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THE EVOLUTIONARY UNDERPINNINGS OF MACROECOLOGY

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The fields of adaptive speciation and macroecology have made many significant advances in recent years. Research in adaptive speciation has elucidated the mechanisms of ecological speciation and sought to explain how selection can divide a single lineage into multiple independent lineages (e.g., Schluter 2000; Rundle and Nosil 2005; Nosil et al. 2009). Concomitantly, macroecologists have characterized the large-scale distributional patterns of the earth's biodiversity and advanced theory to explain the turnover of taxa within space and time (e.g., Gaston and Blackburn 2000; Blackburn and Gaston 2003; Smith et al. 2008). Although seemingly directed at the same goal, understanding the origin and maintenance of diversity, these two fields have developed along somewhat independent lines. There is an obvious connection between the two and no evolutionary biologist would doubt the importance of ecology in facilitating speciation and no ecologist would doubt the importance of speciation in facilitating diversity. Beyond that, however, there has been little dialogue about how these two fields can integrate and form a much stronger understanding of the genesis of biodiversity. Butlin, Bridle, and Schluter designed the book, *Speciation and Patterns of Diversity*, to stimulate thought and discussion about the interconnectedness of macroecology and evolutionary biology.

The book is a result of the *2007 Annual Symposium of the British Ecological Society* entitled *Speciation and Ecology*. The goal of the symposium was to foster ties between the fields of macroecology and adaptive speciation. The resulting edited volume goes a long way toward enlightening the reader of the importance of blending evolution with macroecology. The main thesis of the book is to take the evolutionary mechanisms that are responsible for generating species and examine their consequences for patterns of diversity—a melding of mechanism and pattern that will lead to an understanding of process. The editors assembled leaders in the fields of macroecology and adaptive speciation to provide perspectives of where we are both ecologically and evolutionarily with regards to patterns of diversity. This is no small feat given that the topic encompasses all of the earth's biodiversity—past and present. These leaders have offered their views and challenges for understanding the evolutionary ecology of speciation and how mechanisms of speciation may determine patterns of diversity.

The result is a careful examination of the key issues currently being studied with regards to speciation and its role in generating patterns of diversity. This book is not an in-depth look at one particular aspect of diversity, nor is it a cursory look at all topics. Instead, it is a well-balanced book that explores mechanisms of speciation and the consequences for the patterns of diversity that we observe. The taxa discussed in the book range from microbes to mammals. If I have one complaint about the breadth of taxa, it is that plants are sorely missing. They are featured on the cover, but are only mentioned in passing in one of the chapters. As has historically been the case in the development of speciation theory, plant speciation mechanisms and patterns have rarely been integrated with animal speciation. Perhaps one day that will be remedied.

The overall tone of the book is set by the following statement from the editors—"We have not subdivided the book because we are reluctant to separate parts of a spectrum." (Preface, p. x). This statement is an excellent view of how we should think about speciation and patterns of diversity. The hierarchy from individuals, to populations, to species, to higher taxa is a continuum (spectrum) as are the approaches used to studying them. Moreover, there are a variety of mechanisms that influence speciation, and which mechanism is most important may vary with the taxa studied, the present ecological conditions, and the history of a lineage. Indeed, as Butlin, Bridle, and Schluter state in the first chapter, it is difficult to determine which mechanism (geographic separation, local adaptation, sexual selection etc,) is primarily responsible for generating most biodiversity. Although not explicit in the book, my favorite take away message from reading the book is that we need to start thinking about how to partition the importance of various speciation mechanisms when examining large-scale patterns of diversity. Rather than champion one mechanism, a better, more fruitful tact will be to elucidate how each mechanism comes into play as diversity unfolds.

