Does Competition Drive Diversity of Species?

By Emily Singer

The red-billed scythebill, a woodcreeper from the ovenbird family, has a long, curved beak.

In 1982, a few large ground finches took up residence on the tiny island of Daphne Major in the Galapagos. Compared with the island's existing population of medium ground finches, the invaders had an advantage: large beaks that could more efficiently crack open the seeds of the Jamaican feverplant, one of the island's biggest bird food bounties. The newcomers began to flourish, eating many of the seeds and forcing the diminutive natives to forage for smaller options.

The two kinds of birds lived in relative harmony until 2003, when a two-year drought decimated the food supply for both species, pushing them to the brink of starvation. The bleak conditions favored a subset of medium finches that had smaller beaks; they had never been able to crack feverplant seeds, and their diet consisted solely of small seeds. Free from competition with the large ground finches, the smaller-beaked members of the medium finch clan survived the drought and passed along their petite features to the next generation. The average beak size in medium ground finches shrank in a swift and lasting change to the species. Peter and Rosemary Grant, biologists at

Princeton University who have been studying Galapagos finches for 40 years, tracked the change, publishing their results in Science in 2006. It became a textbook example of an evolutionary tenet known as "character displacement."

In Darwinian evolution, organisms compete for resources, and the winners get to pass their genome to future generations. According to these rules, two similar species using the same resources in the same environment will be forced to compete with each other. If both are to survive, they will need to become more distinct from each other over time. The famous naturalist E. O. Wilson, along with collaborator William Brown, dubbed this pattern character displacement in the 1950s and proposed that it explains much of the diversity among the world's organisms.

Joseph Tobias, an evolutionary biologist at Oxford University, suggests that character displacement may not be as common as previously thought.

"It's one of the main Darwinian ideas for explaining why species are different," said Joseph Tobias, an evolutionary biologist at Oxford University. But some scientists, including Tobias, are now questioning the data supporting character displacement as a driving force in the evolution of diversity. A report published last year examining 144 studies found that few met the strongest criteria for character displacement. Scientists often failed to rule out other possible explanations, for example, or to show that the change resulted from a heritable trait. And in February, Tobias and collaborators published a large-scale study in Nature that questions how widespread character displacement is in nature. Focusing on ovenbirds, a family of birds that, like Darwin's finches, have evolved different beak sizes, they found little evidence that character displacement was responsible for differences in the species if the ages of the species are taken into account. That is, given enough time, species tend to diverge, or become more different from each other, even without interspecies competition.

Tobias and Peter Grant, among others, contend that robust examples of character displacement are relatively rare. If that indeed means that the phenomenon itself is rare, rather than just difficult to reliably detect, scientists would need to reconsider the role of competition in the evolution of diversity.

"We're not saying that character displacement doesn't occur, but it's probably rarer than people think," Tobias said. "The implication of our study is that almost all of the species differences [in ovenbirds] that people have attributed to character displacement are actually the result of time."

Some in the field view the provocative claim with skepticism. "I don't think this spells the death of

character displacement," said Daniel Simberlofff, an ecologist at the University of Tennessee, Knoxville who wasn't involved in the project. "We need a lot more studies to know if this is a general phenomenon."

A Swinging Pendulum

Like many scientific theories, character displacement has gone in and out of favor. After Wilson and Brown coined the term in the 1950s, "just about everyone saw it everywhere," said Jonathan Losos, an evolutionary biologist at Harvard University whose 144-study review published last year examines the history of character displacement. "Any difference between coexisting species was attributed to competition." But often there was little supporting it, and by the 1980s, the pendulum had swung the other way.

"It was a contentious period," said Yoel Stuart, a postdoctoral researcher at the University of Texas, Austin, and co-author of the review with Losos.

In response to some of the criticism, scientists adopted more stringent criteria for concluding that character displacement was truly driving two species to become more different from each other. According to these guidelines, researchers should rule out other drivers of diversity, such as random chance or subtle differences in the two species' habitats. Studies of character displacement should also show that the species under study truly compete, and that the differences among species, such as smaller beaks, are a heritable trait. In the 1990s, character displacement regained popularity as more rigorous studies emerged.

Anolis lizards in the Lesser Antilles tend to be medium-size if they live on an island without lizard competitors, like this Plymouth Anole, but either small or large if two species share an island.

