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Editor

Bird Species

How They Arise, Modify and Vanish

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Cover illustration: Coal Tit *Periparus ater melanolophus* (current status) or Spot-winged Tit *Periparus melanolophus* (common sense for many decades in the past)? Marker-gene sequences place it in the trans-Eurasian Coal Tit assemblage, its song fits in as well, but its plumage is much more colorful than that of other Coal Tit subspecies. Photograph taken near Rakchham, Himachal Pradesh, India, on 10 October 2012 by Gunjan Arora.

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In this book, ornithologists from around the world elaborate on various aspects on how the fascinating diversity of birds found on Earth has formed, how bird species change in time and space, and how they get lost—for natural reasons and under increasing pressure from human activities.

Foreword

According to the compilation used in this book, 10828 species of birds fall into 40 orders. One of these 40 orders, the Passeriformes, arose relatively recently, yet contains 60% of all bird species. The order Passeriformes comprises three suborders. One suborder, the oscines, contains 45% of all recognized bird species, which are found on all continents. The second, the suboscines, contains 15% of all species, mostly confined to South America. The third, the New Zealand wrens, contains just two extant species. What accounts for the large differences in diversity and distribution across the bird portion of the tree of life? They ultimately trace back to differences in speciation rates, extinction rates, and dispersal. Research on speciation, and even research on *bird* speciation, has grown tremendously over the past 15 years. Research on extinction has also grown tremendously, but for birds this has been largely concerned with present-day extinctions and not what happened before humans. Research on bird dispersal is undergoing a revolution, not only through the use of phylogenetic reconstruction and advanced analytical techniques, but through real-time tracking. Up-to-date reviews of the burgeoning literature are needed to keep us informed. Several fine ones are included in this compilation.

One issue that is being revolutionized by new methods for quantifying species traits, including the use of genomic data, is in the species definition itself. Clearly if we talk about speciation, extinction, and dispersal, we need to know what is supposed to be speciating, what is going extinct, and what is dispersing. George Sangster in Chapter 2 of this book gives a good introduction to this contentious issue. As someone who generally employs the biological species concept, I take this opportunity to expand upon some of his remarks.

The introduction of molecular dating in the late twentieth century led to surprisingly old dates, generally millions of years, separating even the youngest species that breed in the same place. These species, if crossed, are likely to produce infertile hybrids, as a result of genetic incompatibilities, and the failure to interbreed maintains their distinctive features. Now, a broader survey and the application of new genomic analyses have led to the discovery of several examples of very young co-occurring species, including the parasitic *Vidua* finches of Africa, Darwin's ground finches, and the *Sporophila* finches of South America. These may truly have recently formed. Other species came together, before they were completely reproductively isolated and whose co-occurrence has led to ongoing hybridization, gene flow, and genetic homogenization across most of the genome. Whatever the reason, they provide the focal point for the debate over species concepts. Young species are recognized as species, because they co-occur, but remain distinct. They are good *biological* species, because they rarely hybridize (premating isolation) and also because hybrids have low fitness generally for ecological reasons (postmating isolation). They are defined by the reproductive isolating mechanisms that keep them apart, which thereby maintain lineage distinctiveness among sympatric forms, and the study of biological speciation is the study of how such mechanisms arose. But according to various phylogenetic concepts, such young species should not be considered species at all, because the vast majority of the genetic variation present is not restricted to such species; hence, lineages are not (yet) distinct. This view has been most strongly promoted by Robert Zink, e.g., in his discussions of Darwin's finches (Zink 2002).

