Low extinction rates made California a refuge for diverse plant species

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The remarkable diversity of California's plant life is largely the result of low extinction rates over the past 45 million years, according to a new study published in the journal *Evolution*. Although many new species have evolved in California, the rate at which plant lineages gave rise to new species has not been notably higher in California than elsewhere, researchers found.

Botanists have long recognized California as a biodiversity hotspot. With more than 5,500 native plant species, 40 percent of which are "endemic" (occurring nowhere else), California has more species and more endemic species than any other U.S. state, and is more species rich than most other places on Earth. The new findings highlight the importance of California as a refuge for plant species that might have gone extinct in other regions during the climatic shifts that occurred in the distant past.

"It seems that California has been an important refuge for plant lineages for a long time," said coauthor Kathleen Kay, assistant professor of ecology and evolutionary biology at the University of California, Santa Cruz. "These findings speak to the importance of protecting areas in California so that it can continue to be a refuge for biodiversity in the future."

First author Lesley Lancaster, now at Lund University in Sweden, became interested in collaborating with Kay after taking a course from her as a graduate student at UC Santa Cruz. She and Kay developed the project together after Lancaster received a postdoctoral fellowship to

study plant evolution at the National Center for Ecological Analysis and Synthesis at UC Santa Barbara.

"Because California has so many unique and relatively young plant species, it was long assumed by biogeographers and naturalists that high speciation rates were the cause of California's biodiversity," Lancaster said. "It turns out that these species have not arisen at a particularly high rate in California compared to elsewhere. Instead, features of California's climate, topography, and latitude have preserved these species, allowing us to see them today, when they may have simply gone extinct if they had arisen elsewhere."

Lancaster and Kay are the first to tackle the question using modern methods of phylogenetic analysis. They studied 16 different plant lineages that are well represented both within and outside of California, and each lineage includes California endemic species. Using DNA sequence data to reconstruct the evolutionary "family trees" of these lineages, plus fossil records to calibrate the dates when different branches of each tree diverged, they were able to estimate historical rates of speciation, extinction, and migration across the California border.

Some of the study's key findings differ from long-standing ideas about the origins of California's extraordinary species richness that were set forth in a landmark study published in 1978, "Origin and relationships of the California flora," by Peter Raven and Daniel Axelrod. That classic work, which was based on analyses of fossil data and current distributions of plants, emphasized high speciation rates as an important contributor to high plant biodiversity in California.

Raven and Axelrod also hypothesized that the onset of the wet-winter, dry-summer Mediterranean climate in California 3 to 5 million years ago was a key factor that promoted high rates of speciation and led to the

species richness that now characterizes California's flora. All the regions of the world with a Mediterranean climate (California, the cape of Africa, Southwestern Australia, the west coast of Chile, and around the Mediterranean sea) are currently plant biodiversity hotspots, and California does have a large number of relatively young species.

Lancaster and Kay's study, however, indicates that the onset of the Mediterranean climate did not affect speciation rates in California in most lineages. "Instead, low extinction rates over longer periods of time are responsible for species richness in California, and possibly in other Mediterranean regions as well," Lancaster said. "All of these regions share characteristics that predate the onset of the Mediterranean climate and that may have favored species persistence in each of these localities."

According to Kay, California's topographical diversity probably has played a critical role in preserving species richness. "People have talked about the topography fostering speciation, and it does play a role in that, but it plays a bigger role in preventing extinction by creating different niches and allowing lots of species to coexist," Kay said. "Topography also provides refuges, and the mountains are particularly important in preventing extinctions during times of climate change."

In a changing climate, species living on mountains can stay in the same temperature regime by shifting their elevation, moving relatively short distances compared to species on flat land that would have to shift their latitude by hundreds of miles to stay in the same temperature range. California's mountains are also important for their influence on precipitation, capturing the moisture in air masses coming off the Pacific Ocean, Kay said.

The new study did support several of Raven and Axelrod's conclusions. For example, they had predicted that cold-adapted lineages would have

lower rates of speciation in California than warm-adapted lineages, which Lancaster and Kay confirmed. They also proposed that the onset of the Mediterranean climate facilitated the immigration of desert-adapted plants. Lancaster and Kay found that desert-adapted plants colonized California more recently than other lineages, arriving on average around 5 to 6 million years ago, in comparison to an average of around 17 million years ago for non-desert lineages.

"We just don't have a lot of evidence that the Mediterranean climate spurred speciation," Kay said. "Our work shows that the causes of the diversity we see now are more ancient than the Mediterranean climate itself."

In addition to topography, important features of California and other Mediterranean climate regions are their latitude and their location on the west coast of a continent, Lancaster said. Latitude is important because it allowed these regions to avoid glaciation during periods when global temperatures were cold and northern latitudes were covered in ice. During periods of global warmth, being situated where easterly air currents bring moisture onto the land from the ocean has kept these regions from becoming deserts.

"These regions are likely diverse because they are some of the only non-tropical regions to have been able to avoid historical periods of either desertification or glaciation," Lancaster said.

Provided by University of California - Santa Cruz