David B. Neale
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The Conifers: Genomes, Variation and Evolution

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The authors of this volume are sincerely pleased to dedicate our work to the many postdoctoral scholars, graduate students, research assistants, and undergraduate interns who provided the hard work, enthusiasm, and creativity to so many research projects the authors collaborated on over the years. Thanks to you all, we look forward to your ongoing contributions to our understanding of the genetics of forest trees.

Foreword

Conifers, and related gymnosperms, are among the world's oldest groups of organisms. I learned that in my first year at university while training as a forester, and even now, as a forest geneticist nearing the end of my scientific career, I still find this fascinating. Conifers evolved during the era of the dinosaurs and continue to dominate large expanses of forest around the world, even after the subsequent evolution of the angiosperms, which are exceedingly more species-diverse. What was in the DNA of conifers that made them so durable? In *The Conifers: Genomes, Variation, and Evolution*, David Neale and Nicholas Wheeler review and synthesize findings from traditional genetic studies and the most recent molecular genetic research that helps elucidate why conifers may have persisted for millions of years.

Humans have long valued conifers for their exceptional wood properties. Straighter in form, and possessing stronger yet lighter wood than most angiosperms, they have been important construction materials throughout the world for thousands of years. Today, conifers are an important forest resource in many countries. Early in the twentieth century, scientists recognized the significance of conifer genetics to the practice of forestry. Common garden studies by pioneering geneticists showed that many conifer species had considerable levels of genetic variation, making them highly suitable to "improvement" using classic breeding techniques developed on domestic plants and animals. Many traditional conifer breeding programs were subsequently initiated, practicing recurrent selection in order to improve desired traits — such as growth, resistance to disease and insects, and, more recently, adaptability to changing environments. In the 1980s, molecular genetics studies of forest trees also became a key element to understanding their basic biology. Using the technique of protein electrophoresis, these molecular approaches enhanced our knowledge of conifer genetics and became instrumental to understanding conifer mating dynamics, informing seed production practices, and developing forest tree genetic resource management programs.

As molecular biology techniques improved through the 1990s and onward, significant resources were invested in molecular genetics and genomics research due, in large part, to the progress and promises of the human genome project. While traditional forest genetics and tree breeding research waned around the world, largely due to fundamental shifts in the economics of forestry investments, forest tree molecular geneticists were keeping pace with the genomic advances occurring in most other organisms (e.g., *Arabidopsis* and humans). During the turn of this

century, study objectives changed to more scholarly questions, along with divergence in the terminology and vernacular used by forest tree breeders and forest tree molecular geneticists. To address this, Neale and Wheeler have neatly clarified the terms used in modern molecular genetics of conifers and, more importantly, have presented the most recent information of conifer genetics in a modern synthesis that integrates many aspects of their quantitative and population genetics. The book is presented in an understandable way, highlighting recent breakthroughs in gene structure and gene families, comparative genomics, phylogenetics, and landscape genomics, for example, but also identifies the interesting challenges ahead in genomics research of these marvelous organisms. Any new forest geneticist must now be versed in both classical and modern population genetics and quantitative approaches, as well as molecular genetics terminology, techniques, and bioinformatics of genomics. *The Conifers: Genomes, Variation, and Evolution* provides a much needed unification of these topics and should be required reading for new students of conifer molecular biology and genomics.

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Preface

The study of the genetics of forest trees began more than 100 years ago, coincident with the rediscovery of Mendel's classic works. For three quarters of the twentieth century, conifer genetics was dominated by the study of phenotypic variation in provenance trials (Chap. 8), species hybridization trials (Chap. 15), disease and insect resistance (Chap. 14), and development of tree breeding methods, all of which suggested most traits in trees were quantitatively inherited. Furthermore, many traits were adaptive and varied in response to environmental factors such as temperature and moisture.

Forest genetics research approaches, funding sources, and personnel began changing significantly in the mid-1970s as biochemical and DNA marker development allowed for population genetic and mating system investigations. These neutral markers were subsequently used to characterize the genetic basis of quantitative traits (Chaps. 9 and 11) and enhance our understanding of conservation genetics (Chap. 13) and phylogenetics (Chap. 16). Recent developments in high-throughput genome sequencing technology have resulted in a quantum leap in our knowledge of conifer genomes (Chaps. 2, 3, 4, 5, 6, 7, 12, and 17). We anticipate this knowledge will continue to increase rapidly, as it has for so many other organisms. A review of the state of knowledge in conifer forest genetics therefore seems appropriate.