The editors cleverly arranged the chapters to create their spectrum. Jody Hey (Chapter 2) starts by evaluating the ways in which we currently delimit species and points to the fact that with an increasing reliance on genetic techniques, we need to develop objective ways for species diagnosis. There are inherent biases in using statistical tests of divergence—larger sample sizes will always lead to the detection of some level of divergence among groups. The crux of the problem is whether this divergence is enough to warrant species designation. Hey suggests that combining statistical tests of divergence with estimators of divergence such as migration and time since divergence may provide a more robust method for determining whether groups are on separate evolutionary trajectories. This point is important when evaluating the next series of chapters about microbial diversity. Genetic tools are now the status quo for determining and assigning microbial species.

The next three chapters are focused on speciation and diversity in the microbial world. The reader is confronted with the following problems—what do we do with asexual species, why are there so few protist species given the limitless niches they could fill, and can we derive a general theory for understanding microbial diversity? The foundations of speciation theory have been built mainly on the patterns and processes in the multicellular animal world. Do we need to abandon these ideas to understand speciation and diversity in the microbial realm? Perhaps the best answer is maybe. Barraclough and colleagues (Chapter 3) address the issue of whether asexual taxa diversify into distinct evolutionary units. If so, what governs this diversification and how does this compare to patterns of divergence in sexual organisms? Bell (Chapter 4) next examines protist diversity and suggests that low levels of gene transfer and recombination mechanisms, the protists' answer to sex, are what helps to keep protist diversity low. In addition, high rates of global dispersal also help to spread genes across populations and may slow the process of diversification. It will be interesting to see whether Bell's suggestions hold in the coming years as we see an explosion in the number of microbial species as more and more sediments, water samples, and air samples are subjected to molecular analyses. Based on what is currently known about microbial diversity, Curtis and colleagues (Chapter 5) point to a more mechanistic basis of microbial diversity. They suggest that microbial communities and their diversity—whether low or high—may best be understood by examination of free energy. They propose a link between mutation rate, the amount of free energy available to an organism, and species diversity. They cite results that suggest bacteria with energy stress appear to have lower rates of mutation and evolution when compared to species living in less energy-stressed environments. Both experimental evolution and community comparisons in the microbial world will have much to offer in testing this idea.

The spectrum then shifts to the theoretical with a look at the limits of adaptation and patterns of biodiversity and patterns of adaptive radiation. Bridle and colleagues (Chapter 6) suggest a link between the ability of a species to adapt and its distribution in space and time. In their chapter, the importance of stabilizing selection, shifting selection optima and genetic variation are discussed with respect to the rate of local adaptation. The chapter is geared to understanding population level processes that could drive the formation of diversity. Gavrilets and Vose (Chapter 7) then develop and test a theoretical model to determine the order of change in key parameters necessary for an adaptive radiation. One of the interesting outcomes is that divergence in ecological characters evolves much earlier than divergence in mating characters and that mating characters are quite dynamic and their differentiation is more continuous rather than discrete. The results suggest that local adaptation via ecological selection is quick, but there will likely be some degree of gene flow among species because complete nonrandom mating will take longer to evolve. Hence, changes in the selective environment may have to persist relatively long to gain complete reproductive isolation. This does not mean, however, that speciation is not possible.

From this part of the spectrum, the book then turns to examination of niche divergence and ecological speciation. Nosil and Harmon (Chapter 8) argue that an increase in niche dimensionality leads to an increase in genetic divergence. It is an interesting premise and one that makes intuitive sense. A greater number of niche dimensions potentially cause increased divergent selection on a greater number of traits. This may be the precursor to ecological speciation. Seehausen (Chapter 9) takes up on this line of reasoning in examining the levels of trait divergence in the cichlid

