For the birds. The Clark's nutcracker prefers pinecones with thinner scales (*inset*, *right*), but with squirrels around, the cone's scales are thicker (*inset*, *left*).

EVOLUTIONARY ECOLOGY

Variable Evolution

Researchers are discovering the intricacies of relationships in which one organism sometimes influences the evolution of another and sometimes doesn't

Coevolution is a tale of intimacy. Two species—a parasite and its host; a pollinator and its plant—evolve in lockstep, adapting ways to deal with willing, and sometimes unwilling, partners. But occasionally, evolution gets off track.

In north-central Nevada, for example, the Clark's nutcracker has a cozy relationship with certain pine trees: The birds carry off seeds and cache some of them for future use, helping new seedlings get started. For its part, the pine tree has made extracting seeds child's play by evolving short cones bursting with seeds that are covered by thin, easy-to-remove scales. But in the Rocky Mountains, a ménage à trois has developed, in which the pine trees are torn between defending their seeds against squirrels and helping out the nutcracker. As a result, the birds must make do with long, heavy cones with thick scales and relatively few seeds. Coevolution has practically stalled out.

When biologists first started thinking about coevolution some 40 years ago, they didn't appreciate this complexity. Over the years, they have marveled at bird bills exquisitely shaped for feeding efficiently on products of specific plants, and they've learned about arms races in which snakes, insects, and other predators develop ways to outwit the ever-better defenses of their prey. But there have been nagging inconsistencies in many of these observations: Some species pairs don't have the same adaptations everywhere.

Ecologists have found that, in organisms from birds to bacteria, coevolution is not a sure thing. "The interactions between pairs of species have different intensities in different ecological settings," says May Berenbaum, an entomologist at the University of Illinois, Urbana-Champaign. A decade ago, evolutionary ecologist John Thompson of the University of California, Santa Cruz, came up with a theory to explain these geographical variations in coevolution and coined the term "geographic mosaics." And in the past few years, because of its relevance to understanding evolution, biodiversity, and species invasion, there has been "a surge in interest" in the theory, says Richard Gomulkiewicz, an evolutionary biologist at Washington State University in Pullman.

Coevolution's mosaics

Thompson proposed that the survival advantage provided by coevolution was inconsistent because environmental conditions, and hence the forces of natural selection, differ from place to place. In retrospect, this idea seems self-evident, but at the time "people generalized [what they found] from one location and extrapolated to everywhere else for that species," says Craig Benkman, an evolutionary ecologist at the University of Wyoming in Laramie.

If researchers looked more broadly at different populations of interacting species, Thompson predicted, they should discover "hot spots"—with intense interactions between partner species and rapid coevolutionary change—and "cold spots"—areas where the two species have little influence on each other's evolutionary trajectories. Environmental factors, including the presence of other species, should affect hot-spot distribution by making coevolution more or less advantageous to the partners. The mobility of the partners should matter as well: Gene flow from one set of coevolving populations to another should speed or impede the evolution of specializations.

Thompson's fellow ecologists were skeptical at first. "Many of us were left wondering how to address such a complex set of processes and were frustrated with the lack of very specific, testable predictions," says Edmund Brodie III, an evolutionary biologist at the University of Virginia, Charlottesville. Recalls Thompson, "The criticism I got was 'Show me the data.'"

Today, however, the theory is much more palatable. In 2005, Thompson published a book, *The Geographic Mosaic of Coevolution*. He and other theoretical biologists have come up with more detailed models to predict how species might change over space and time, helping field researchers focus their studies. In 2006, the number of publications was expected to be double that of 6 years ago. "We're suddenly seeing the data for a whole variety of interactions," Thompson says.

Third-party interference

Even as Thompson was first formulating his geographic-mosaic theory, Benkman was coming to similar conclusions based on his long-term studies of crossbills and other birds that feed on pine seeds. In the 1990s, his work suggested that the presence of squirrels in certain pine forests of the Rocky Mountains influences cone shape and scale size. Now he and Adam Siepielski have extended that work with a careful look at the ecological and evolutionary crosstalk between squirrels, Clark's nutcrackers, and pine trees in western North America. They find the geographic mosaic and the cold and hot spots Thompson envisioned.

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The squirrels and birds both eat seeds, but only the nutcrackers help the tree by dispersing some seeds: A single bird can carry off up to 98,000 seeds a season, sometimes as far as 22 kilometers. When squirrels harvest cones, few seeds ever germinate. In 2004 and 2005, Siepielski and Benkman looked at limber pine or whitebark pine forests with or without squirrels and assessed cone and seed characteristics as well as bird and squirrel consumption of seeds.

