What's a tree to do?

Interactions between nutcrackers, squirrels, and bird-dispersed pines

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Seed dispersal strategies are an important facet of the natural histories of plants. Most plants benefit from seed dispersal by having their seeds moved from the immediate vicinity of the parent plant, thereby reducing the chances of seed predation and competition with their siblings, among other benefits. Limber pine (*Pinus flexilis*) is among the 20 pine species that rely on birds, namely Clark's nutcrackers (*Nucifraga columbiana*), to disperse their seeds. Unlike most pines, bird-dispersed pines lack the wings on the seeds that slow their descent to the ground allowing them to be dispersed by wind. If you watch a group of nutcrackers in the fall, you will see them using their bills to shred the tough cone scales or reaching between open cone scales of limber pine to remove the seeds. During the fall an individual nutcracker will bury up to an estimated 98,000 seeds a year! Nutcrackers rely on these seeds throughout the winter and spring and into early summer as a resource for themselves and their offspring. However, many buried seeds are not retrieved by nutcrackers and some may germinate into new trees before beginning the cycle anew.

The interaction between nutcrackers and limber pine is an example of mutualism. Both nutcrackers and the trees benefit from the interaction. Trees provide nutcrackers with a nutritious food while the nutcrackers disperse the seeds. But there are costs. Many of the seeds are eaten, and in some years no cones are produced. Hence the interaction is very dynamic. Nutcrackers, however, are not the only animals that eat the seeds of limber pine. In fact, the most important seed predator of limber pine is likely the pine squirrel (*Tamiasciurus* spp.), which is common to many of the coniferous areas throughout the Rockies

and Sierra Nevada. Like nutcrackers, squirrels remove large numbers of seeds each year from limber pine and other conifers. Unlike nutcrackers, however, squirrels are a seed predator, not a seed disperser—the pines do not benefit from having their cones harvested by squirrels. Because squirrels do not provide a benefit like nutcrackers, this creates a conflict of interest where both nutcrackers and squirrels coexist with these conifers.

Trees that minimize cone harvest by pine squirrels while maximizing seed harvest by nutcrackers will produce the most seedlings. These trees have a reproductive advantage and therefore come to represent more and more of future generations. This is simply how natural selection causes populations to evolve over time. One of the most important functions of conifer cones is to protect seeds, so what you might expect is where pine squirrels occur, seeds are well defended by larger cones. Where pine squirrels are absent, such well-defended seeds are not necessary. Thus, in regions where pines squirrels are absent we expect trees that invest less in seed defenses should be more attractive to nutcrackers and have more of their seeds dispersed. Over time, these trees that are producing more seeds and allocating less to defenses should increase in the population. I have measured tree preferences of both pine squirrels and nutcrackers, which is a way to measure natural selection exerted by these animals, and not surprisingly, they strongly prefer to forage on trees with less-defended cones.

If you look at limber pine cones from mountain ranges in the Great Basin where squirrels have been absent for 10,000 or more years, and compare these cones to limber pine from throughout the Rockies or Sierra Nevada where squirrels are present, you will notice they are very different. Cones in the Great Basin are much smaller, with thinner cone scales, than cones in the Rockies or in the Sierra Nevada, but even though the cones are smaller they have twice as many seeds. This makes sense when we consider the preferences of squirrels (as seed predators) and nutcrackers (as seed dispersers), and is a wonderful example of how natural selection influences conifer cone structure.

These patterns are also replicated in another related bird-dispersed pine, whitebark pine (*Pinus albicaulis*), which occurs throughout the Rockies and Sierra Nevada, and further supports the hypothesis that these pines are evolving in response to the balance of natural selection exerted between nutcrackers and pine squirrels.

This work highlights the importance of taking a broad perspective on how organisms interact in nature. It also emphasizes why protection of numerous areas is important, because interactions between organisms do not occur in the same way in every location, and this diversity of interaction is as important to conservation as are the species themselves.