

Ecological speciation in wild tomatoes.

Keywords: adaptation, drought, ecological speciation, hybrid fitness, natural selection.

Ecological speciation occurs when divergent selection on two populations results in reproductive isolation (1). This isolation can be pre- or postzygotic (1). Postzygotic isolation, essentially reduced hybrid fitness, can in turn be intrinsic or extrinsic. Intrinsic isolation occurs when genetic incompatibilities cause hybrid sterility or inviability, while extrinsic isolation occurs when hybrids are less fit because they fall between parental niches (1, 2).

Intrinsic isolation should occur across all environments, while the appearance and magnitude of extrinsic isolation depends on environment. The dependence of extrinsic isolation on environment suggests that it may be more easily overcome during environmental changes (see (3)). While it is agreed intrinsic and extrinsic isolation mostly likely both contribute to speciation, little is known about their relative importance as species barriers.

One way to understand the relevance of extrinsic isolation is to study the selection acting on hybrids in the wild. Previous studies have shown that hybrids can be less fit than parent species (4), more fit (5), or that this relationship can vary depending on the environment measured (3, 6, 7). Often F1s display higher fitness than parents because of heterosis (8); including F2s and backcrosses can allow us to determine if hybrid fitness is truly reduced compared to parents. Using backcrosses will also reveal cytonuclear interactions (9).

As an NSF fellow, I plan to use tomato species to examine the importance of extrinsic reproductive isolation. *Solanum* Sect. *Lycopersicon*, hereafter referred to as *Lycopersicon*, is an appropriate group for investigating the role post-zygotic extrinsic isolation plays in speciation. The group contains 13 closely related diploid species that share a high degree of genomic synteny. The distribution of *Lycopersicon* species spans a wide range of habitats and environmental gradients and much work has been done to identify and understand environmentally adaptive traits in *Lycopersicon*. In addition, much is known about the genetic basis of intrinsic postzygotic isolation between tomato species (10).

I will focus on two closely related tomato species: *Solanum lycopersicum* var. *cerasiforme* and *S. pimpinellifolium*. *S. pimpinellifolium*'s range is limited to the west coast of the Andes while *S. l. cerasiforme* is found on the eastern and western sides of the Andes, including the wet environments of the Amazon basin. However, the *S. l. cerasiforme* populations on the eastern side of the Andes, where *S. l. cerasiforme* is sympatric with *S. pimpinellifolium*, may be the result of introduction.

A study of nine *S. l. cerasiforme* accessions and ten *S. pimpinellifolium* accessions found significant between species variation in morphological traits. These differences were related to the habitats in which these accessions were collected. For example, *S. pimpinellifolium* had on average smaller leaves, with a lower water content, and greater leaf/mass area (all traits associated with drought tolerance) than *S. l. cerasiforme*. As would be expected from trait and environmental differences, *S. pimpinellifolium* took longer to wilt in drought conditions than *S. l. cerasiforme* (11).

There was also significant within species variation for traits in *S. l. cerasiforme* and *S. pimpinellifolium*, and this variation was sometimes associated with climatic

gradations within the species ranges. For example, days to wilting was correlated with mean annual precipitation in *S. pimpinellifolium* but not in *S. l. cerasiforme*. The lack of association between drought tolerance traits and climate in *S. l. cerasiforme* could be due to the fact that *S. l. cerasiforme* individuals often occur near agricultural fields or irrigation ditches, and so might avoid drought that nearby *S. pimpinellifolium* individuals in different microclimates would experience (11).

I plan to investigate fitness in hybrids between two *S. l. cerasiforme* accessions and one *S. pimpinellifolium* accession. I will use one *S. l. cerasiforme* accession from west of the Andes and one accession from east, where *S. l. cerasiforme* is in sympatry with *S. pimpinellifolium* and may have been introduced recently. Each pair will include the two parent accessions, F1 and F2 reciprocal hybrids, and reciprocal backcrosses between F1s and parents, resulting in 16 genotypic groups per pair, or 32 genotypic groups total.

While the most convincing evidence of extrinsic isolation would be fitness measurements from a field study in situ, as a first experimental investigation, laboratory manipulations can act as a simulation of field conditions. Since the largest differences between *S. l. cerasiforme* and *S. pimpinellifolium* traits occurs in traits associated with drought tolerance, in my manipulative experiment, I propose to grow hybrids and parents under three water regimes: highly restricted, moderate, and ad libitum (based on drought responses observed in 11). I will estimate fitness using a number of fitness correlates: survival, growth rate, total number of inflorescences and fruit produced in a predetermined time span, and the mean number of seeds per fruit (from a subsample of fruit).

Differential or reduced fitness of F2 hybrids and backcrosses compared to parents in drought or non-drought conditions would be consistent with extrinsic isolation mechanisms. Comparisons between the two accession pairs could reveal within-species variation in extrinsic reproductive barriers. In addition, variation in fitness depending on the direction of the cross would suggest that cytonuclear interactions play a role. These results could form the basis of a further in situ study under more natural field conditions in South America.

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