

Swiss Stone Pine – Portrait of a Mountain Forest Tree

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"Here and there such a warrior still stands faithfully at his post, with shattered shaft, and stretches his arm out defiantly from the rocky scree like a battle axe, or cowers like an old man bent down on his crutches by the storm of life."

(Schnidrig 1935)



Fig. 1. Steadfast Swiss stone pines in a dynamic habitat: patchy, mixed-age stand above the Aletsch Glacier (Canton Valais).

The Swiss stone pine (*Pinus cembra* L.) stands out among the pine tree species of the Alpine region (fig. 1). It “crowns” the timberline, its altitudinal range explaining why it is sometimes also known as the “Queen of the Alps”. The stone pine also stands out for various biological characteristics. As well as its capacity for physiological adaptation, its interaction with the spotted nutcracker (*Nucifraga caryocatactes*) as a seed disperser is of particular note. And then the Swiss stone pine also plays an important ecological and economic role as the main tree species of the stone pine-larch forest community, especially in the Alps. Rapid climate change does pose a major challenge, however. The long-lived Swiss stone pine can only move up the slopes slowly in response to the increasing competition as other tree species also migrate to higher altitudes.

Biology and ecology of Swiss stone pine

Many of the biological properties and characteristics of the Swiss stone pine (see profile) are related to its adaptation to its habitat. Swiss stone pines can reach a great age, and must therefore also survive long phases with inhospitable weather conditions. Over the years, mechanical damage (caused by wind, snow load, lightning) can result in bizarre growth forms, as described very figuratively by Schnidrig (1935; fig. 2). Multi-stemmed Swiss stone pines are also to be found. These arise when young trees fuse together as they grow, or when the crown shoots split.

The stone pine can be distinguished from the other pine species within its range through its clusters of five needles and closed cones (fig. 3a). The pollen of these monoecious trees is spread by the wind, so pollination can take place over long distances. Cross-fertilisation is favoured by this, although self-pollination is also possible (SALZER and Gugerli 2012). The female cones can contain more than 100 large, nutrient-rich and non-winged seeds which, as with all gymnosperms, have no real pericarp. Despite their hard shell, they are thus not “nuts” in the botanical sense. The maturing of the seeds over two years is probably one of the reasons why the development of the cones varies considerably over the years; seed years occur about every third year; a full mast occurs only every 4–10 years (ULBER *et al.* 2004).

The seeds are spread almost exclusively by the spotted nutcracker (Mattes 1982). The cones growing in the top third of the crown are carried away by the bird, which extracts the seeds. The bird buries the seeds as a food reserve. If they are not eaten during the winter, they can germinate the following spring. It is from these seed caches that the often closely packed groups of young Swiss stone pines develop (see fig. 6c).

Distribution area

The current distribution area of the Swiss stone pine covers the entire Alpine arc; the species is also scattered in the Carpathians, often in small stands (fig. 4, small map). Its altitudinal distribution stretches in the Alps from about 1500–



Fig. 2. Sometimes bizarre growth forms reflect the harsh conditions to which the Swiss stone pines are exposed in the high altitude forest – conditions which they defy over decades.

2400 m a.s.l., although young Swiss stone pines can occur in favourable locations up to 2850 m a.s.l. The natural forest limit would in fact be 200–300 m higher, but has been pushed down in many places as a result of clearing in favour of alpine farming. In the lower Carpathians, the timberline and thus the area colonised by stone pine is accordingly lower (1300–1700 m a.s.l.).

In Switzerland, the two main Swiss stone pine areas are in the Engadine valley and the canton of Valais. In the northern Alps, Swiss stone pine stands are to be found mainly in the St. Gallen Oberland, Glarus, the Bernese Oberland,



Fig. 3. a) Developed pine cones with female inflorescences and b) male inflorescences.

Fribourg, and the Vaud areas. On the southern side of the Alps, the stone pine reaches central Ticino.

Over the last few centuries, the Swiss stone pine has been intensively used over a wide area, even over-exploited in many places, and cleared to establish alpine pastures. This has severely reduced its presence or even caused it to disappear. A historically wider area of distribution is shown by field names referencing Swiss stone pines [“Arven” in German], such as “Arvenbüel” above the village of Amden (Rikli 1909). In the Swiss Alps, this loss of range is likely to have been significant in areas such as the Oberhalbstein and Surselva regions (Grisons) or the Lötschental valley (Valais), but also in the northern Alps (e.g. Fribourg).

Colonisation history

Like all species found in the Alpine region today, the Swiss stone pine has an eventful history. The area available for the stone pine has varied constantly with the repeated advances and retreats of the glaciers in central Europe.

Fossil plant remains (pollen, macro-remains) show that the Swiss stone pine probably survived the last ice age along

Profile of Swiss stone pine

Classification: Gymnosperms (Gymnospermae) – pine family (Pinaceae) – pines (*Pinus*) – *Pinus cembra* L.; nearest relative: *P. sibirica*

Range: Alps, Carpathians

Habitat: (Supra-)subalpine altitudinal zone, with larch (*Larix decidua*) and spruce (*Picea abies*); generally well supplied with water, acidic raw humus soils, predominantly north- and west-facing; avoids hollows

Growth shape: upright, up to 25 m; often with multiple trunks or candelabra-shaped as a result of damage

Age: mostly up to max. 400 years, “Methuselah” stone pines anecdotally over 1000 years old

Reproduction: monoecious/with separate female (cones; fig. 3a) and male inflorescences (Fig. 3b) on the same plant; reproductive from about 40 years (in cultivation also earlier), seed development over two years; mature seeds weigh 150–270 mg

Dispersal: Pollen by wind, seeds mainly by spotted nutcracker

Identifying features: 5 needles per cluster, needles triangular in cross-section; whitish wax stripes on 2 sides; young shoots reddish-yellow and tomentose; closed, purple-tinged, rarely green cones with non-winged, hard-shelled seeds

Occurrence in Switzerland: 5.7 million trees (>12 cm trunk diameter), 1.2 % of the number of trees nationwide; 2.9 million m³ (0.7 %) of volume of standing timber; increase of 9 % in both of these values since NFI3 (2004–2006) (National Forest Inventory NFI4, 2009–2017)

Names: English: Swiss stone pine, arolla pine; German: Arve, Arbe, Zirbe, Zirbelkiefer, Zir(b)m; French: arole, arolle, pin cembro, pin des Alpes; Italian: cirmolo, pino cembro; Romanish: gembru, gembra, (d)schember

