So far and no further

Plants are the subject of Prof. Yvonne Willi's research at the Department of Environmental Sciences – in particular populations at the border of a species' range. The evolutionary biologist aims to understand why plants are able to adapt to some extent and why they encounter limits.

Sequoia, gingko and coconut palm – these trees can be found together only in a botanical garden. Here, the most diverse specimens from all over the world meet in one place. This would not occur in natural habitats, because like all living organisms, plants have adapted to particular environments through natural selection. And this is why, one would search in vain for cacti in the Alps or edelweiss in a rainforest.

"Nature films in particular tell stories about how species are able to adapt perfectly to their environment," says Yvonne Willi, Professor of Plant Ecology and Evolution. "In reality, however, this is often not the case. We study where and why populations are unable to adapt optimally. The fact that species cannot adapt to all kinds of conditions is indeed very important for the maintenance of biodiversity."

The limits of adaptation are particularly visible at the edges of a species' range. This can be the geographic edge of a species' distribution or the edge of elevational distribution. Until today it remains unclear why certain species only occur in specific climatic zones and why they are unable to gradually adapt to changing climatic conditions and therefore spread further.

Alpine plants

"In the Alps, each species has its niche in regard to elevation and is generally not found below or above a certain altitude," explains Yvonne Willi. "We focus on the warm and cold margins of distribution in order to understand which climatic aspects are limiting." To study this, she compares dozens of *Brassicaceae* species from different locations in Switzerland, from the lowlands to alpine regions. Such macro-ecological and -evolutionary comparisons of species revealed some astonishing findings: Alpine plant species are not particularly resistant to cold temperatures, but they can capitalize on short periods of warmth.

"In experiments carried out in climate chambers, the greenhouse and in field experiments on the Calanda mountain near Chur, we could show that high-alpine *Brassicaceae* species grow and reproduce very fast under warm conditions," says Yvonne Willi. "They are the winners when it comes to growth and development. But this comes at the expense of size and lifespan. The plants are less robust, do not live very long and remain small, like we generally see with alpine plants." This cost-benefit relationship is crucial and defines the line for the limit of adaptation. How quickly a species can complete the

Yvonne Willi has been a Professor for Plant Ecology and Evolution at the Department of Environmental Sciences at the University of Basel since 2015. She was born in Canton St. Gallen and studied Biology and Biochemistry at the University of Zurich, after which she worked in cantonal nature conservation. She then did her PhD under the supervision of the plant ecologist Prof. Markus Fischer at the University of Zurich, where she investigated questions dealing with the evolution under small population size.

crucial life processes during one vegetative period affects the upper elevational limit. The lower limit is determined by how well a species can deal with stress and tolerate heat, drought or snow-free frost.

Hurdles to species spread

Yvonne Willi also studies the causes of geographic range limits, using the North American sand cress *Arabidopsis lyrata* as her model system. "For geographic range limits, the demographic history of a species plays an important role. Typical for plants in the northern hemisphere is their recent spreading towards northern areas at the end of the last ice age, with the glacial retreat. During this migration, the genetic composition of populations was perturbed by random change."

Populations at the periphery have gone through many demographic bottlenecks, or they remained small and isolated in the southern margins. As a consequence, they lost genetic variation. Furthermore, they accumulated a load of deleterious mutations. And finally, genetic drift worked against directed selection leading to poorly adapted populations at the edges. "In contrast, populations in the center of distribution are the most genetically diverse and fittest. Less fit populations can also persist, but their lower fitness becomes critical at the edge of the distribution."

In rare cases, populations at range edges may exceed this limit. Based on genomic sequence analysis and demographic modelling, Willi's team could identify a population breaking with the usual pattern and bringing forth a new species. "We were able to date this event quite precisely to about 12,000 years ago. This coincides with the time of retreating ice in that region," says Yvonne Willi. "This new species then has spread widely in North America because, among other reasons, it was able to pollinate itself. Although genetically depleted, its range is now larger than the one of the parental species – occasionally something magical happens."

In the face of climate change

When considering plant adaptation, the theme of climate change is inevitable. From a purely ecological point of view, warmer does not necessarily mean worse; some plants benefit from the changes. Globally, distributions and diversity of species are shifting. But from an evolutionary perspective many questions arise. Numerous species are likely to disappear. "This takes us back to our high-alpine *Brassicaeae*, which are set up to optimally use warm periods but remain small. They seem to have bet on the wrong horse and are no longer competitive."

The problem is that climate change is occurring very rapidly. Plants have adapted to their environments over a long period of time and suddenly there is a dramatic turnaround. They cannot keep up. Adaptations to climate are very complex, genetically difficult and slow. Especially adaptations to higher temperatures take a long time, many thousands of generations.

"Plants are important for our climate in every respect, including the climate of cities. Trees provide humid air and cooling. They can reduce temperatures up to two or three degrees, which is not trivial. And above all, plants will play a major role when we change our lifestyle to climate-friendly." ■