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Flowering plants outcompeted conifers

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ABSTRACT

It is commonly accepted that the burst in diversity of flowering plants, between 125 and 80 million years ago, had a negative impact on the diversity of other plant groups such as conifers (plants with cones). The diversity of conifers is strongly linked to the increasing diversity of flowering plants since 66 million years ago, thus attesting to the role of competition between plants.

Picture of the Madeleine waterfall in New Caledonia, a protected site where seven endemic conifer species are in the middle of mostly flowering plants.

Image credits: Fabien Condamine

As evolutionary biologists, one of our major objectives is to understand how competition for resources regulates the appearance and extinction of species and can lead to the increase or decline of entire groups of species. This is particularly difficult to study because each group has different diversity trajectories over time, with a range of different species being created and becoming extinct.

There are two models that fossil evidence supports for how one group of organisms replaces another: the "double-wedge" model, in which one group of species declines while the other prospers, and the mass extinction model, involving an extinction event that wipes out one group while allowing another to diversify (e.g. dinosaurs and mammals). When two groups of organisms occupy similar habitats and the long-term diversity of one gradually increases while that of the

other decreases, we can naturally conclude that competition has taken place between the two. However, such a diversity pattern may also result from opposite responses to physical changes.

In our study, we investigated the decline of conifers, which are a group of cone-bearing plants that include cedars, junipers and pines. Conifers are a good example of competition between two groups during evolution. Since the "Cretaceous period" ended 66 million years ago, conifer-like species (also known as gymnosperms) declined to only 1100 species, whilst plants that produce flowers and bear their seeds in fruits rapidly diversified to around 300,000 species. Because of their current dominance, it is generally thought that flowering plants have replaced gymnosperms.

To evaluate the long-held hypothesis that the increased diversity of flowering plants has led to the decline of conifers, we analyzed historic plant DNA and fossil data to estimate processes of conifer diversification. Models estimating creation of new species and extinction were then used to corroborate the results between DNA and fossil data and to overcome the general difficulties in estimating diversification rates, particularly extinction rates.

Using these data covering the history of conifers (350 million years), we found that conifer species diversify at low rates throughout their history, but this low rate is punctuated by bursts of new species appearing during warming events. Our most important result is that the extinction of conifers drastically increased in the middle Cretaceous period (100-110 million years ago) and has remained high since then. In the last 66 million years, conifers are in decline as there were more extinctions than appearances of species.

We carried out further analyses to understand the causes of this long decline. We used data models to elucidate the impact that flowering plant diversity and climate change (variations in temperature and atmospheric carbon) had on the diversification of conifers. The Earth has generally cooled down over the last 65 million years so temperature is an important factor to consider.

These models estimate that the extinction rate of conifers is related to flowering plant diversity, so that conifer extinction increases as the flowering plants increase. These models better explain diversification than models with climate, although climatic cooling also favors extinction. Thus, the results support the hypothesis of an active replacement of conifers, implying that direct competition with flowering plants has increased conifer extinction during the expansion of flowering plants towards an ecological and evolutionary dominance in a period of global cooling.

During the last 66 million years, flowering plants have dominated terrestrial ecosystems, in terms of diversification dynamics, geographical occupation (except for boreal regions), and ecological or physiological innovations. Previous studies have suggested that flowering plants may have outcompeted conifers due to advantages such as rapid growth, varied reproductive systems such as insect pollination, new chemical defense systems and tolerance to climatic stress. These features probably gave flowering plants a competitive advantage over conifers from the Cretaceous period, which eventually led to conifer decline.

Our study of an ancient and relatively species-poor group of plants deepens our understanding of how diversity is regulated over time and in relation to multiple external factors. Using ecological models of evolution, genetic and fossil data, this study provides strong support for a widespread hypothesis of competition between groups of species over time. Our study illustrates how entire branches of the tree of life can actively compete for ecological dominance under changing climatic conditions. Such a methodological framework could shed light on long-term interactions between organisms for many other groups.