In this monograph, our goal is to summarize and synthesize this body of work, specifically for conifers, in a manner that would be useful for practicing professionals in conifer genetics and genomics research but also for those from other fields of forestry and plant biology who might be curious as to what has been learned over 100+ years in this small discipline. The monograph is organized into three major parts, Genomes, Variation, and Evolution, and we have tried to synthesize and cross-reference across all chapters and sections. We have not included the very extensive literature in applied conifer breeding and tree improvement research, and instead refer readers to other important works in this area (Wright 1976; Namkoong 1979; Zobel and Talbert 1984; Mandal and Gibson 1998; Kumar and Fladung 2004; White et al. 2007; Plomion et al. 2011).While our search and summary of the relevant literature is certainly not exhaustive, we have sought to provide a comprehensive view with a modest (over 1600) number of exemplary citations.

Finally, the authors of this monograph have enjoyed and been rewarded by our years of making small contributions to this discipline of forest genetics working

individually and for much of our careers together. We have benefitted from knowing and working with a substantial number of the scientists, past and present, who have defined the forest genetics discipline. We are using this moment to give a little something back to the discipline that has given us so much. It is our perspective on the evolution of our discipline over the last 100+ years (Wheeler et al. 2015) that has shaped our final chapter (Chap. 18).

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The Conifers

1

The conifers are a diverse and ancient group of seed plants of monophyletic origin that arose more than 300 million years ago (Rothwell and Scheckler 1988). They are uniformly distinguished by their naked or exposed ovules during pollination, a trait they share with the cycads, the monotypic genus *Ginkgo*, and the gnetophytes. Collectively, these four taxa comprise the gymnosperms, which, along with the flowering plants (angiosperms), constitute the seed-bearing plants (Fig. 1.1).

The conifers are not easily circumscribed or defined. While there are many traits commonly associated with conifers, exceptions to most character states exist. Conifers are typically single-stemmed, evergreen trees with separate male (simple) and female (compound or reduced) reproductive structures (strobili or cones) either on the same (monoecy) or different plants (dioecy). Conifer wood possesses tracheids, bordered pits, and frequently, resin canals. Conifer lignin polymers are comprised almost entirely of coniferyl alcohol monolignol monomers (guaiacyl lignin), lacking syringyl elements common to most angiosperms (Boerjan et al. 2003). Leaves are simple, mostly needle- or scale-like, and often resinous (Fig. 1.2). Molecular studies indicate conifers possess a single copy of a large (~25 Kbp) inverted repeat element in the chloroplast genome (Strauss et al. 1988; Strauss and Doerksen 1990; Raubeson and Jansen 1992), while all other plants tested have two copies.

Notable exceptions to commonly held views of what defines a conifer include the shape and persistence of their leaves and the form of their female strobili. At least 15 species of conifer from five genera (*Larix, Pseudolarix, Taxodium, Metasequoia*, and *Glyptostrobus*) annually shed their leaves, and species like *Nageia wallichiana* or members of the genus *Agathis* might easily be mistaken for broad-leaved trees with their flat, wide leaves. Species of the genus *Phyllocladus* (Podocarpaceae) are essentially leafless, sporting instead modified, flattened, and photosynthetic branches that resemble celery tops. Many species have distinctly different leaf forms for juvenile and mature foliage.