The results were similar irrespective of the pine species. Nutcrackers preferred cones with thinner scales and more seeds, characteristics of the squirrel-free stands. But forests with squirrels had wider, heavier cones with thicker scales and fewer seeds that were harder for the birds to retrieve, Siepielski and Benkman report in the May issue of *Ecological Monographs*. Thus, squirrel-infested forests represented cold spots. "The presence or absence of the squirrel drives the interaction between the pines and the nutcrackers," says Benkman.

Sometimes three-way interactions can lead to new species, Benkman and Julie Smith of Pacific Lutheran University in Tacoma, Washington, reported in the April issue of *American Naturalist*. The newcomer, the South Hills crossbill, lives in pockets of Idaho forest where squirrels are absent. There, unusually thick scales have resulted in bigger bills, which in turn eventually led to changes in birds' calls. With that change, the birds' attractiveness to crossbills from elsewhere diminished. "The selection is so different with and without squirrels, it's causing one population to speciate from the others," says Benkman.

Arms races

Berenbaum has also found that a third species can throw a wrench in the works of coevolution. Over the past 15 years, she and entomologist Arthur Zangerl, also from the University of Illinois, had found a tight correspondence between the types of toxins produced by wild parsnip and the detoxifying capabilities of parsnip webworms found in the United States. Both plant and caterpillar are native to Europe, with the parsnip arriving in North America about 400 years ago, followed by the webworm about 250 years later.

What's striking, notes Berenbaum, is how quickly the webworm and the parsnip established a tight correspondence once the two met up in North America. Zangerl has analyzed the toxin profiles of herbarium specimens of wild parsnips from collections that date from 1836 to the present. His 2005 analysis shows that within 20 years of the webworm's arrival, the toxin content increased. And, judging from the U.S.–based webworm's current ability to chow down on parsnip with impunity, the webworm has rapidly improved its ability to break down parsnip toxins. "That's something we don't see happening in the European samples," Zangerl notes. The reason is the presence of a third player in Europe: Webworms there often munch on hogweed, a less toxic plant that's not present in North America, Berenbaum and Zangerl reported in the December 2006 issue of *Ecology*.

At the University of Virginia, Brodie is examining another coevolutionary tale, that between toxic newts and their snake predators. He and his colleagues have found hot spots—where garter snakes are rapidly evolving resistance to ill effects from snacking on newts—and cold spots, where resistance to the newt poisons has not evolved. They are now looking to see whether other predatory snakes have the same hot and cold spots. "If so, it is pretty strong evidence that there are major geographic or biogeographic patterns that influence the mosaic and not simply some stochastic process," Brodie says.

Chemical warfare. Wild parsnip battles the parsnip webworm by evolving ever-more-potent toxins in its tissues.

CREDITS (TOP TO BOTTOM): ARTHUR ZANGERL/UNIVERSITY OF ILLINOIS

Brodie hopes to investigate how gene flow affects these geographic mosaics. When resistant snakes move into an area populated by vulnerable individuals, for example, they should have the advantage and "warm up" a cold spot. Brodie knows that mutations in a gene for a sodium channel in muscle confer resistance to the newt poisons, and he and his colleagues are sequencing this gene with the hope of using single-base differences between individuals as a way to monitor gene flow throughout the mosaic.

To date, though, the most solid evidence that gene flow plays a major role in geographic mosaics comes from an experiment in which Thompson and his colleagues monitored how quickly bacteria evolved resistance to bacterial viruses (which in turn develop ways to evade this resistance). In 2004, he, Samantha Forde in his lab, and Brendan Bohannan of the University of Oregon, Eugene, first showed that the intensity of this arms race depended on how nutrient-rich the environment was, with resistant bacteria evolving faster in richer media. But when the researchers put bacteria from rich media in with bacteria with suboptimal nutrients, the evolution of resistance sped up in those communities, thereby changing the coevolutionary dynamics.

Working out how geographic mosaics arise, and why, has important ramifications. Agencies charged with protecting borders against invasive species are struggling to predict the worst offenders. "The geographic-mosaic theory can be a tool for improving predictions," says Berenbaum. And Benkman thinks the data to date on the effects of a third-party species suggest caution to wildlife biologists thinking about reintroducing species, particularly mammals, into areas where they have not lived for centuries. Finally, conservation policies need to consider how species might differ genetically across space, and how the coevolutionary paths they travel might vary. "If in conserving biodiversity we aim to represent the full array of the species, then we need to cover a broad sweep of these areas," says Jeremy Burdon, an evolutionary biologist at the Commonwealth Scientific and Industrial Research Organisation Division of Plant Industry in Canberra, Australia.

For these reasons and others, testing the geographic-mosaic theory has increasing appeal. "People are motivated to see if these different processes are present and if they are important," notes Gomulkiewicz. And Paul Rainey, an evolutionary geneticist at the University of Auckland, New Zealand, agrees: "There is a huge opportunity here for research."

–ELIZABETH PENNISI