fish *Pundamilia*. He argues that populations of two species occur along a speciation transect with a single variable population at one end and two sibling species at the other. Differences in niche dimensionality with respects to the ecology of spawning sites and lake turbidity increase as one moves from the highly variable population through intermediate populations to sibling species. For *Pundamilia*, reproductive barriers due to sexual selection and signaling environments lead to adaptive divergence. Mallet (Chapter 10) suggests, however, it is the incompleteness of reproductive barriers that may also facilitate divergence. He examines speciation in the *Heliconius* butterfly mimicry complex and the patterns reinforce the theoretical results of Gavrilets and Vose. Mating among diverging species does not necessary preclude adaptive speciation. Instead, Mallet argues that perhaps introgression of mimicry genes among *Heliconius* species may be a key factor in generating the various mimicry complexes in South America. Funk (Chapter 11) completes this part of the spectrum by proposing a detailed framework for investigating ecological speciation. His major point is that studying ecological speciation is a multi-faceted endeavor that will require analyses within populations, among populations and among species complexes. Thus, it will require population biology, ecology, evolutionary biology, population genetics, and phylogenetics to gain a deeper understanding of the overall importance of ecological speciation in patterns of diversity.

From ecological speciation, the book shifts toward larger community patterns. For instance, Schemske (Chapter 12) examines the potential reasons for differences in diversification in the tropics and temperate regions. He argues that biotic interactions may be the key to understanding enhanced diversity in the tropics. In particular, he suggests that biotic interactions are stronger in the tropics and represent a moving selective optimum that can facilitate speciation. The strength of biotic interactions may be reduced in temperate climates due to increased strength of the abiotic environment on species survival. Furthermore, abiotic factors may be less likely to present moving selective optimum. Phillimore and Price (Chapter 13) examine whether temporal patterns of speciation are predicted by our current knowledge of ecological speciation models. In general, they suggest that initially speciation rates are high with initial ecological opportunity, but as niches fill, speciation events decrease and become stable. Thus, ecological speciation is an important component of early diversification, but not later in a clade's evolution.

Ricklefs (Chapter 14) expands this line of reasoning by examining the importance of regional processes in patterns of diversity. He suggests that regions have species carrying capacities that help shape the number of species within a region, and that lineages are "competing" within regions and are affected by density-dependent effects as well as changes in environmental conditions as regions fill. He also points out the difficulties of using phylogenies to examine patterns of diversity. Extinctions are not represented in a phylogenetic tree, yet are an important component of understanding patterns of diversity. Purvis and colleagues (Chapter 15) continue this argument in more detail by looking at the temporal patterns of diversification rates. They conclude that attempts to estimate diversification rates are biased because of lack of data on extinction, and suggest that neither paleontological nor phylogenetic data alone are suitable for obtaining good estimates of diversification rates. They suggest that a model system approach may be the best way to examine macroevolution. Currently, there is no single system for which we have a good understanding of its complete history of diversification and this limits our ability to test models of diversification. One of the better model systems is the fossil record of North American mammals. Alroy (Chapter 16) uses paleontological data to examine the speciation/extinction problem and estimate turnover rates for various mammal groups. The results suggest that mammalian diversity and turnover rates are constrained and there are a number of potential reasons. Clearly, differentiating among them will require more process-oriented research and an understanding of the speciation mechanism.

What the reader will learn from the seemingly hodge–podge assortment of taxa and concepts is (1) how evolutionary mechanisms that generate species have a central role in observed patterns of diversity, (2) there is no single approach for studying diversity, but there are complementary approaches that should be integrated, (3) our understanding of speciation mechanisms and their role in patterns of diversity has come far, but there is still much that remains, and (4) it is time to venture across our different subdisciplines if we are to truly come up with a synthetic view of patterns of diversity.

In every chapter along the spectrum, each of the contributors has outlined current approaches and suggested avenues for further study. There is much to be gained from each chapter in terms of learning about different approaches to studying patterns of diversity and exploring the implications of mechanisms of speciation to the genesis of diversity. There are many advanced concepts and techniques illustrated in the book, but it would serve as an excellent basis for a semester-long graduate seminar. Graduate students will profit immensely from exposure to the different approaches to studying diversity, macroevolution, and ecological speciation as well as learn what the next avenues for research are. For more seasoned researchers that peruse the table of contents, you will see the classic topics in studying diversity, but what you are going to miss by not digging deeper, are the sparks of newly forming connections between macroecology and adaptive speciation.

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