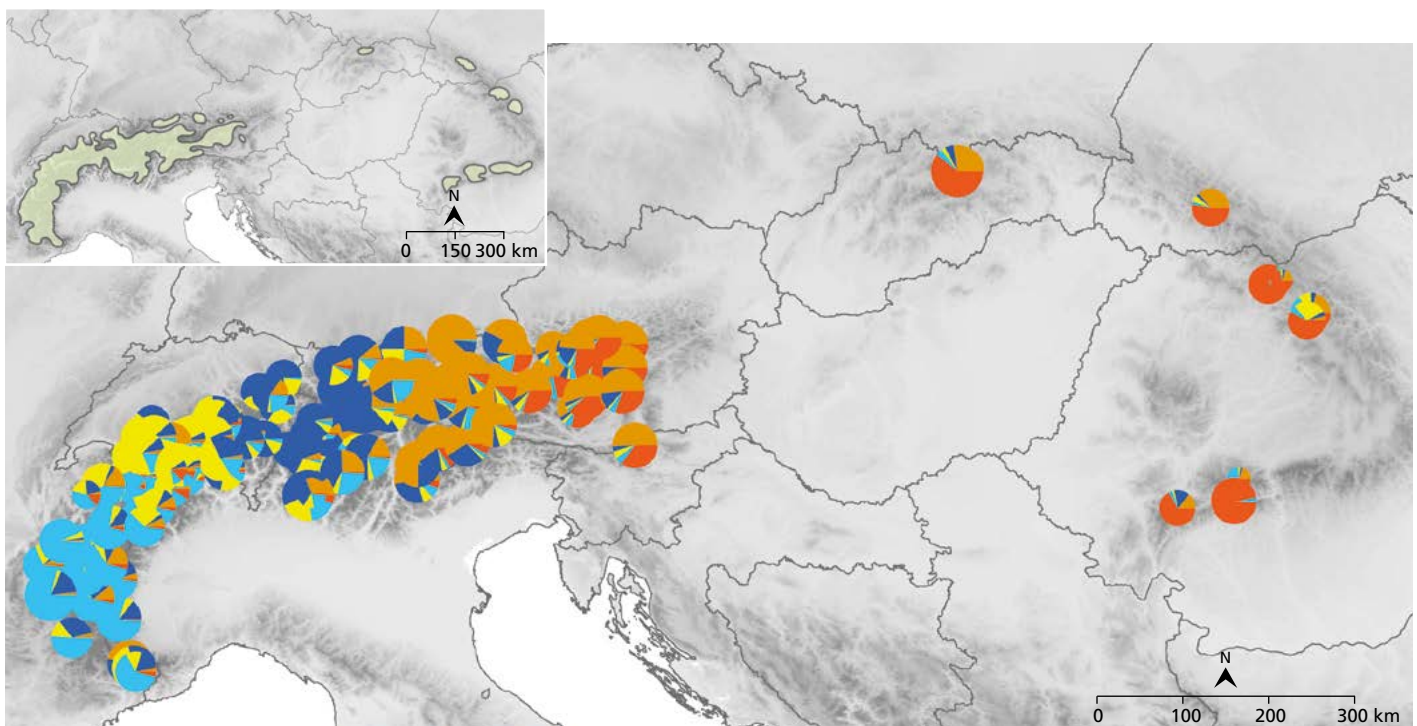


Fig. 4. Genetic structure of the Swiss stone pine in its natural range. The circles each mark a genetically investigated stand. The colours in the circle diagrams represent the proportions of each of the five genetic lineage groups. Small map: natural range of the Swiss stone pine in the Alps and Carpathians. Source: Gugerli *et al.* 2023, small map: Euforgen.

the central and eastern southern edge of the Alps, in the Hungarian lowlands, and around the Carpathians (Gugerli *et al.* 2023). Its return to the Alps was mainly westwards into the eastern Alps and northwards/westwards into the central and western Alps. The Carpathians were mostly recolonised from nearby populations.

This history of migration to and fro is also reflected in the spatial genetic structure, which reveals five genetic lineages along the east-west axis of the Carpathians and the Alps (fig. 4). The eastern group dominates primarily in the Carpathians and is likely to have originated mainly from refugial areas close to the Carpathians; it reveals a genetic link to the eastern Alps. The three genetic groups in the western Alps became differentiated as they returned after the maximum spread of the last ice age. Two genetic groups dominate in Switzerland, corresponding respectively to the two main areas in the east and west (Engadine and Valais). Knowledge of this spatial pattern makes it possible to detect the transfer of seed over long distances, for example, or to select suitable seed sources (provenance).

Site requirements

In the high-altitude forests of the Alps, larch and spruce also occur in varying proportions alongside the Swiss stone pine. The larch is considered a pioneer tree species, while the stone pine becomes dominant in the course of succession (climax tree species). Swiss stone pine and larch predominate especially in the central alpine, continental regions of the Alps, which are characterised by large temperature differences during the day and year and relatively low precipitation. In oceanic conditions, with higher precipitation, spruce trees are usually mixed in with the Swiss stone pine.

Swiss stone pines grow mainly on sites with medium soil moisture (Ott *et al.* 1997). This is probably why they are mainly found on sites facing north, north-west and north-east. The most favourable soils are consistently moist and contain some clay. Long-lying snow has a negative effect, because fungal infections are more pronounced (Senn and Schönenberger 2001). A good layer of raw humus is important, so that the



Fig. 5. Winter conditions present special challenges for the stone pine.

soil pH is acidic even if the underlying layer is calcareous. Stone pines are occasionally found on exposed rocks; thanks to their deep roots, they can nevertheless tap into water and nutrients.

But if the distribution of the Swiss stone pine seems rather limited in comparison with its potential, it is not just because of its specific site requirements. Competition from the shade-tolerant, faster-growing spruce, as well as over-exploitation in the past have also contributed to its loss of area in many places.

Physiological adaptation

As an alpine tree species that grows up to the tree line, the Swiss stone pine hardly ever occurs in a pure stand, but almost always together with larch and spruce. It therefore makes sense to compare the physiological characteristics of the Swiss stone pine with those of these two species, which at least partly occupy the same ecological niche.

The Swiss stone pine grows at the bioclimatic extremes at which trees are still found at all in Europe (Casalegno *et al.* 2010). The appearance and survival of the species is basically limited by low temperatures, the length of the growing season, summer temperatures, and summer precipitation (this applies to all tree species that occur at the tree line). These limitations include the fact

that growth below 5–7 °C is only possible to a very reduced extent (Körner 2012), and the time period for even this growth is determined by the length of the day (Etzold *et al.* 2021). The Swiss stone pine tolerates very cold winter temperatures, to below –40 °C, almost better than the spruce and the larch. In contrast to these two species, however, the Swiss stone pine does not compete well in dry environments and seems to be more dependent on a balanced water regime than other tree species (Casalegno *et al.* 2010).

Winter precipitation is particularly important for the occurrence of Swiss stone pine (Oberhuber 2004), because it influences the amount of snow and thus the duration of snow cover (fig. 5). This is an important factor in connection with damage caused by *Gremmeniella* shoot dieback (see below). On the other hand, the Swiss stone pine is less sensitive than larch and especially than spruce to frost-desiccation, i.e. when water evaporates from the needles and is not replenished from the ground due to frost (Christersson and Fircks 1990).

The Swiss stone pine is considered very sensitive to ozone (Buchholcerová *et al.* 2021; Dalstein *et al.* 2002). Along with its low drought tolerance, the Swiss stone pine's ability to compete with spruce and larch could decline regionally under the predicted climate changes.

No Swiss stone pines without spotted nutcrackers

It is impossible not to recognise or hear the 32–35 cm tall spotted nutcracker (*Nucifraga caryocatactes*), with its blackish brown, white-spotted plumage, its black tail with a white terminal band on the undertail, white undertail vents and characteristic, long and chisel-like beak, and its distinctive call (fig. 6a). This inhabitant of the coniferous forests of central and south-eastern Europe is represented by various subspecies in the boreal belt of Eurasia, as far as Japan (Glutz von Blotzheim and Bauer 1993). In Switzerland, its breeding range is in the Alps and the western Jura (Knaus *et al.* 2018). The native subspecies *N.c. caryocatactes* is a distinctly sedentary bird, and master of stockpiling.