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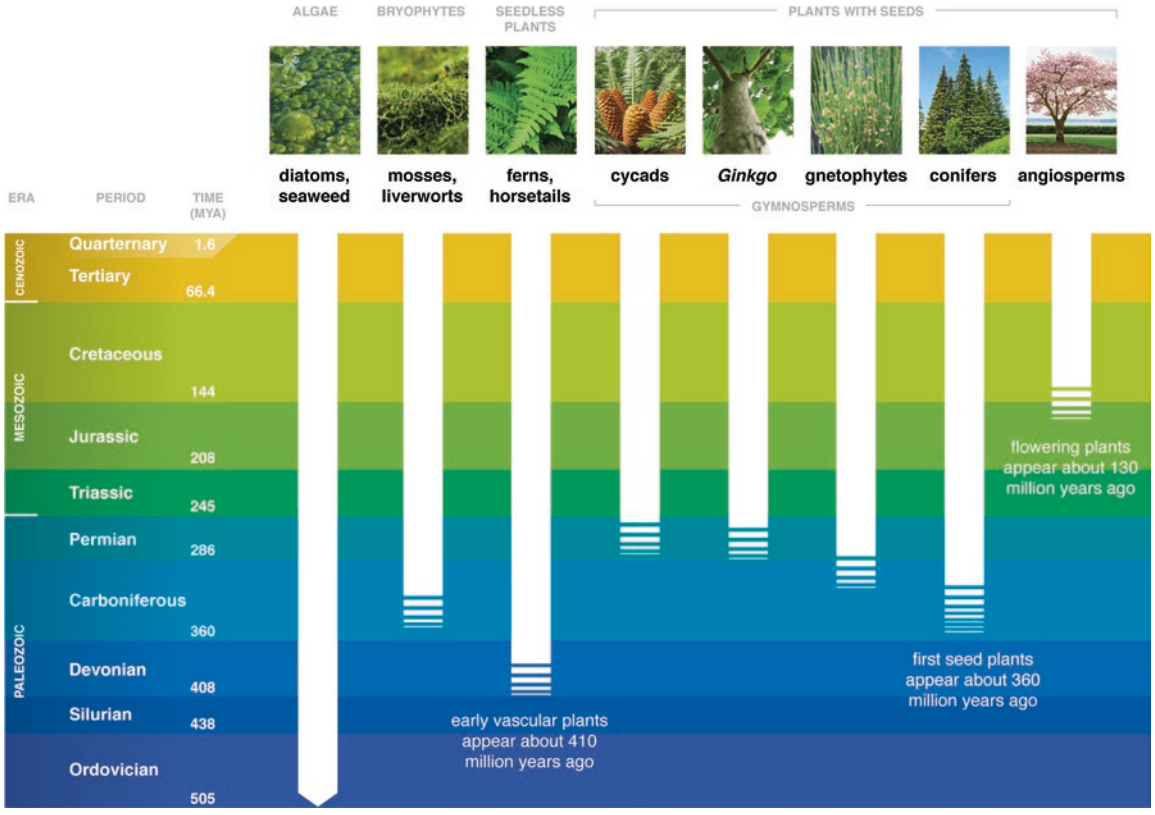


Fig. 1.1 Extant land plant taxa and their estimated evolutionary beginnings. The algae and bryophytes lack vascular elements. The earliest vascular plants, including modern ferns and their allies, are seedless, reproducing via spores. The conifers, along with the cycads, *Ginkgo biloba*, and gnetophytes, constitute the gymnosperms. Along with the angiosperms, gymnosperms represent today's seed-bearing plants

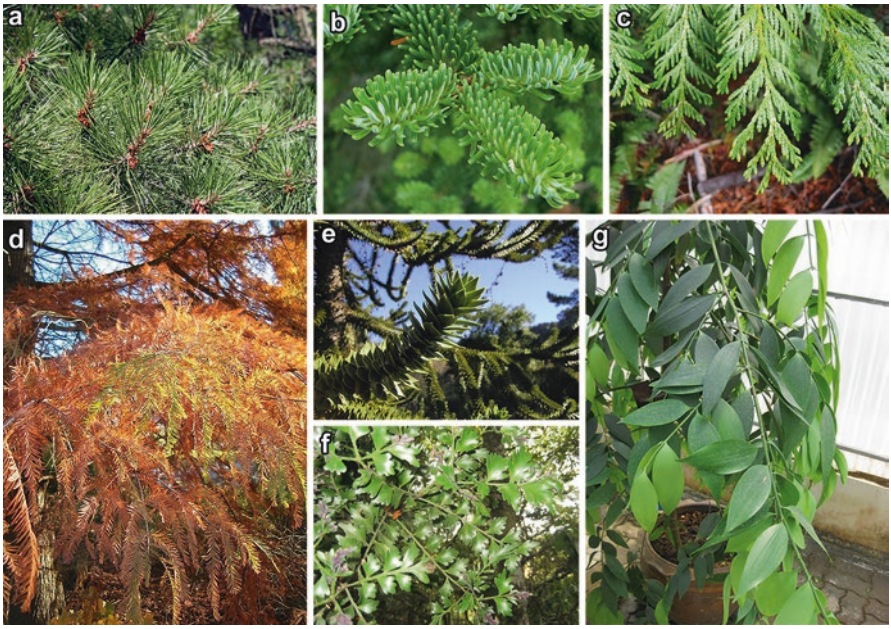


Fig. 1.2 Conifers have evolved numerous foliage types to cope with variable and often challenging environments. Residents of the Northern Hemisphere are familiar with members of the Pinaceae genera (**a**) *Pinus* and (**b**) *Abies* and the Cupressaceae genera (**c**) *Thuja* and (**d**) *Taxodium*, the latter a deciduous conifer. Less familiar to most are the Southern Hemisphere conifers such as (**e**) *Araucaria*, (**f**) *Phyllocladus*, and (**g**) *Nageia*

