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PERSPECTIVE

Coevolution, local adaptation and ecological speciation

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Coevolution is one of the major processes organizing the earth's biodiversity, but it remains unclear when and how it may generate species diversity. The study by Parchman *et al.* (2016) in this issue of Molecular Ecology provides the clearest evidence to date that divergent local adaptation in a coevolving interaction may lead to speciation on one side of an interaction but not necessarily on the other side. Red crossbills in North America have diversified into ecotypes that specialize on different conifer species, use different calls and vary in the extent to which they are nomadic or sedentary. This new study evaluated genomic divergence among nine crossbill ecotypes. The authors found low overall genomic divergence among many of the ecotypes, but the sedentary South Hills crossbills, which are specialized to eat the seeds of a unique population of lodgepole pines, showed substantial divergence from other crossbills at a small number of genomic regions. These results corroborate past studies showing local coadaptation of the morphological traits of South Hills crossbills and lodgepole pines, and premating isolation of the South Hills crossbills from other populations. Together, the past and new results suggest that local coevolution with lodgepole pines has led to reduced gene flow between South Hills crossbills and other crossbills.

Keywords: birds, coevolution, speciation, species interactions

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Hypotheses on how coevolution may fuel the process of speciation range from those invoking speciation as an indirect outcome of the coevolutionary process to those suggesting more direct effects (Althoff *et al.* 2014; Hembry *et al.* 2014; Clayton *et al.* 2015). Ehrlich & Raven's (1964) classic paper on coevolution suggested that reciprocal selection may indirectly lead to speciation if novel mutations allow populations to radiate into new adaptive zones where they are temporarily free of their coevolving partners. The evolutionary result would be starbursts of speciation evident at higher taxonomic levels, rather than parallel speciation of coevolving taxa. Some more recent studies have focused on hypotheses of how coevolution may directly affect speciation through local adaptation. In that sense, speciation through coevolution, sometimes called diversifying coevolution, becomes a form of ecological speciation.

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This study of South Hill crossbills suggests both direct and indirect effects of coevolution on speciation. The genomic analyses indicate that divergence of the South Hills crossbills from other crossbill populations is likely driven by local coevolution (Fig. 1). Using the results of this study and their other studies over the past several decades, Parchman and colleagues argue that local coevolution with lodgepole pines has resulted in resource-based density dependence, which, in turn, reduces gene flow with other populations. Divergent selection on South Hills crossbills contributes to reproductive isolation from other crossbill populations. Reduced gene flow is therefore a consequence, rather than the initial driver, of divergence.

These results help clarify the relationships among reciprocal selection, coadaptation and speciation. There is no necessary connection among them. Reciprocal selection could lead to coadaptation of traits in interacting species without any direct effect on speciation, or it could lead to speciation in one species but not in other species. Rarely, it could lead to speciation on both or all sides of an interaction. The general process that connects reciprocal selection, coadaptation and speciation is the geographic mosaic of coevolution. Selection acts differently on interactions in different environments (geographic selection mosaics), is reciprocal in only some environments (coevolutionary hotspots and coldspots) and is continually reshaped through gene flow and genomic processes that alter the combinations of alleles available to selection (trait remixing). The study of South Hills crossbills shows that these components of the coevolutionary process can sometimes result in a local population of one of the interacting species becoming reproductively isolated from other populations.

The results of this study combined with other studies of these coevolving crossbills and conifers show that interpretation of the connections between reciprocal selection, adaptation and speciation demands a deep understanding of the natural history and ecological processes shaping species interactions combined with well-chosen molecular approaches. The insights from this study were possible only because past studies have carefully assessed the ecological interactions between crossbills and conifers in many populations and environmental settings (Smith & Benkman 2007; Benkman *et al.* 2010; Parchman *et al.* 2011; Benkman & Mezquida 2015). These past studies have evaluated