The spotted nutcracker feeds mainly on the seeds of the stone pine. As the seed-bearing cones grow in the uppermost third of the crown, they are easily accessible for the bird. It collects the stone pine seeds from late summer onwards, and hides them in the ground as winter reserves. To do this, it extracts the stone pine seeds from the cones, directly in the crown, by wedging the cones in a so-called “anvil” (branch fork, tree stump; fig. 6b), or on the ground. Its strong beak for working the cones, throat pouch for transporting the seeds, and its skilled flying ability give the spotted nutcracker a great advantage over competitors such as squirrels, voles, great spotted woodpeckers

and Eurasian nuthatches when it comes to harvesting. Mattes (1982; 1978) showed in his studies in the Upper Engadine Stazerwald forest that outside the nesting season, the spotted nutcracker flies distances of up to 15 km in search of food. It carries an average of 41 stone pine seeds in its throat pouch, although it can carry more than 100.

The reserves it builds up are crucial for its overwintering and the nesting period. Depending on the supply of cones, each bird hides between 45 000 and 100 000 stone pine seeds per year, with an average of 5.7 seeds per cache (Mattes 1982). The bird has to find them under the snow in winter and dig them out, often with a great deal of effort. The recovery rate of around 80 % is thus all the more astonishing. The seeds that remain buried are enormously important for the spread of the Swiss stone pine.

For the Stazerwald forest, Mattes (1982) calculated that from the buried annual stockpile of a pair of spotted nutcrackers with two chicks, in a season with average cone production, around 8400–15 600 seeds per hectare of forest area are left behind for pine regeneration. These can germinate the following spring. Since several seeds are buried per cache, one often finds clusters of seedlings (fig. 6c), of which usually only one will develop into a tree. With its highly specialised feeding be-

haviour, the spotted nutcracker makes an important contribution to the continued survival of the Swiss stone pine forest. For this reason, the bird is also known as a “feathered forester” in German. However, new studies show that, contrary to popular belief, the caches are not usually created on sites that are favourable for germination. Spotted nutcrackers prefer to bury the seeds in places where they are unlikely to rot, and thus where the establishment conditions for stone pine seedlings are poorer (Neuschulz *et al.* 2015). Biotic factors (ground vegetation, seed foraging by rodents and other birds) play a more important role for the development of the seedlings than site conditions (Neuschulz *et al.* 2018). Moreover, it has been demonstrated in the Davos landscape that the majority of seed caches are in breeding territories below the current range of the Swiss stone pine, in subalpine spruce forest, where conditions are unfavourable for Swiss stone pine regeneration (Sorensen *et al.* 2022).

Ultimately, the decisive factor for the Swiss stone pine is how many seeds remain in sites that are favourable for the establishment of seedlings. Seed caches in clearings within existing forest areas and above the tree line, as they occasionally occur, may be of great importance for the Swiss stone pine in the current context of climate change.

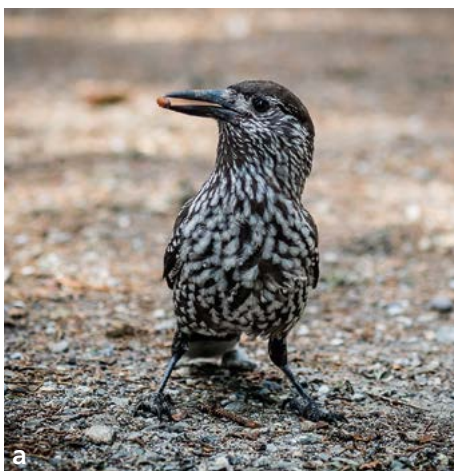


Fig. 6. a) Spotted nutcracker (*Nucifraga caryocatactes*) with a stone pine seed in its beak. b) Remains of nutcracker-processed stone pine cone in an “anvil”. c) Clusters of young stone pine growing from a spotted nutcracker’s seed cache.

Wood structure and annual rings

The wood of the Swiss stone pine is quite light in colour compared with other coniferous woods. The reason for this is the early wood formed from May onwards, which makes up the largest part of the annual rings in the Swiss stone pine (fig. 7). The individual cells of the early wood, which begin to form as soon as the soil reaches temperatures of around 1.5 °C (Gruber *et al.* 2009), are relatively large and thin-walled and thus appear lighter in colour. By contrast, the late wood cells formed from the end of July or beginning of August are smaller and have thicker cell walls, giving the late wood a darker appearance. In comparison with other coniferous species such as larch, however, the late wood cells are still thin-walled. Overall, this wood structure results in a low-density wood that is soft and easy to work with.

The onset of growth, 20–30 days before it starts in spruce and larch, is remarkably early (Rossi *et al.* 2014). At the upper limit of the forest, effective growth in terms of actual cell expansion starts in all three tree species almost simultaneously however, around mid-May. It ends in early autumn for the Swiss stone pine and the larch, earlier than for the spruce (Rossi *et al.* 2014).

The wood cells of the stone pine make up about 90% of the wood body; the rest is formed by medullary rays and resin canals (fig. 7). Resin canals are common in representatives of the genus *Pinus* and thus also in Swiss stone pines. The resin canals are formed by epithelial cells that secrete resin into the hollow intercellular space.

Today's Swiss stone pines are up to 400 years old (Nicolussi *et al.* 2009), but the oldest specimens can reach an age of 800–1000 years, indicating their potential for longevity (Carella 2022; Nicolussi *et al.* 2009; Carrer *et al.* 2007). However, in old trees the heartwood is usually rotten, which means that the innermost annual rings are not preserved and the maximum age is underestimated. The short growth period at the upper tree line limits the tree's productivity to such a degree that the annual rings are only about 1 mm wide on average (Carrer *et al.* 2007). The growth itself is favoured by warmer temperatures in July/August and in the

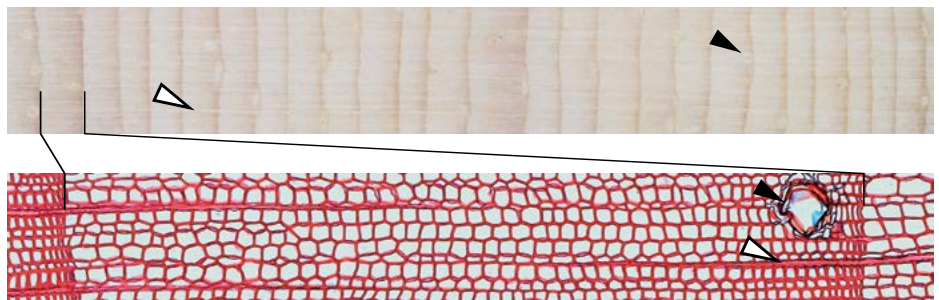


Fig. 7. Above: View of annual rings at a macroscopic and microscopic level, with growth direction from left to right. The polished, lightened surface of a trunk coring sample makes the late wood visible as a narrow darker stripe. Bottom: a coloured fine cross-section showing the typical cell structures of a single annual ring. Black lines: tree ring boundaries; black arrow: resin canal; white arrow: medullary ray. Source: Dendro Science WSL.

