ECOLOGY

Eco-evolutionary effects of keystone genes

The rapid evolution of specific genes within species can drive ecological changes

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There is increasing evidence that genetic evolution can occur rapidly enough to affect the ecological dynamics of populations and communities (1-3). To better predict the future of ecosystems, it is necessary to understand how evolutionary changes within species influence and interact with ecological changes through processes known as "eco-evolutionary dynamics" (4). On page xxx of this issue, Barbour et al. (5) demonstrate that a gene affecting a plant's resistance to herbivory also influences the persistence of the food web through the gene's effect on plant growth (see the figure). Subsequent studies of natural selection in the wild can help understand how variations of such "keystone genes" can be maintained (6, 7). The maintenance of genetic variation in keystone genes is required for eco-evolutionary dynamics to be perpetual rather than transient.

It is important to determine the genes that underlie eco-evolutionary dynamics because genetic details, such as the number and biological effect of genes that affect traits, are expected to influence evolution. In this context, by identifying a gene with marked ecological effects, the study by Barbour et al. offers several key insights. The authors constructed an experimental food web in the laboratory, which comprised a predator (a parasitoid wasp that attacks aphids), two herbivores (two species of aphids that eat plants), and the plant *Arabidopsis*—also known as thale cress, a model genetic organism. They monitored three genes in the cress that showed variation in the wild. The genes were chosen because of their role in controlling chemical biosynthesis that could affect resistance to herbivory.

Barbour et al. observed that one of the genes, *AOP2*, affects the persistence of the food web. In other words, this gene affects extinction risk and the collapse of the wider community in the experimental ecosystem. Specifically, the null allele (an allele is a variant of a gene), which is a loss-of-function mutation that occurs in natural thale cress populations, reduced the extinction risk for the species in the food web. Critically, these effects are pronounced, with the null allele reducing extinction risk by 16% relative to the average allele, and by 29% relative to the *AOP2+* allele, a specific *AOP2* genetic variant. Just as keystone species have disproportionately strong effects in communities relative to other species (10), *AOP2* is a keystone gene that has strong effects on ecological dynamics (11, 12). The authors combined their results with ecological modeling to elucidate the mechanisms underlying the observed effects of *AOP2* on food web dynamics. Their analysis revealed that the gene affects extinction by altering species' intrinsic growth rates in a manner that allows the parasitoid and the dominant aphid species to coexist. Thus, the results also inform the mechanisms by which species co-exist--a major theme in ecology (13).

Given the revelation brought by these results, perhaps the most pressing question that needs answering is whether the variation at keystone genes is maintained over the long term, and if so, what are the mechanisms that preserve this variation over time (6, 7)? These are important questions because genetic variation is the fuel for evolution. If the variation is lost, eco-evolutionary dynamics will not occur except following variation introduced by the occasional mutation or gene flow. In classic population-genetic models of adaptation, genetic variation is expected to be lost as natural selection acts in a single, consistent direction that favors beneficial alleles in the population (6). Through this process, natural selection causes one allele to replace all others, eliminating genetic variation from the population.

In contrast to this view of directional selection and the loss of variation, the ecological genetics literature emphasizes 'balancing selection', where heterozygotes (i.e., individuals with two different allele copies at a gene) have higher fitness than homozygotes or where selection fluctuates over time and is dependent on the environmental or genetic context (7). In such instances, the selection is not uniform and genetic variation can be maintained. Determining how selection acts on keystone genes in the wild is thus required to predict whether eco-evolutionary dynamics will be brief and transient (as predicted by directional selection), or more pervasive and perpetual (as predicted by balancing selection) (1-3).

Another future direction concerns the genetic architecture of traits that exhibit ecological effects (4, 8-9). Although traits controlled by single genes of large effect certainly exist, such as the *Agouti* gene affecting coat color in mice (8), many traits exhibit continuous phenotypic variation underlain by many genes (14). In such cases, individual genes have minor effects on trait variation. Moreover, not only genes but also the environment influences trait expression.

Additionally, even apparent cases of single genes with strong effects on a trait may represent multiple genes that are tightly linked (i.e., physically located) on the same chromosome, as occurs in 'supergenes' (9). Studying such complex genetic architectures is more challenging than studying single genes, as evidenced by difficulties in genetic mapping of human disease and complex behavioral traits (14). Testing how traits underlain by many genes affect ecological dynamics is a challenging, yet important, avenue for future work. A caveat is that even if major effect loci are relatively rare, they could be more likely than minor effect loci to exert marked ecological effects (1).

Further studies that combine disciplines such as ecology, genetics, and mathematical modeling are likely to invigorate the field of eco-evolutionary dynamics. Although simple systems are a powerful and useful starting point for such work, most eco-evolutionary systems are more complex because of the interactions and feedback among and within ecological and evolutionary processes, and complex communities and trait genetics (1-3). This complexity of eco-evolutionary systems must be unraveled to fully understand if these dynamics will be gradual or abrupt, and how the dynamics can be characterized by tipping points in ecosystems (15). Such knowledge will inform the importance of evolution for ecological dynamics and biodiversity.

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Figure 1. A keystone gene in a plant affects food web dynamics. Using an experimental community, comprised of a plant, aphids, and a parasitoid, Barbour et al. (5) demonstrate that a gene affecting the resistance of thale cress (pictured above) to herbivory also influences extinction risk in the community.