# CONIFEROUS TREES

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## Contents





## Summary

The diversity of conifers expressed in numbers of species is small in comparison with that of flowering plants. However, the 630 extant species are very diverse, ranging from creeping dwarf shrubs to the tallest trees in the world. They occur on all continents

inhabitable to vascular plants, and are found in almost all major land ecosystems, from tropical forest to arctic tundra. They evolved as a distinct group about 300 million years ago, and were once the dominant type of woody plants on earth. Their importance, both ecological and economic, is still far greater than their limited species diversity would suggest. Exploitation, forest degradation and habitat destruction have brought about 25% of this biodiversity under the threat of extinction. This article summarizes current knowledge, and discusses the various issues in more detail by means of brief accounts of 20 example species of important coniferous trees.

## 1. Introduction

In comparison with the flowering plants, which when all taxonomy is finally done may add up to 300 000 species, conifers are a small group of woody seed plants, with a mere 630 species. In this group, as in all botany, new species are still being described, but it is the author's opinion that, with the exception of occasional new discoveries such as the rather spectacular Wollemi pine (*Wollemia nobilis*) in Australia in 1994, this is more a matter of taxonomic concepts than of discovering new species. Here at least, a complete inventory stage is being approached, save for a few areas such as New Guinea, Myanmar, and the Venezuelan-Brazilian border, where novelties may still be found, although the discovery of Wollemi pine indicates that surprises elsewhere should not be ruled out. What is now needed in this group more than the distinction of yet another (dubious) species of pine, is a critical revision evaluating the inventory so far, and pulling together all the evidence, including that found by new techniques such as DNA analysis. Despite its small size, however, conifers are remarkably widespread and diverse. They are also a well-studied group of seed plants, although knowledge is much biased towards a relatively few species important in forestry and horticulture. In this general overview given in Section 2, the account is not restricted to trees (if only because the definition of a tree seems difficult to agree upon), but includes the many shrubby forms as well. In Section 3, where examples of important conifers are discussed, the emphasis is on undisputed trees.

## 2. General Overview

The conifers are a group of gymnospermous woody plants including two formerly recognized classes or orders: Coniferopsida (Coniferales) and Taxopsida (Taxales), but excluding other gymnosperms such as cycads, gnetums, ephedras and the two unique gymnosperms *Ginkgo* and *Welwitschia*. There is evidence, both from the fossil record and from phylogenetic analysis, to support the theory that conifers are a monophyletic group, i.e., derived from a common ancestor. The fossil record of conifers is relatively abundant, with few major gaps in time, and goes back almost 300 million years to the Upper Carboniferous (Pennsylvanian). However, that common ancestor is not known. There were during the Upper Carboniferous and Lower Permian several lineages of primitive seed plants present, leading either to groups now extinct, or to some still extant, and relationships have not yet been resolved unambiguously. Another complication is that the early conifers of the Permian and Triassic appear not to belong to extant families, but became extinct some long before modern groups appeared. Among the oldest of present conifer families is the Araucariaceae (which have existed since the Jurassic, 160 million years ago), closely followed by the Cupressaceae

(Taxodiaceae) and the Podocarpaceae. Pinaceae appeared with early pines (*Pinus*) in the Lower Cretaceous, 120 million years ago. Not only do conifers therefore vastly antedate any flowering plants (angiosperms), they were the dominant trees nearly everywhere (although sharing forests with glossopterid gymnosperms in southern Gondwana) through much of the Mesozoic. As late as the early Tertiary (the Eocene, 50 million years ago), although flowering plants had by then become dominant on most continents, conifers still extended from the tropics to the high polar regions. Many genera are known that are now extremely limited in their distribution, e.g., *Araucaria*, *Metasequoia*, *Sequoia*, and *Sequoiadendron*, from fossils found across America and Eurasia. Some were even present in both supercontinents—Gondwana and Laurasia, as exemplified by *Araucaria*, which disappeared entirely in the Northern Hemisphere, and *Sequoiadendron*, which is now absent from the Southern Hemisphere.