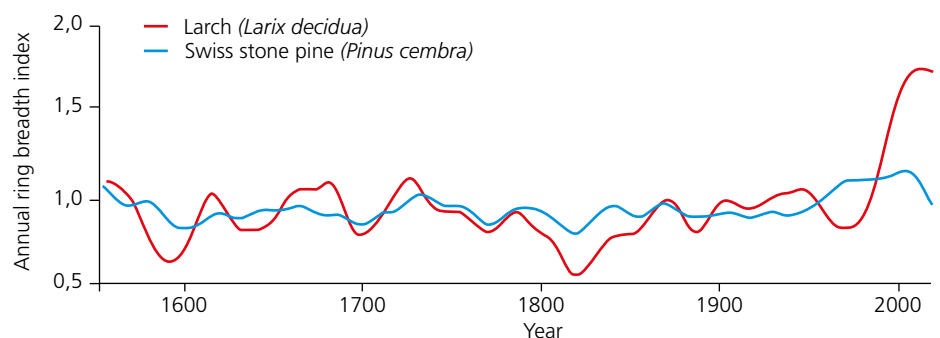


Fig. 8. Influence of climate change on tree growth, shown as tree ring width index averaged over 32 years. The warming of recent years has been accompanied by a decline in growth in the case of the Swiss stone pine, but not in the case of the larch. Source: Carella (2022).

preceding autumn, as well as by high winter precipitation (Carella 2022; Carrer *et al.* 2007; Oberhuber 2004). However, local site conditions such as nutrients, competing ground vegetation and microclimatic conditions also influence tree growth, especially at the tree line (Gruber *et al.* 2018, 2009). A case study in the Avers valley (Canton Grisons) shows that the Swiss stone pines at lower altitudes have been growing less well since the 1980s. This is in contrast to the larch, which apparently benefits from climate warming (fig. 8; Carella 2022). In addition to changing environmental conditions, this trend could also be due to current utilisation and the denser stand structure resulting from it (increased competition, especially for the Swiss stone pine). This result should thus be corroborated by further studies.

Utilisation

The earliest evidence of the utilisation of Swiss stone pine comes from a spring

catchment in St. Moritz dating from the Bronze Age (1400 BC). From the 16th century onwards, it is known to have been put to a variety of uses in addition to its use as fuelwood in the salt works, for example. This soft, easily workable wood was used to make utensils for mountain agriculture, such as bowls, vessels for milk, and spoons. Due to its antibacterial and insect-repelling properties, Swiss stone pine was popular for furniture used to store goods (cupboards, flour chests). To this day, the wood is used for furniture and in interior design, as in the panelled stone pine parlours often to be found in the Engadine valley. For a long time, Swiss stone pine was considered less valuable than larch and spruce, so prices for it were lower. Although the demand for Swiss stone pine increased with the construction boom of the 1970s, a downturn came in the 1990s: “cosy” stone pine parlours were no longer in demand, and the entire value chain suffered as a result of the dwindling demand (Bisaz 2004). This crisis was the starting point for an

initiative to investigate the health benefits of Swiss stone pine. The main finding from this study was that as a result of Swiss stone pine wood in the bedroom, the human heart saves 3500 beats a day, i.e. one hour of cardiac work, leaving people feeling more rested (Grote *et al.* 2003). Terpenes are responsible for this effect, and pinene in particular. Pillows were thus also filled with wood shavings to ensure restful sleep. This image and marketing campaign for a natural product has made the healthy and positive properties of the Swiss stone pine and its wood widely known. Although sales of Swiss stone pine have recovered in the last 20 years, the volume of wood sold represents only 0.7 % of the wood processed in Switzerland and is therefore only of regional importance.

In addition to wood, forest litter was also used as fodder and animal bedding in certain regions until the middle of the 20th century. This had serious repercussions for the regeneration of the Swiss stone pine: because the raw humus layer was removed, not only the seed bed was raked off, but often also the seedlings developing in it. Out of concern for forest regeneration, litter and cone use was restricted or banned in many areas from 1900 onwards. As well as being limited by the use of litter, natural regeneration was further hampered by the hunting of

spotted nutcrackers, which was financially rewarded in some regions until the 20th century because the bird was wrongly considered to be a pest that would eat too many stone pine seeds (Hess 1916).

Nowadays, more non-forestry products are being produced (fig. 9). This commercial use of the Swiss stone pine is regulated by cantonal law in Switzerland and usually requires a permit. The tasty and nutritious stone pine seeds (often called pine nuts) are becoming increasingly important, although these usually come from the Siberian stone pine (*P. sibirica*). Another non-forest product is essential oil distilled from needles and branches. Such aromatic oils with the typical scent of stone pine are used unprocessed or as an additive in soaps, creams, disinfectant sprays, room fragrances, but also for flavouring cheese. The needles are added to sausages, herbal teas, spices and even ice cream. The dark red stone pine or Swiss stone pine liqueur is made from unripe cones. Colourless stone pine brandies can be made with cones, seeds or needles.

In addition to the value chain of its products, for which no figures are available, the stone pine also has an intrinsic and above all an aesthetic value. Both these symbolic, centuries-old trees, marked by wind and weather, and the

richly structured stone pine or mixed stone pine forests they form are much admired and appreciated. The quality of the stone pine landscape is an important argument used to underline the attractiveness of tourist destinations and thus for local value creation.

Seed harvesting, breeding and reforestation

Stone pine cones are harvested from the standing tree from mid-August for the purpose of breeding in the nursery. Before the seeds can germinate, they need post-harvest maturation (stratification). The harvested cones are stored in moist sand at varying temperatures between 5 and 25°C for eight to ten weeks, until they disintegrate. The seeds are then extracted from the cones by rubbing, and cleaned. They are then stratified again (warm-cold-warm) for another twelve weeks in peat/sand substrate until they can be stored at 3 to -5°C for three to seven years.

The substrate of the seedbed in the open ground should have a pH value of 4.5–6.0. If germination is successful, the seedlings remain in the seedbed for two to three growing seasons. When the young plants have reached a size of 8–10 cm, they can be transplanted into a pot. This may only be done outside the vegetation period. The pot size should be increased gradually. It is important that the stone pines are not cultivated in a substrate that is too wet, because they prefer well-drained soils.

The WSL Research Institute has been examining ways of promoting the Swiss stone pine in mountain forests for over 50 years. Numerous reforestation projects have been realised for this purpose and scientifically monitored for decades. Whenever possible, the stone pine should however be regenerated naturally, even if this takes decades. Microsites play a decisive role here in the success of regeneration.

Reforestation projects with Swiss stone pine are usually associated with high costs, as it takes up to five years just to grow the seedlings. Transport in the mountain forest and distribution of the seedlings to the planting holes is also expensive and costly in terms of time and effort. The trials with Swiss stone pines have shown that potted plants



Fig. 9. A diverse range of products made from Swiss stone pine contributes to regional value creation.



Fig. 10. a) Grubbing mattock in use for hole planting. b) Microterraces to protect young plants from sliding snow.

have clear advantages over bare-rooted plants. The better growing success of potted plants compensates for the higher costs in comparison with bare-rooted plants. The nutrients provided in the substrate with plants in containers (quickpots) ensure a continuous supply, including with water. This way the roots are protected in the container and reach the planting hole fresh, which significantly reduces the shock of planting.

In the often steep terrain with stony soils, the excavation of the planting holes is laborious. The classic hole plant-

ing method with the grubbing mattock has proved successful (fig. 10a). On south-facing slopes with winter snow movement (snow gliding), microterraces (small berms; fig. 10b) help to reduce mechanical damage to the young plants. The stones dug out of the planting holes can be laid on the small terraces and shield the soil. On southern slopes, they reduce dehydration; on northern slopes, the stones help store warmth.