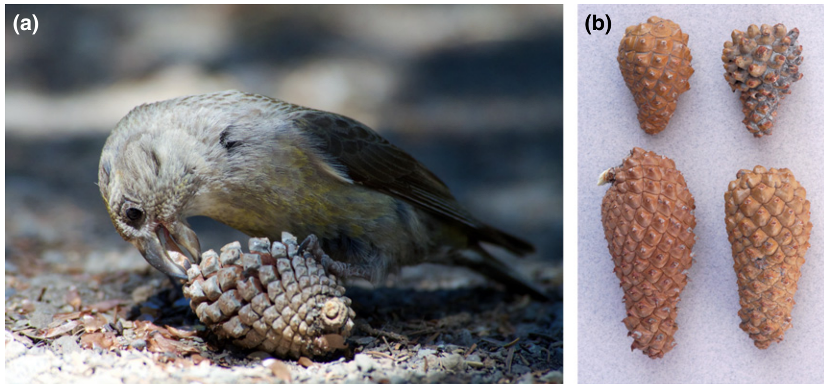

Fig. 1 Crossbills and lodgepole pines. (a) A South Hills crossbill lifting a lodgepole pine seed with its tongue and (b) lodgepole pine cones from different geographic regions. The top two cones are from regions in which crossbills are present, but the pines coevolve mostly with red squirrels. The bottom two cones are from the South Hills, where pine squirrels are absent and the pines coevolve with crossbills. Regional differences in cone morphology impose divergent selection on the birds. Photographs courtesy of Craig Benkman.

patterns of density dependence in these birds, experimentally manipulated traits to understand the foci of selection and assessed the actual structure of selection on those traits in multiple ecosystems. The authors know how and why the traits and ecological outcomes of these interactions vary geographically. The genomic results for these crossbills corroborate the past ecological results suggesting that, during the process of local coevolution, these birds have become reproductively isolated from other crossbill populations.

More generally, this study is important for yet another reason: it suggests that even relatively long-lived species may undergo speciation during remarkably short periods of time through coevolving interactions with other species. Parchman and colleagues suggest that speciation in South Hills crossbills may have occurred over the past 6000 years. Post-Pleistocene environmental changes have altered the distribution of lodgepole pine in the Rocky Mountains, eventually leading to conditions favouring local coevolution and a sedentary population of crossbills in the South Hills. Unlike adaptation to physical environments, coevolution between or among species produces direct genetic feedbacks generation after generation, continually altering and fine-tuning selection on populations. Consequently, speciation driven by local coevolution may sometimes be faster than speciation driven by adaptation to local physical environments.

The view of evolution as a slow and stately process that occurs over a long period of time is being replaced, through studies like this one, with a view of evolution as a relentlessly dynamic combination of ecological and genetic processes (Thompson 2013). Local adaptation and strong divergence among populations constantly ebb and flow as environments change and the balance between selection and gene flow tilts and retilts across space and time. As the geographic ranges of species shift, and species interact in different ways in different places, new evolutionary and coevolutionary solutions arise. Occasionally, as with the South Hill crossbills, a new or incipient species may arise, sometimes rapidly, from the geographic mosaic of coevolution.

As examples accumulate of adaptation and coadaptation driven by the geographic mosaic of coevolution, we are left with the question of why there are still few convincing examples of speciation fuelled by coevolutionary mosaics. There seem to be at least two reasons. It is easier, although still plenty difficult, to show that the traits of two or more species are coadapted in at least some ecosystems or regions than it is to show that reciprocal selection has caused reproductive isolation among some populations. Showing that speciation has been driven by coevolution requires a combination of molecular, ecological, geographic, phylogeographic and phylogenetic data that can take decades to accumulate. Also, many more studies focus on one side of interactions than on both, or all, sides. Demonstrating that coevolution has driven, or at least influenced, speciation requires understanding how reciprocal evolutionary change has led to reduced gene flow among populations of at least one of the interacting species. Hence, although the opportunities for evaluating ecological speciation are increasing, the opportunities for assessing whether coevolution contributes to ecological speciation remain limited. That is why the ongoing studies of these crossbills have become increasingly important for our understanding of the coevolutionary process. By linking together so many different kinds of results, and knowing where and why the coevolutionary hotspots and coldspots occur, these studies continue to provide new insights into how the coevolutionary process may fuel the diversification of life.

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