Not all conifers bear woody cones, as the name might imply (Fig. 1.3). The yews and related taxa in the Taxaceae and the podocarps (Podocarpaceae) generally bear a single seed atop or surrounded by a highly reduced or modified structure, often fleshy and colorful. Cones of the genus *Juniperus* (Cupressaceae) are composed of fleshy, fused scales, and are often referred to, erroneously, as berries. In short, fruiting structures of the conifers are highly variable and reflect strong selective pressures associated with modes of seed dispersal.

Tree form is another trait which varies considerably among conifers. While most conifer species grow as single-stemmed trees with strong apical dominance, multi-stemmed, shrubby species such as *Juniperus horizontalis* and *Lepidothamnus laxifolius* seldom surpass a meter in height. The most widely distributed conifer in the world, *Juniperus communis*, often grows as a low shrub, especially at higher latitudes and a subspecies of *Pinus mugo* (*P. mugo* ssp. *mugo*) is characterized by having multiple stems and short stature even though across much of its native range it is tall and single-stemmed. Many conifer species exhibit the *krummholz* growth habit near tree-line, an apparent response to adverse growing conditions.

Perhaps the greatest challenge to the traditional concept of what defines a conifer is found on the island of New Caledonia. There grows the only known heterotrophic

Fig. 1.3 The seed-bearing structures of conifers are highly diverse. The woody "pine cone" typical of the genus *Pinus* (**a**) is perhaps best recognized while the upright cones of the genus *Abies* (**b**) dry and disintegrate on the tree. The highly modified fruiting structures of *Taxus* (**c**) and *Podocarpus* (**d**) encourage seed dispersal by birds and small mammals

conifer, *Parasitaxus usta*, a small tree of 1–1.5 m, lacking chlorophyll, which survives as a parasite, growing on the roots of another conifer, *Falcatifolium taxoides*. Both species belong to the Podocarpaceae.

In summary, extant conifers are a highly diverse group of taxa representing descendants from a single common ancestor following millions of years of evolution. While most taxa share many traits in common with subsets of other taxa, there are few easily identified traits that characterize them all. The burgeoning field of genomics likely holds promise for expanding our knowledge of what constitutes a conifer (Chap. 3).

Conifer Taxonomy

Taxonomic classification of the conifers is a dynamic process, from the relatively recent discovery of new genera and species (Jones et al. 1995; Farjon et al. 2002) to ongoing revisions at virtually all taxonomic levels up to division, driven by new morphological studies, the rapid expansion of molecular studies of organelle and nuclear genomes, and the completion of monographic treatments. Disagreements frequently exist on the naming and recognition of species, genera, and even families (reviewed in Farjon 2008; Eckenwalder 2009; Farjon 2010; Gernandt et al. 2011).

Conifers have been variously recognized at the level of division or phylum (Pinophyta, Coniferophyta), class (Pinosida, Coniferae), subclass (Pinidae; Cronquist et al. 1966), and order (Coniferales), the latter considered widely accepted (Gernandt et al. 2011), though Christenhusz et al. (2011) recognized three different taxa at the level of order: the Pinales consisting solely of the family Pinaceae, the Araucariales which includes the Araucariacea and Podocarpaceae, and the Cupressales with families Sciadopityaceae, Cupressaceae, and Taxaceae. Taxonomic support for these six families, given recent morphological and molecular studies, appears strong and those six are adopted here, though recent treatments (Farjon 2001, 2008; Farjon and Filer 2013) recognize as many as eight families, including Cephalotaxaceae and Phyllocladaceae with the previous six (Fig. 1.4).

Classification of species and genera has fluctuated to an even greater degree over the last 60 years. Dallimore et al. (1967) accepted 53 genera, while more recent treatments recognized as many as 71 (Farjon 2001, 2008, 2010; Eckenwalder 2009; Gernandt et al. 2011; Christenhusz et al. 2011; Table 1.1). This increase in genera has been coincident with a general decline in the number of recognized species, though this number too remains elusive to define, with a range of 546 to 670, as noted in recent treatments (Table 1.1). The highly variable estimates likely result from how accepted taxa are treated at the species and subspecies levels.

