will be able to enlist all ecological possibilities and genetic realities. Still, if we discover the plethora of theoretical opportunities, as well as the multitude of empirical divergences, we can perhaps use theory as a mental framework to connect the first with the second. We hope the workshop and this special collection have advanced that cause.

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