Losos' studies of Anolis lizards in the Lesser Antilles highlight a major challenge in studying character displacement — different evolutionary histories can result in the same ecological pattern. In work published in 1990, Losos reported strong evidence that character displacement among lizards in the northern islands had resulted in the islands having one smaller and one larger species. The southern islands similarly had habitats with one large and one smaller species of the lizards. However, the likely explanation for this situation in the south was that the animals were two different sizes when they arrived. Without knowing the history of when two species come together,

determining the forces at play can be difficult. The end result of both processes looks the same. “That’s one of the biggest sticking points in these studies,” Losos said.

Character displacement remains popular today, but some scientists insist that stronger evidence is needed to show that this phenomenon is the true driver of differences among competing species. “I think people have gone overboard and returned back to the state of play in the ’70s where people see character displacement everywhere,” Losos said, though he thinks that today’s studies present better evidence than their 1970s counterparts. Despite a huge proliferation in the number of potential examples of character displacement, conducted more rigorously than earlier efforts, fewer than 40 percent of the 144 studies that Stuart and Losos reviewed met most of the gold standard criteria. “With 20 years of rigorous research, we still have few cases,” Stuart said.

Peruvian Glaciers to Bolivian Deserts

An avid bird watcher from the age of 11, Tobias has traveled to the plains of Patagonia, Bolivian deserts and the high cloud forests of Panamanian volcanoes and has spied on about 5,000 species, more than half of the world’s birds.

These explorations revealed a pattern familiar to any naturalist: Where two similar species live in the same habitat, they are generally more different than species that live apart, said Tobias, now 44.

“The underlying assumption is that it’s because of character displacement,” he said. But Tobias began to doubt that assumption after coming across exceptions to the pattern. A study of Amazonian antbirds, for example, revealed that two species that compete for resources use very similar songs. “There may be many scenarios where competition does not produce divergent selection” and may in fact drive the opposite pattern, in which a specific characteristic starts to converge, Tobias said.

In 2007, Tobias and collaborators launched their in-depth study of ovenbirds, a diverse family of small, insect-eating birds that live mainly in South America. Different ovenbird species have adapted to rocky ocean shorelines, snowy mountains, scorched deserts and tropical rainforests. Like finches, ovenbirds have a variety of beak sizes and shapes, an important indicator of food preference that makes them ideal for studying evolution. In ovenbirds, “some [beaks] are long and down-curved, like a scythe, for probing into crevices in tree bark,” said Jason Weir, an evolutionary biologist at the University of Toronto who was not involved in the study. “Others have short dagger-like bills.”

Most studies of character displacement have focused on only a few species, but Tobias’ team compiled information on 350 ovenbird lineages, including species and subspecies, culling data from a vast set of resources: bird specimens from museums; recordings of bird songs, some more than a century old; geographical data collected during expeditions and from other sources; and a highly detailed evolutionary history of ovenbirds. “The scope of the study is pretty amazing,” said Stuart, who was not involved in the research.

To study the role of competition in evolution, Joseph Tobias and collaborators mapped out the evolutionary relationships and variation in beak size among 350 lineages of ovenbirds.

For each lineage, the researchers compared the youngest, most closely related species living in the same area and the youngest, most closely related species living in different areas. When they looked at the data, they found a pattern that Darwin and most biologists would have predicted — the lineages living together were more different than those that lived apart.

But Tobias and colleagues suspected that species that cohabit tend to be older than those that live apart. That's because new species usually form in isolation, so it makes sense that the youngest don't typically share habitats, Tobias said. This pattern was familiar to some evolutionary biologists, but Tobias said few ecologists had considered the implications. "You can't just compare things living together with those living apart," Tobias said. As a species ages, it has more time to evolve, so "you have to take into account how old they are," he said.

When the researchers accounted for the age of each ovenbird lineage — an unusual step in studies of character displacement — the differences vanished. "We find no evidence there is any kind of bump up in differences between lineages that come together," Tobias said.

Instead, they found that the youngest species living together tend to be much older than the youngest species with distinct habitats; the former split from their common ancestor an average of 10 million years ago, compared to approximately 4 million years for the latter.

The researchers concluded that diversity isn't driven by competition between cohabiting species.

The differences they see may simply be the result of species having more time to evolve. “An important finding of their study is that it takes a long time for these species to diverge enough to be able to invade each other’s geographical range with little or no competitive interaction,” said Peter Grant, who was not involved in the study.