Planting should only take place on selected microsites with small groups of trees (three to five stone pines). Favour-

able microsites are raised terrain and areas around old tree stumps or wood that has been left lying across the slope. Wet, cool, grassy depressions in the terrain (hollows) where the snow disappears relatively late are unsuitable as sites. Competition from tall herbs and dense reed grasses are also problematic, as they increase the risk of frequent fungal diseases. During the first 20 years, Swiss stone pines are susceptible to fungal diseases (especially *Gremmeniella* shoot dieback), which spreads under long-lasting snow cover (Merges *et al.*

Reforestation and verification of provenance

In the past, Swiss forests were heavily overused. Damage caused by events such as landslides, mudflows and avalanches increased. In the second half of the 19th century, people came to the conclusion that it was going to be necessary to reforest sometimes extensive areas as a countermeasure. This was not always successful, as the example of the canton of Fribourg shows (Fragnière *et al.* 2022). According to forest archives, at least 450,000 Swiss stone pines were planted there between 1885 and 1952. Despite extensive follow-up searches, only about 650 Swiss stone pines could still be found there in 2020 (0.15 %). This enormous failure is probably related to the fact that the stone pines were

planted on unsuitable sites. It was likely mostly bare-rooted young plants that were used for planting (fig. 11), and these probably dried out during transport or had difficulty becoming established once planted.

Genetic studies of the Swiss stone pine stands in the canton of Fribourg revealed a clear distinction between local, naturally regenerated and planted stands (Sonnenwyl 2021). The trees still present in the planted stands came from eastern Switzerland, and partly from even further east (probably South Tyrol). This identification of foreign provenances is possible thanks to our knowledge of the genetic structure of the Swiss stone pine in the Alps (cf. fig. 4).



Fig. 11. Farmer bearing a load of bare-rooted young spruce plants for the reforestation of the Schwyberg area, 1943. Swiss stone pines are also likely to have been transported and planted in this way. Source: BCU Fribourg.

2020). This has become very clear in the high-altitude reforestation project on the Stillberg mountain (Davos, Canton Grisons), where practically all the Swiss stone pines in depressions and between avalanche barriers with long snow cover died due to *Gremmeniella* shoot dieback (Barbeito *et al.* 2013). Planted stone pines are susceptible to game damage. Wild ungulates cause damage to the trees by rubbing and striking the trees with their antlers as well as browsing (fig. 12). Especially in areas where there are no old trees, the game pressure on this tree species is huge. Reforestation without game protection measures therefore has little chance of success.

Genetic diversity

Genetic diversity is an important component of biodiversity and describes the diversity within species. It can be determined using molecular genetic methods. Its description facilitates a better understanding of ecological and evolutionary processes in connection with geographical location and environmental conditions. Genetic analyses of conifers such as the Swiss stone pine are often a considerable challenge financially, however, because the genome of



Fig. 12. Antler-rubbing and stripping damage caused by cloven-hoofed animals usually leads to the death of the young trees.

Habitat suitability

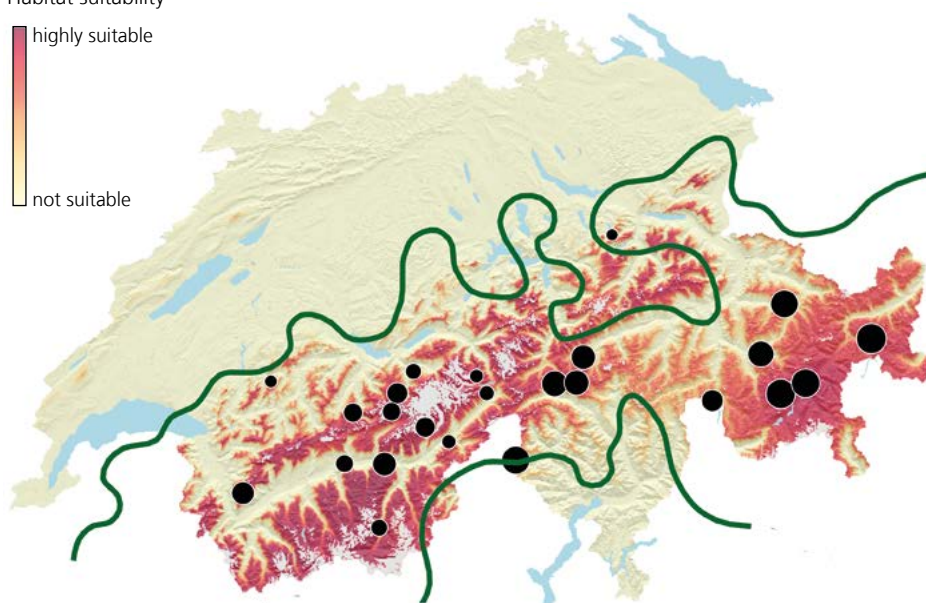
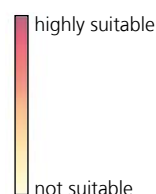


Fig. 13. Neutral genetic diversity of 24 Swiss stone pine stands as a function of geographical location and habitat suitability. The red part of the map shows the degree of habitat suitability. The green line marks the northern and southern limits of the range. The larger the circle, the higher the genetic diversity. The neutral genetic diversity correlates with marginal location, but not with habitat suitability of the stands. Modified from Dauphin *et al.* (2020).

the Swiss stone pine is almost ten times larger than that of humans. Genetic diversity is divided into two categories:

Neutral genetic diversity: This is the diversity of genes that have no influence on fitness. This diversity is influenced by gene flow, changes in population size and random genetic changes (= genetic drift). These so-called neutral processes affect the entire genome. Patterns of neutral genetic diversity also provide information on kinships (e.g. for proof of provenance).

Adaptation-relevant genetic diversity: This is the diversity of genes that have an influence on fitness. It therefore plays a role in adaptation to the environment and is characterised by natural selection, which acts on individual gene regions and leads to adapted populations over many generations.

In 24 Swiss stone pine stands studied, the neutral genetic diversity was generally higher in large stands in the centre of the range than in small stands near the northern and southern range limits (fig. 13; Dauphin *et al.* 2020). The genetic diversity relevant for adaptation,

on the other hand, varied independently of the geographical location. It correlated partially with habitat suitability, however: stands in suitable habitats had a smaller adaptive genetic diversity than stands on the edge of the ecological niche. This is not a contradiction, because natural selection in suitable, stable habitats leads to a reduction in the genetic diversity relevant for adaptation, while populations on the edge of the niche are not yet optimally adapted and therefore still contain non-adapted genetic variants. These findings can help to protect, promote and manage genetically diverse stands, in that suitable seed sources can be selected, for example.

Swiss stone pine forest habitat

The stone pines and the stone pine-larch forest are a species-rich habitat in the transitional area between the forested and treeless alpine zones. Swiss stone pine stands often show gaps in their canopy due to the meagre conditions for germination and growth. Where alpine cattle do not graze intensively, moss-rich dwarf shrub heathers with alpenrose (*Rhododendron ferrugineum*), blueberry (*Vaccinium myrtillus*),

lingonberry (*Vaccinium vitis-idaea*) and bearberry (*Arctostaphylos uva-ursi*) cover the ground. Under the crowns there is often only a thick layer of raw humus. These forests also provide a habitat for numerous insects, and are colonised by other seed-eating vertebrates in addition to the spotted nutcracker. The scattered stands favour the occurrence of ground-feeding bird species such as common chaffinch, mistle thrush, song thrush, ring ouzel, tree pipit, citril finch, western Bonelli's warbler, common redstart, Eurasian green woodpecker and black grouse. Red deer, chamois and mountain hare also benefit from the loose stand structure. Rare species such as the twinflower (*Linnaea borealis*) or the alpine clematis (*Clematis alpina*) find their ecological optimum in the stone pine forest (Delarze *et al.* 2015).

