

Genetic and Ecological Divergence in the *Pinus flexilis*–*Pinus strobiformis*–*Pinus ayacahuite* Species Complex: Clues to Understanding Speciation in Pines

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North America is a secondary center of diversification of the genus *Pinus*. Most of these speciation events are fairly recent, producing a pattern of widespread shared polymorphism and fuzzy species boundaries. Among five-needle pines, the relationships among *Pinus flexilis*, *Pinus strobiformis*, and *Pinus ayacahuite* have been particularly difficult to determine. To understand the speciation process and the phylogenetic relationships in this species complex, we evaluated genetic and ecological differentiation using multilocus sequence data and ecological niche model comparisons. Our results show Late Pliocene–Early Pleistocene divergence and a contrasting pattern of differentiation between genes and ecological niche. Cytoplasmic and housekeeping nuclear genes show a clear differentiation of *P. ayacahuite*. However, ecological niche differences and candidate genes for drought tolerance show a strong differentiation in *P. flexilis*. Significant correlation was found between genetic distance and environmental distance in some of these candidate genes, as well as evidence of natural selection in *P. flexilis*.

This discrepancy among genes could be evidence of a genomic mosaic product of ecological speciation in *P. flexilis*. In adaptive speciation, only those genes

under natural selection would become differentiated, whereas in allopatric or parapatric speciation, differentiation would occur in the entire genome. Additionally, the ecological differentiation of *P. flexilis* could represent a barrier to gene flow with its sister species.

The differentiation of *P. flexilis* at the ecological and candidate gene level suggests that adaptive divergence has played a role in speciation. This means that despite their long generation times, pines can adapt to new environments relatively quickly, and that local adaptation could be an important factor in causing population structure and speciation in other five-needle pines. Considering the broad latitudinal range of this species complex, it is also possible that divergent selection could be acting on other genomic regions that were not sampled in this study, which in turn would explain the differences between the tropical *P. ayacahuite* and subtropical *P. strobiformis*. Therefore, more work is needed to characterize the genetic structure in these pines at the genomic level.

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