Indeed, previous research by Tobias’ team suggests that ovenbird species only start to overlap geographically once they are different enough to peacefully coexist. Species with the most similar beaks and ecologies took longest to cohabit, Tobias said. “It’s not necessarily that evolution isn’t happening; it’s just not driven by interaction among species,” Tobias said.

Evolution in Action

Having plunged itself into an evolutionary debate, the ovenbird study has received mixed reviews. Many experts applaud its unprecedented scope and the effort to look at the large-scale effects of evolutionary forces. “The overarching question they pose is an important one in evolution,” said David Pfennig, an evolutionary biologist at the University of North Carolina, Chapel Hill. One of the biggest issues in evolutionary biology is understanding how microevolutionary processes, mechanisms that happen within species, influence larger ecological patterns, he said. To what degree do they explain broad observations, such as the diverse range of body shapes we see? By looking at many species of ovenbirds, “this is one of the few studies that gets directly at this issue,” Pfennig said.

But some say it’s too soon to conclude that the findings will hold true more broadly. “All we can say is that there isn’t a strong signal for [character displacement] in this taxonomic group,” Weir said. “But it’s an extremely interesting starting point to explore this in other groups.”

It’s also difficult to rule out character displacement in this group of birds entirely. Pfennig points out that the traits that Tobias’ team examined in ovenbirds are mostly morphological — beak and leg size. But it’s possible that competition among species has driven the birds to evolve different behaviors, such as foraging during different times of day. “Many species undergo this kind of divergence,” he said.

The one behavior that Tobias’ team studied — bird song — did appear to shift in response to competitive species, but in the opposite direction than traditional character displacement would predict. Birds with overlapping ranges tended to have more similar songs, a pattern of convergence rather than divergence. Ovenbirds sing for largely territorial reasons, warning other birds to stay out. Tobias theorizes that a signal recognized by both the singer’s species and related competitor species deters more birds. This may represent a different flavor of character displacement, in which certain characteristics are driven to become more similar.

Islands and Archipelagoes

Tobias and collaborators propose that character displacement might be most important for environments, such as islands and archipelagos, with fewer species that come into contact earlier in their evolutionary history. Indeed, the best examples, such as Darwin’s finches, come from these environments.

If there are only two competing species on an island, they might have more unoccupied ecological niches in which to expand. Darwin’s finches, for example could evolve to specialize on smaller seeds. “But on a continent, there is less evolutionary wiggle room,” Weir said, because other competing species have already occupied these niches.

But scientists are divided about the idea. Some say that fewer species may simply make it easier to see character displacement. “I think it’s just harder to document on continents,” Simberloff said. “People study phenomena on islands because they are simpler systems.”

The findings also highlight the need to take evolutionary history into account in studies of character displacement, an issue that has been ignored in the past, largely because that data was hard to come by, Weir said. Many of the existing studies held up as examples of character displacement “are invalid without a time component,” he said.

Catching evolution in action, as the Grants did with their finches, is a powerful alternative, because researchers don’t need detailed evolutionary histories. “The real advantage is that you can actually see what happens,” Losos said. Theirs and other recent studies have demonstrated just how quickly evolution can occur, making it feasible to measure changes as they unfold. “Years ago, we thought evolution was too slow to see these things change, but it’s not,” Losos said. “Evolution can occur rapidly when natural selection is strong.”

One of the best opportunities for catching character displacement in the act comes from the study of invasive species. “We have inadvertently set up situations where character displacement might occur by introducing species that might be competitors,” Losos said. Despite the shortfalls of many existing studies, he said, “I am convinced that character displacement is a common phenomena.”

Scientists predict that the ovenbird study will provoke a round of similar research in the next few years to test whether the same pattern — that species differences are mostly linked to the age of the species rather than competition among species — is true in other groups. Tobias and collaborators are already expanding their approach to many more of the world’s birds, including other members of the roughly 1,200 species group known as suboscines. (Ovenbirds belong to this group.) They also plan to study character displacement and other evolutionary questions for the 5,500 species of passerines, which encompass more than half the world’s bird species. The effort will rely on evolutionary maps currently under construction by researchers at Louisiana State University and elsewhere.

Scientists hope that in the next 10 years, studies that take species age into account, as well as the invasive species efforts that Losos describes, will clarify the role of competition in the evolution of diversity.

“My overall opinion is that character displacement may be fairly common,” said Peter Grant, whose studies of Galapagos finches are considered one of the strongest demonstrations, “though far from universal [and] generally small in magnitude.”

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