Although Swiss stone pines are not among the top tree species in terms of lichen diversity, more than 100 lichen species have been observed on this tree species in Switzerland (Stofer *et al.* 2019). The eye-catching beard, fruticose and foliose lichen species are in the minority, with a share of about 40 % compared to crustose lichens. Six species are endangered species on the Red List (Scheidegger *et al.* 2002). The wolf lichen (*Letharia vulpina*; fig. 14b) is frequently found. Its bright yellow colour makes it very conspicuous. The toxic vulpinic acid that gives it its colour also prevents it from being eaten; in former times it was even used to poison wolves.

The stone pine is not only a substrate for lichens. It lives in obligate symbiosis with mycorrhizal fungi such as boletes (fig. 14a), russula and cortinari. Fungal threads completely surround the fine roots of the stone pines (fig. 14d). This enables the exchange of nutrients and sugars between the fungus and the host tree and is particularly important at the marginal sites of the occurrence of Swiss stone pine, where nitrogen-poor raw humus soils and rocky sites predominate. The diversity of the mycorrhizal fungal partners increases with the age of the Swiss stone pines, and their species composition varies according to site and exposure (Mandolini *et al.* 2022). Frequently found is the stone pine bolete (*Suillus plorans*; fig. 14c). This fungus occurs exclusively with the stone pine.



Fig. 14. Typical fungi (a, c, d; slimy boletes *Suillus* spp.) and lichens (b; wolf lichen, *Letharia vulpina*), which grow with and on stone pine. a) Mycorrhizae and fruiting body of the bolete mushroom *S. flavidus* on a stone pine seedling in a nursery. The stone pine bolete (c; *S. plorans*) forms typical nodule mycorrhizae (d) and produces an extensive network of thick mycelial strands that ensure the transport of water and nutrients over long distances.

The Swiss stone pine is not considered to be a hotspot for fungal diseases (Dubach *et al.* 2022). It is mainly infected at the regeneration stage. Two species play a particular role in this (Nierhaus-Wunderwald 1996): the snow blight (*Gremmenia infestans*, syn. *Phacidium infestans*) and Scleroderris dieback (*Gremmeniella abietina*; fig. 15). These fungi grow unnoticed during the dormant phase, and are thus barely disturbed by any defensive reactions of the affected trees. In the case of the Swiss stone pine snow blight, the dead needles initially turn olive-grey. Once the snow has melted, they dry out quickly, turn brown, bleach during the summer, and become brittle. Dead needles remain in white clusters on the shoots for a long time. In Scleroderris dieback, a brownish red discolouration appears first at the base of the needle. Later, bare, dead one-year-old shoots become noticeable.

Another fungus that causes damage to the stone pine is *Cenangium ferruginosum*, the pathogen causing shoot dieback of pine. It usually grows as a saprophyte on the bark of various pine species (*Pinus* sp.). If trees are weakened by drought, frost or insect damage, the fungus can also occur parasitically. Numerous stone pines and Scots pines with symptoms of damage were observed in 1992 and 2010 in the cantons of Grisons and Valais as a result of drought stress. Such events are likely to occur more frequently under expected future climate conditions.

Two invasive pine needle diseases pose a further threat to the Swiss stone pine: red band needle blight and brown spot needle blight (Dubach *et al.* 2022). Neither of these pathogenic fungi has been observed in the natural range of the Swiss stone pine in Switzerland to date.



Fig. 15. Examples of damage to the Swiss stone pine caused by fungal infection: a) *Scleroderris* die-back and b) snow blight.

Physiological needle cast is often considered a symptom of fungal disease. However, it is in fact a natural ageing process of the needles, which mostly occurs in older generations of needles and is promoted by stress situations, such as drought.

Of all coniferous species, it is the genus *Pinus* that is colonised by the highest number of herbivorous insects, and also the highest proportion of specialist spe-

cies (fig. 16). Among pines, however, the number of insects found on the stone pine is significantly lower than on the Scots pine, black pine and Swiss mountain pine (*P. sylvestris*, *P. nigra* and *P. mugo*). Two species are considered to be Swiss stone pine specialists: the aphid *Cinara cembrae* and the sawfly *Xyela alpigena* (fig. 16).

A whole range of insects has already caused damage to Swiss stone pine in

Switzerland, including various aphids, sawflies, weevils, long-horned beetles, bark beetles, as well as ermine moths, leafroller moths and grass moths (fig. 17). With all groups, there was also infestation over large areas. The stone pine leaf miner ermine moth (*Ocnerosoma piniariella*), the small eight-toothed spruce bark beetle (*Ips amitinus*), the small stone pine bark beetle (*Pityogenes conjunctus*) and the stone pine aphid (*Pineus cembrae*) are the species causing the most frequent reports of damage to stone pines in Switzerland (fig. 17).

Swiss stone pine in climate change

Climate change is causing most forest habitats to become warmer and drier in summer. Tree populations can respond in four different ways to avoid a loss of vitality or even local extinction (fig. 18): Some individual trees are able to tolerate environmental changes without genetic changes (phenotypic plasticity); stands can move up the slope to cooler locations through seed dispersal (migration); they can acquire genetic variants suitable for warmer conditions through genetic exchange (gene flow); or they

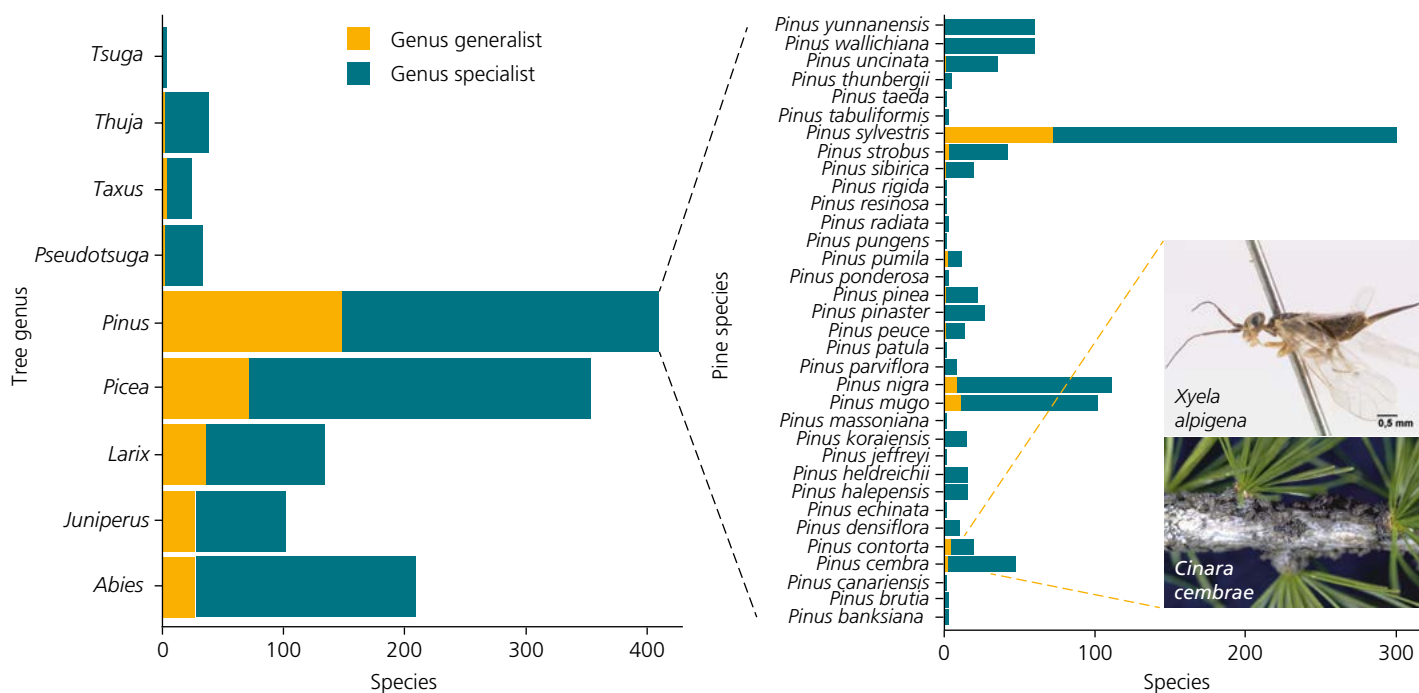


Fig. 16. Number of species of herbivorous arthropods (insects and arachnids) recorded on different conifers and pine species (reference area Germany, according to Brändle and Gossner unpubl.). A distinction is made between host specialists and host generalists of a tree genus (left) or pine species (right). The pictures on the right show the two stone pine specialists *Xyela alpigena* and *Cinara cembrae*.