A good indication of the relict nature of present-day conifers is given by the following figures. There are 8 families: Araucariaceae (3 genera), Cephalotaxaceae (one genus), Cupressaceae (including the former Taxodiaceae, 28 genera), Phyllocladaceae (one genus), Pinaceae (11 genera), Podocarpaceae (18 genera), Sciadopityaceae (one genus), and Taxaceae (five genera). Three families have only a single genus, and the Japanese *Sciadopitys verticillata* is the only species in its family. Of 68 genera, 30 have but a single species, and 39 are considered endemics; in many instances a genus falls in both categories. Furthermore, these are mostly concentrated in a few of the conifer regions recognized in the IUCN Conifer Action Plan, notably Japan and environs, China and environs, Australia and the SW Pacific. Particular small areas can be extremely diverse: the maximum diversity and endemism is reached on the island of New Caledonia in the SW Pacific, with 43 conifer species, all endemics. Some of these are extraordinary, such as the only parasitic conifer, *Parasitaxus usutus*, and the only rheophyte, *Retrophyllum minor* (both Podocarpaceae). New Caledonia is in many respects a mini-cosmos reflecting what happened to conifers worldwide until recent human interference.

Apart from extinction, there were two trends: adaptive specialization to narrowly defined, extraordinary ecosystems, eventually resulting in endemism and loss of diversity; and an opposite diversification by colonization of new habitats, spread and subsequent speciation caused by separation of populations. Most of the 30 monotypic genera and many of the 39 endemics belong to the first category, while usually the larger genera, notably *Abies*, *Picea*, *Pinus* (Pinaceae), *Juniperus* (Cupressaceae), and *Podocarpus* (Podocarpaceae), are good examples of the latter. Of these, the pines (*Pinus* spp.), with 108 species, are not only the largest genus in conifers, but also the most diverse, and include evolutionary relicts as well as evolving species. As a general ecological rule, it is often emphasized that conifers can only be successful where flowering plants fail, and especially as regards the relict endemics, there is certainly some evidence for this. Both paleoendemics and evolving new species that occupy vast tracts of continents are often adapted to adverse climatic and/or edaphic conditions where angiosperms, it is assumed, could not follow. But as a general principle, this is less convincing. Not only have many flowering plants evolved into forms equally well adapted to cold, darkness, aridity or lack of nutrients, but with an evolution time of 120 million years and more than 250 000 extant species, it is highly unlikely that there could be many habitats suitable to conifers but not suitable to any angiosperm. Conversely, there are many species of conifers that thrive under conditions quite favorable to

angiosperms as well, such as those conifers that dominate the temperate coastal rainforests around the Pacific Ocean, or the montane forests further inland both in Asia and North America. Adaptation to fire in fire-prone ecosystems is found in both angiosperms and conifers; the same is true for acidic, nutrient-deficient soils, long periods of water deficiency or the reverse—persistent waterlogging. In all these cases, it can merely be observed that coniferous trees can evidently compete successfully enough to maintain themselves. Furthermore, on closer observation of successional stages, it is true even in the boreal coniferous taiga that there are phases in which angiosperms dominate after periodic disturbances, e.g., fire or wind damage, slowly to be replaced by conifers.

This leads to mosaic patterns of forest vegetation, often with a phase of mixed angiosperm-conifer stands. Particularly in coastal temperate rainforests, longevity of conifers seems to be the only advantage by which they can eventually survive angiosperm domination. Longevity and slow growth are often two sides of the same coin, and result in a strategy of perseverance, until the next episodal disturbance clears away most of the competition, after which regeneration can occur. There are many conifers with life spans lasting well over a millennium, and several which can live two to four millennia. Most of these, but not all, occur in arid habitats (which may have selected for slow growth and tenacity), and the champion is *Pinus longaeva* in eastern California and Nevada, with a few trees nearing 5000 years old. However, *Fitzroya cupressoides* (Cupressaceae) in Chile may well be longer lived—a maximum ring count of 3620 years was taken from a hollow tree (there are no existing solid trees of large size; this species grows in extremely wet climatic conditions.

Conifers, then, although most likely diminished in diversity and abundance compared with their heyday in the Mesozoic, but are still an extremely widespread and diverse group of plants. They are found on all continents except Antarctica, and from fire-prone tropical pine savannas to extreme climatic conditions at the treeline or beyond in high mountains, from temperate evergreen rainforests on ocean shores, to semi-deserts in the interior of continents. Soils can be sandy, rocky, peaty, dry or wet, and even toxic with heavy metals. This tolerance of such a wide range of climatic and edaphic conditions is remarkable for such a relatively small number of species, and is undoubtedly the result of a very long evolution. For these reasons, conifers are very important ecologically, as they provide forest cover or other permanent or periodic vegetation to animals and humans in all these habitats.