Taxonomic diversity of families ranges widely (Farjon 2008; Farjon and Filer 2013). The Pinaceae has ~231 species in 11 genera, the largest of which is *Pinus* with ~113 recognized species. The other large families are the Podocarpaceae

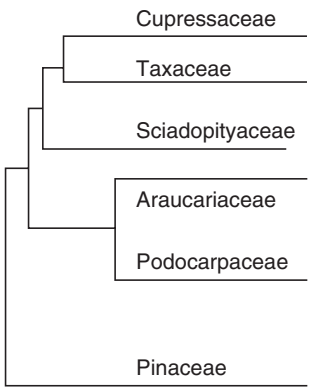


Fig. 1.4 Cladogram of the six conifer families most frequently recognized today. (Adapted from Gernandt et al. 2011). Some authorities recognize two additional families: the Cephalotaxaceae, here subsumed in the Taxaceae, and the Phyllocladaceae, here subsumed in the Podocarpaceae

Table 1.1 Reported number of conifer taxa for family, genus, and species as listed in four recent authoritative treatments

	Number of taxa			
Taxon	A	B	C	D
Family	8	6	6	6
Genus	69–70	71	67	69
Species	615–630	670	546	–

A = Farjon (2008), Farjon and Filer (2013)
B = Gernandt et al. (2011)
C = Eckenwalder (2009)
D = Christenhusz et al. (2011)

(18 genera, 175–190 species, including the phylloclads) and Cupressaceae (30 genera, 135 species). Of the 30 genera in the Cupressaceae, 17 are monotypic (Farjon 2008). The Araucariaceae (3 genera, 37–41 species), Taxaceae including the formerly recognized Cephalotaxaceae (6 genera, 36 species), and Sciadopityaceae (1 genus, 1 species) are considerably smaller. Enumeration and descriptions of all conifer species and their distributions are provided in excellent references by Eckenwalder (2009) and Farjon and Filer (2013).

Though diverse and seemingly species-rich, the conifers in general may be in decline and have been since the Mesozoic, an era some paleobotanists have referred to as the Age of the Conifers. As many as 20 conifer families, 12 of which are now extinct, have been recognized and it has been estimated the Jurassic flora may have had as many as 20,000 conifer species (Debazac 1964 cited in Farjon 2008). Clearly, a great deal of diversity has been lost in the last 65 million years, and the existing inventory of conifers includes many species struggling to survive. Farjon (2008, pp. 184–185) lists 39 species considered to be relicts that are currently known to exist in a single locality, often confined to a few square kilometers. The International Union for Conservation of Nature Red List of Threatened Species (IUCN 2017), which tracks the status of organisms worldwide, listed 196 of the 605 conifer species reviewed to be vulnerable, endangered, or critically endangered in 2015. In some cases, such as with *Abies beshanzuensis*, the number of known living trees can be counted on one hand (Yang et al. 2013). Some genera and families are significantly more threatened than others (Table 1.2), no doubt a reflection of their evolutionary past and their inability to adapt to new and changing conditions, as well as range fragmentation, human development, and mismanagement. A more thorough look at the evolutionary history of conifers and their relationships to one another is explored in Chap. 16.

Geographic Distribution and Biogeography

Conifers are widely distributed across much of the world's landmasses, occurring on all continents excepting Antarctica (Fig. 1.5, Farjon and Filer 2013). They form extensive, circumboreal forests across North America and Eurasia, the largest

Table 1.2 The number of species listed as vulnerable, endangered, or critically endangered for select genera as noted in the IUCN Red List (April 2015)

	Status					
Genus	Vulnerable	Endangered	Critically endangered	Total threatened	Number of species in genus	Percent of species threatened
Abies	4	7	4	15	46	32.6
Agathis	4	5	–	9	16	56.3
Amentotaxus	3	2	–	5	6	83.3
Araucaria	5	6	1	12	17	70.6
Cupressus	4	3	–	7	15	46.7
Dacrydium	2	3	1	6	21	28.6
Juniperus	4	7	2	13	53	24.5
Picea	7	6	2	15	36	41.7
Pinus	7	9	2	18	113	15.9
Podocarpus	11	19	5	35	97	37.1
Taxus	1	3	1	5	8	62.5
Widdringtonia	–	–	2	2	4	50.0