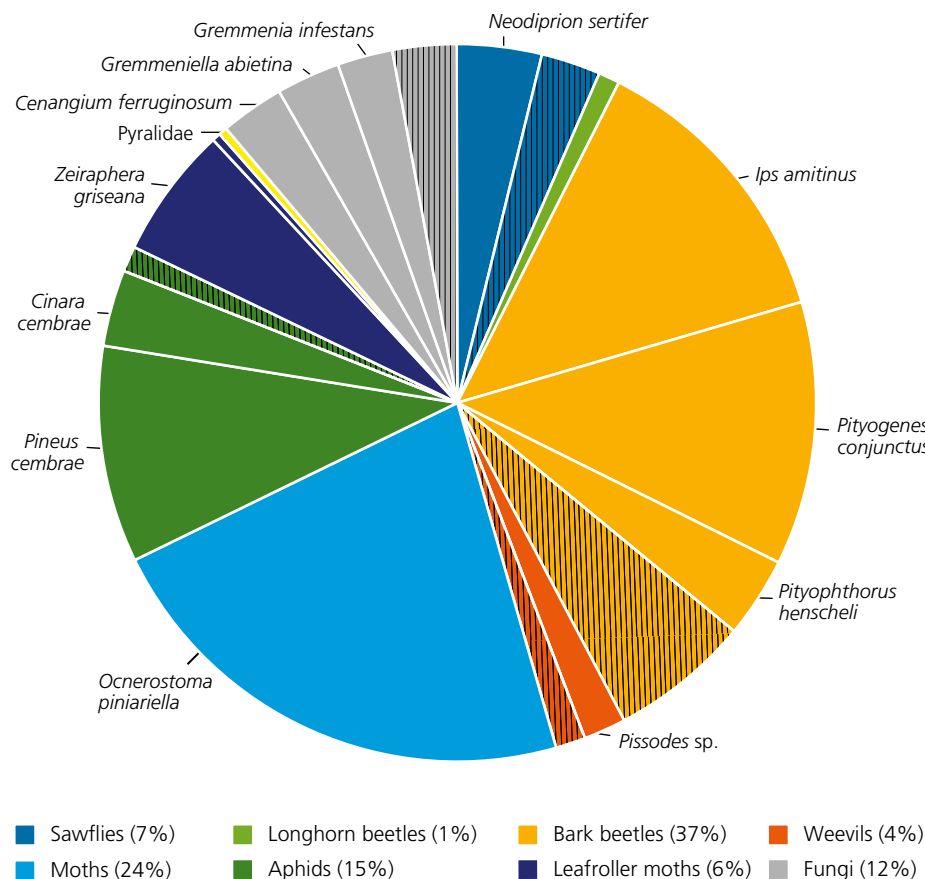


Fig. 17. Percentage of reports of insect or fungal damage to Swiss stone pine (1984–2021). Mentioned species (groups) were reported at least ten times. Hatched colours indicate the remaining species of an insect group or fungi. Source: Swiss Federal Institute WSL.

can adapt genetically to the new conditions over many generations through the natural selection of fit individuals (adaptation).

Dauphin *et al.* (2021) reconstructed the historical climatic conditions and genetic composition of seven Swiss stone pine stands. In the course of the last 150–250 years, it has become slightly drier and significantly warmer in all stands. During the same period, important genetic changes could be detected. However, these were considerably smaller than would be necessary for the stone pine to adapt to the rapid predicted climate changes. In order to avoid the increasing competitive pressure from other tree species in many places and thus to preserve respective forest areas, the Swiss stone pine would have to spread to higher altitudes where the future site conditions would meet its requirements. This is difficult, however, because the spotted nutcracker prefers to bury the stone pine seeds in the already existing forest (Neuschulz *et al.* 2018) and the living conditions governed by topography and soil deteriorate with increasing altitude (due to lack of raw humus). As stone pines are long-lived, have a very long generation time, and genetic adaptation requires

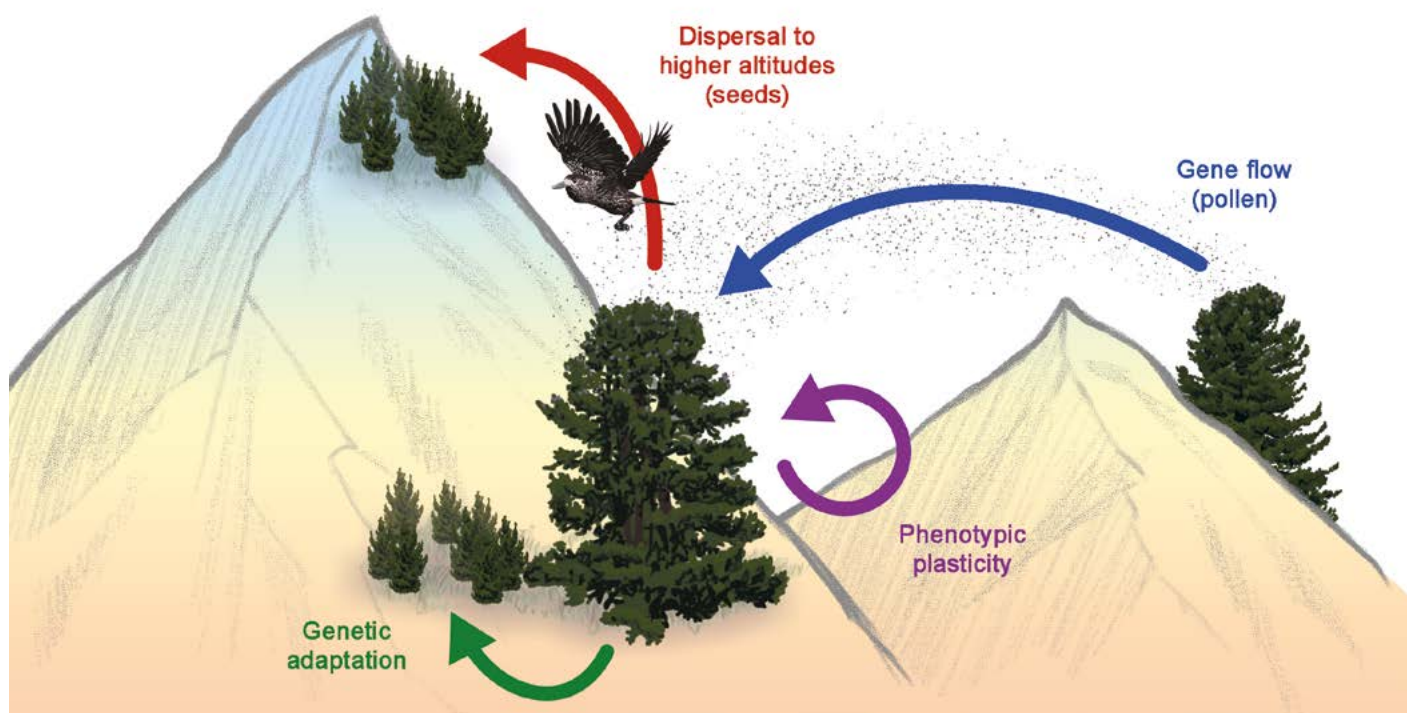


Fig. 18. The four ways in which the stone pine can respond to climate change. Phenotypic plasticity (purple), dispersal to higher altitudes (red), gene flow through pollen from lower-lying stands (blue) and genetic adaptation (green).

many generations, this process can hardly keep up with rapid climate change. There is therefore a risk that certain stone pine stands will become smaller or even disappear in some places.