Natural old growth conifer forests, in which conifers can attain great size and age, are ecosystems supporting a high level of biodiversity. Many species of plants and animals depend on these conifers. Successional cycles in such forests are long and complex. It is not be surprising that such ecological diversity has also led to a great morphological diversity. Conifers range from diminutive decumbent shrubs, to the tallest trees in the world: *Mycrocachrys tetragona* (Podocarpaceae) in Tasmania crawls over rocks or peaty soil to a height of a few centimeters, while *Sequoia sempervirens* (Cupressaceae) along the coast of California reaches 115 meters tall. Some species are among the fastest growing trees in the world, adding 2–3 m stem length per annum in young trees; others are so slow growing, that annual increments of wood cannot be observed without a 20 × magnification. While pollen dispersal has remained primitive (a chance strategy

by wind requiring massive investments), seed dispersal has often involved elaborate mutualism with a range of vertebrate animals, e.g., in some pines and especially in the Podocarpaceae and Taxaceae. There is, therefore, a paradox, in that despite a long and continuing evolution, which has resulted in adaptations to numerous environmental challenges, many conifer species are at present restricted in their occurrence, often as single survivors of greater diversity and spread in the geological past. As a consequence, they are vulnerable to the ever increasing pressures that humans have imposed on their habitats, or directly on the individual conifer species concerned.

The most recent and comprehensive assessment on a world scale has concluded that 25% of conifer taxa (species, subspecies and varieties) are threatened with extinction. The "Global Red List of Conifers" in the IUCN/SSC Conifer Action Plan includes 355 taxa of conservation concern. Seventy conifers are considered Endangered (EN) or Critically Endangered (CR) which means that they will become extinct in the foreseeable future (within decades) should current trends continue. It is to be feared that these trends will in many cases increase rather than decrease, so that extinction will be inevitable. Criteria have been developed in the Conifer Action Plan by which prioritization in the face of such a massive threat of extinction can be given a scientific basis.

Urgent conservation action focused on 43 short-listed species would, if successfully implemented, safeguard at least a major portion of the incredible genetic diversity that was built up over millions of years, and is now facing sudden demise. Even from the more restricted perspective of human utilization, this loss would be severe. Exploration of economic potential has merely scratched the surface of this diversity, traditionally concentrating on a handful of species in the Pinaceae of the Northern Hemisphere. Timber is the most obvious, and by far the largest of exploited resources, but even here the qualities of most conifer species remain poorly known. The recent discovery in *Taxus* of chemical compounds that are very useful as a medicinal drug to fight cancer has emphasized how little is know of other properties besides those of wood in most conifers.

In the following illustrative overview of important coniferous trees, some examples will be given which may highlight the various aspects indicated, from scientific interest, via ecological approaches, to economic aspects. An attempt has been made in this article to cover most families, continents, climatic zones and forest types in which conifer trees occur. This has been done by presenting descriptions of 20 species in Section 3 below—although it is clear that many more species are equally important, and it is emphasized that their exclusion here is by no means an indication of lesser importance in any respect. The arrangement of species adopted is alphabetical by family.

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**Biographical Sketch**

**Aljos Farjon** was born in 1946 in the Netherlands, and pursued his biological studies by self-education. Between 1970 and 1983 he made six extensive expeditions to North America and the Arctic. From 1981 to 1985 he worked as an ecologist for regional Dutch government agencies and meanwhile studied vegetation ecology under the guidance of Dr. J. T. de Smidt of the University of Utrecht and Prof. Emeritus V. Westhoff. In 1985 he became a research associate with the Institute of Systematic Botany (subsequently Herbarium Division) of the University of Utrecht, where he combined taxonomic work on conifers (started in 1983) with part-time ecological work. He has published 80 papers and 7 books in both fields, since 1985 almost exclusively on conifer systematics. In 1993, he was asked by Prof. Sir Ghillean Prance, then Director of the Royal Botanic Gardens, Kew, to join the Department of Plant Sciences of the University of Oxford to complete a taxonomic revision of the pines of Mexico and Central America,

which was published in 1997. At the XVI International Botanical Congress, held in August 1999 at St. Louis, US, he was awarded the prestigious Adolf Engler Medal in silver for this work. In 1995, he was appointed Senior Scientific Officer and Curator of Gymnosperms at the Royal Botanic Gardens, Kew. He is Chair of the Conifer Specialist Group of the IUCN Species Survival Commission, and was asked to chair the program committee of the 4th International Conifer Conference which was held in August 1999 in Wye, England. He has been a Fellow of the Linnean Society of London since 1991.