While in the previous paragraph I gave examples of young biological species in sympatry, much older allopatric populations are often classified as belonging to the same biological species and given the status of subspecies. They are considered to be subspecies and not species, because their inferred reproductive isolation is incomplete and the two taxa would interbreed and collapse back into one, if they came into sympatry. These subspecies may be reciprocally monophyletic in many genes, i.e., already be quite genetically distinctive. Such allopatric forms are "phylogenetic species" harboring substantial amounts of unique genetic variation. Hence, in the literature we have biological species that are not phylogenetic species (young co-occurring forms) and phylogenetic species that are not biological species (older allopatric forms). At present, most classifications and studies of speciation use the biological species concept, relatively easily applied to sympatric forms, but often requiring subjective inference on whether related allopatric taxa would interbreed, if they were to come together. Perhaps we need to move to a clear statement of the species definition being used.

These considerations highlight a major issue associated with biological speciation. Birds are particularly suitable for investigating the way by which reproductive isolation is generated as a result of divergent selection pressures (so-called ecological speciation). Studies of habitat choice, food choice, host choice in parasitic birds, migration differences, timing of breeding, and urban–rural differentiation are all nicely summarized in this book. Sometimes, these selection pressures lead to rapid divergence in ecological traits that enable co-occurrence. Hence, biological speciation can be rapid. But the co-occurrence of such young species, which have no intrinsic isolating barriers, creates the opportunity for interbreeding, hybridization, and species collapse as environments change. So perhaps communities of old co-occurring species were formed after a longer time in allopatry, with first the formation of phylogenetic species, possibly with strong reproductive barriers. In fact, it seems likely that both periods in allopatry and ecologically divergent selection pressures are involved in most biological speciation events. This book sets the stage for what will surely be an important research direction in the next decades: integrating the role of ecologically divergent selection pressures with an understanding of the origin of those genes that drive genetic incompatibilities, i.e., those genes that ensure species are permanently reproductively isolated from each other. They will undoubtedly show that speciation is often a long and protracted process.

In this light, I now return to the question posed at the beginning of this foreword and use our current state of knowledge about speciation, extinction, and dispersal to generate a viable hypothesis for why the oscines are so species rich and why the suboscines are largely restricted to South America. We infer from both fossils and phylogenetic reconstructions that the ancestor to the songbirds arose in the Australian region. It then seems that a great cooling some 34 million years ago (the Eocene/Oligocene boundary) was the time when descendants of that species set off to world domination, spreading north and multiplying as they moved through Asia and into Africa and later over the Bering Strait into North America. (One species that crossed over the Bering Strait perhaps 20 million years ago gave rise to more than 800 species, including tanagers, New World warblers, and New World blackbirds.) South America was the last major land mass to be reached and entry from the north is still going on: Two migratory swallow species have recently started to breed in Argentina. Dispersal through the world in a cooling climate was correlated with extinctions in other orders, as inferred from the fossil record. Extinctions likely affected the suboscines as well, and the late entry of oscines into South America may be one reason why so many suboscines persist there. The reasons for the great success of the oscines are still debated, but are likely to include elements of speciation, extinction, and dispersal. Several authors of chapters in this book emphasize song learning as a possible accelerator of speciation. But other researchers, including Luis Baptista and Pepper Trail (1992) and Storrs Olson (2001), have noted the possible importance of large brains and base intelligence; nests can be constructed craftily and several oscine species store food, very useful in harsh climates. Perhaps attributes such as these promoted successful dispersal and persistence in new locations, thereby accelerating speciation by giving time for reproductive isolation to develop and lowering extinction rates. I find the intelligence argument quite compelling.

Now, millions of years later, we see an intelligent organism moving toward world domination, albeit on a much grander scale than the oscines. This book summarizes aspects of bird speciation, but also pressing issues associated with the other side of the diversification coin, extinction. Timescales of extinction in the past are poorly understood for birds, and extinction addressed here is contemporary. The emergent conclusion is that the time it has taken to produce the diversity of species we now see is completely discordant from current times to extinction. As the fossil record shows for other groups, it will take many millions of years to recover from the extinction wave now in process. The more we learn about contributions of speciation and extinction to diversity, the more obvious it becomes that we need to lower extinction rates. This book is an important summary by showing where we currently are, especially in our understanding of speciation, and what we need to do next.

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