Future prospects

The coming decades are expected to bring a wide range of environmental changes: warmer temperatures, rather less precipitation and longer dry periods. It can thus be assumed that the vegetation levels and thus also the habitat of the stone pines will shift upwards. It will not be easy for the Swiss stone pine: it does not compete well with other tree species advancing from below, and it grows slowly. In addition, the pine tree is almost only able to reach higher altitudes through the spotted nutcracker, and this species predominantly creates its seed caches in the already forested area. Likewise, the raw humus layer, which provides favourable germination and establishment conditions for the Swiss stone pine, is generally lacking above the timberline. At least the mycorrhizal fungi that are important for growth of the trees seem to be present (Merges *et al.* 2018), which should facilitate the establishment of the seedlings. On the other hand, the warmer temperatures in spring are likely to make things more difficult, as damage caused by fungi will increase and more stone pines will die as a result. This depends primarily on how much snow there is and how long it takes for the snow to disappear. Newly introduced pests can also cause widespread damage, as observed with the closely related *Pinus albicaulis* in North America (Shanahan *et al.* 2016).

Not only the climate will continue to change, but also the utilisation of the stone pine habitats: where meadows and pastures are abandoned, forest can develop, something that benefits the Swiss stone pine. It should be noted that



Fig. 19. Swiss stone pines will continue to grace the alpine landscape in the future, even if their distribution is limited in warmer, drier climates.

the reclamation of forest area above today's timberline is in fact reforestation, as the establishment of alpine pastures had often pushed the natural timberline down by 200–300 m. Elsewhere, intensified human activities (e.g. tourism, mountain farming) and high game pressure can have negative effects on natural regeneration.

Finally, longevity could also become a genetic stumbling block, because today's old trees became well established in their youth about 150 years ago in wetter and much cooler conditions — because they were well adapted at that time. These trees continue to pass on their genes to new generations, but these need to prove themselves in a drier and warmer environment (Dauphin *et al.* 2021).

This assessment does not however mean that the Swiss stone pine is on the verge of extinction, and that the Swiss stone pine forest will disappear, as Schnidrig (1935) warned (see quotation

below). Swiss stone pines will remain with us for a long time to come, as they have done for millions of years (fig. 19). It is possible, for example, that at lower altitudes of the Swiss stone pine occurrence, competition could decrease, especially from spruce, if the latter were to come under increased pressure from drought and bark beetles. The area colonised by Swiss stone pine could however become smaller. Especially in marginal areas, where the climate is already subject to very oceanic conditions, the Swiss stone pine is likely to struggle over the next one to two hundred years or even disappear in some places. On the other hand, there is growing interest in Swiss stone pine products and thus also in the silvicultural promotion of this species. In view of global warming, this promotion should focus on the high altitudes, where conditions suitable for Swiss stone pines will continue to prevail in the future.

“Unstilled would otherwise remain the hiker’s silent longing for the rustling of the treetops in the incense-scented stone pine forest; and too late then the nature-lover’s rueful assertion: “What a pity about our magnificent Swiss stone pine forest, the adornment of our mountains”.

(Schnidrig 1935)

Recommendations for forestry practice

In order to preserve stone pine forests as diverse habitats at the transition to the alpine zone under future climate conditions, an integrative approach is needed to protect biodiversity and the various functions and services provided by the forest, which include protection, utilisation and recreation.

When **planting Swiss stone pines**, attention should be paid to ensuring that:

- suitable small sites are selected; and that gullies and snowy depressions are avoided
- the trees are planted in small, well-spaced groups
- the trees are mixed with other high altitude tree species (e.g. Swiss mountain pine, larch).
- regional planting material in pots is used, taking into account a possible shift in altitude under future climate conditions
- where possible, the plants are bred at high altitudes (pre-adaptation)
- planting also above the current forest line is considered

Local conditions and silvicultural **history** are important when assessing where and how to promote the Swiss stone pine. In some areas, the stone pine is very vital and vigorous. There, it can also be contained, to promote biodiversity or to keep the landscape open – for grazing or for tourism purposes, for example. Elsewhere, the Swiss stone pine can be threatened by competition, and needs to be promoted through silvicultural measures.

The two **fungal pathogens** snow blight (*Gremmenia infestans*, fig. 20b) and Scleroderris dieback (*Gremmeniella abi-*

etina) play a decisive role in the regeneration dynamics of Swiss stone pine and influence its spatial distribution. Thick and persistent snow cover promotes fungal infections, and snow fungi also spread via directly neighbouring trees.

The Swiss stone pine prefers open forest structures (fig. 20a). Although it is well adapted to mountain sites, a high stem density is a problem for the stone pine, especially in the shade of faster-growing tree species such as spruce. In order to preserve the Swiss stone pine even in the face of increasing competition, it should be promoted as early as possible through **targeted tending of the young plants** or later by removing competing species. In this way, the Swiss stone pine can also take on functions as a valuable mixed tree species even outside its predicted future distribution area, in the event that the spruce comes under increasing pressure there as a result of beetle damage.

Since land use and the level of **game populations** have a great influence on where the range of the Swiss stone pine can expand at higher altitudes, different stakeholders can potentially work together to define the forest functions of future Swiss stone pine forests.

The traditional use of biomass from the Swiss stone pine and locally processed niche products are of great value. Adapted use increases appreciation of the Swiss stone pine and thus contributes to its conservation and to the ecosystem services of mountain forests. Swiss stone pine forests have a high value as a landscape. For this reason, tourism, forestry enterprises and forest owners should agree on **sustainable utilisation** and thus secure the continued existence of these sensitive habitats.



Fig. 20. a) Scattered Swiss stone pine stand in the Rautialp karst area (Canton Glarus). b) Swiss stone pine infected with the snow blight (*Gremmenia infestans*) near the timberline. The larger tree on the left will cope with the infection. The smaller tree on the right is so badly infected that it will probably die in the next few years.

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Further information

www.wsl.ch/swiss-stone-pine

Illustrations

F. Gugerli (figs. 1, 2, 3a, 6c, 15b), S. Brodbeck (figs. 3b, 5, 6b, 9, 12, 19), E.-L. Neuschulz (fig. 6a), U. Wasem (figs. 10, 16 bottom), BCU Fribourg, Fonds Mülhauser JOMU_40103 (fig. 11), S. Egli (fig. 14a), C. Scheidegger (fig. 14b), G. Martinelli (fig. 14c), A. Liston (fig. 16 top), I. Kälin (fig. 14d), V. Queloz (fig. 15a), S. Wölfle (fig. 18), Chr. Rellstab (fig. 20a), F. Krumm (fig. 20b)

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