Fig. 1.5 The worldwide distribution of conifers. (From Farjon 2008, p. 166)

recognized floristic region in the world (Takhtajan 1986), and they are common to predominant elements in floras throughout North and Central America, large areas of South America, Malesia (the biogeographical region straddling the Indomalayan and Australasian ecozones), Australia, New Zealand, China, and Eastern Africa. Conversely, they are rare or absent in deserts, steppes, the Arctic tundra, alpine regions, and the great lowland tropical rainforests of the Amazon and Congo Basins, predominantly due to ecological preferences and tolerances. The absence of conifers in large areas of otherwise habitable land on the Indian subcontinent, Southern Africa, and southern South America is discussed in some detail by Farjon (2008) and may be variously attributed to historical periods of climate change, the breakup of the supercontinent Gondwana, and vicariance events like mountain building, flood basalts, and continental drift. Conifers are commonly dominant in stressful or extreme environments where water and temperature regimes are limiting to plant growth (Richardson and Rundel 1998) but less successful in ameliorating environments that favor the rapid growth of angiosperms (Coomes et al. 2005).

The study of the distribution of organisms across large geographic regions is known as biogeography, the roots of which date to the studies of Alfred Russell Wallace on the Malay Archipelago (Wallace 1876). Over the last several decades, biogeographical studies seeking to explain the distribution patterns of organismal groupings have been significantly influenced by the near-universal acceptance of plate tectonics or continental drift (Moss and Wilson 1998). For the ancient conifer lineages, which have been evolving for over 300 million years, continental drift helps explain much of the current worldwide distribution patterns of extant taxa.

The consensus theory today is that the Earths' landmasses have moved about on continental plates for at least two billion years (Zhao et al. 2004), periodically forming supercontinents, where all plates are roughly in contact with each other. The most recent of these supercontinents, known as Pangea, likely formed about

300 million years ago (mya), about the time early conifers appear in the fossil record. Pangea began breaking up roughly 200 mya into two minor supercontinents called Gondwana and Laurasia which roughly equate to todays' Southern and Northern Hemisphere landmasses, respectively (Fig. 1.6). The breakup of the land masses had a profound effect on the subsequent distribution of conifer taxa. Extant conifer diversity is largely (90%) contained in major clades (families or subfamilies) that are confined to either the Northern or the Southern Hemisphere (Leslie et al. 2012, Fig. 1.6). The Podocarpaceae and Araucariaceae, early fossils of which occurred on Gondwanan landmasses prior to the breakup of Pangea, remain largely restricted to the Southern Hemisphere, while the Pinaceae, Sciadopityaceae, and Taxaceae are predominantly of Northern Hemisphere origin (Critchfield and Little Jr 1966; Eckenwalder 2009; Farjon and Filer 2013). The large and diverse Cupressaceae are distributed worldwide but are divided into subfamilies that are mostly hemisphere specific: Cupressoideae in the north, Callitroideae in the south (Mao et al. 2012).

Similarly, generic and species diversity in the conifers appears to have been significantly influenced by continental- and hemispheric-scale phenomena like the distribution of oceans, mountain-building, climate change, and continental drift (Leslie et al. 2012). Conifer taxa are clearly not distributed randomly around the world. Farjon (2008, Ch. 24) notes that all extant families, 83% of genera (gen) and over half of all species (sp) occur in 14 centers of diversity around the Pacific Ocean, many of which are islands like Japan (18 gen, 45 sp), New Caledonia (14 gen, 44 sp), and Taiwan (17 gen, 26 sp). In the eastern Pacific, the Pacific Northwest (13 gen, 29 sp), California (14 gen, 48 to 50 sp) and southern Mexico/Guatemala (7 gen, 39 sp) host forests of remarkable conifer diversity. The Klamath Mountains of northwest California alone is home to 35 species (Griffin and Critchfield 1976; Kauffmann 2012), nearly half of which can be found within remarkably diverse forest plots. Around the Pacific, the distribution of rare and endemic species is often coincident with these centers of diversity. Approximately 70% of all conifer species occur in the Northern Hemisphere.

Life History

The conifers are large, long-lived, woody perennial plants that often grow in extensive panmictic populations covering vast portions of the boreal and temperate regions of the world and in mixed stands in tropical and subtropical forests. They are the dominant life forms in a diverse array of ecosystems, demonstrating the capacity to adapt to highly variable climatic and edaphic conditions. Their success and persistence, over 300 million years of continental shifting, climate changes, mountain building and volcanism, must rest in large part with the spectrum of life history traits they exhibit and, by inference, the store of genetic diversity they maintain.

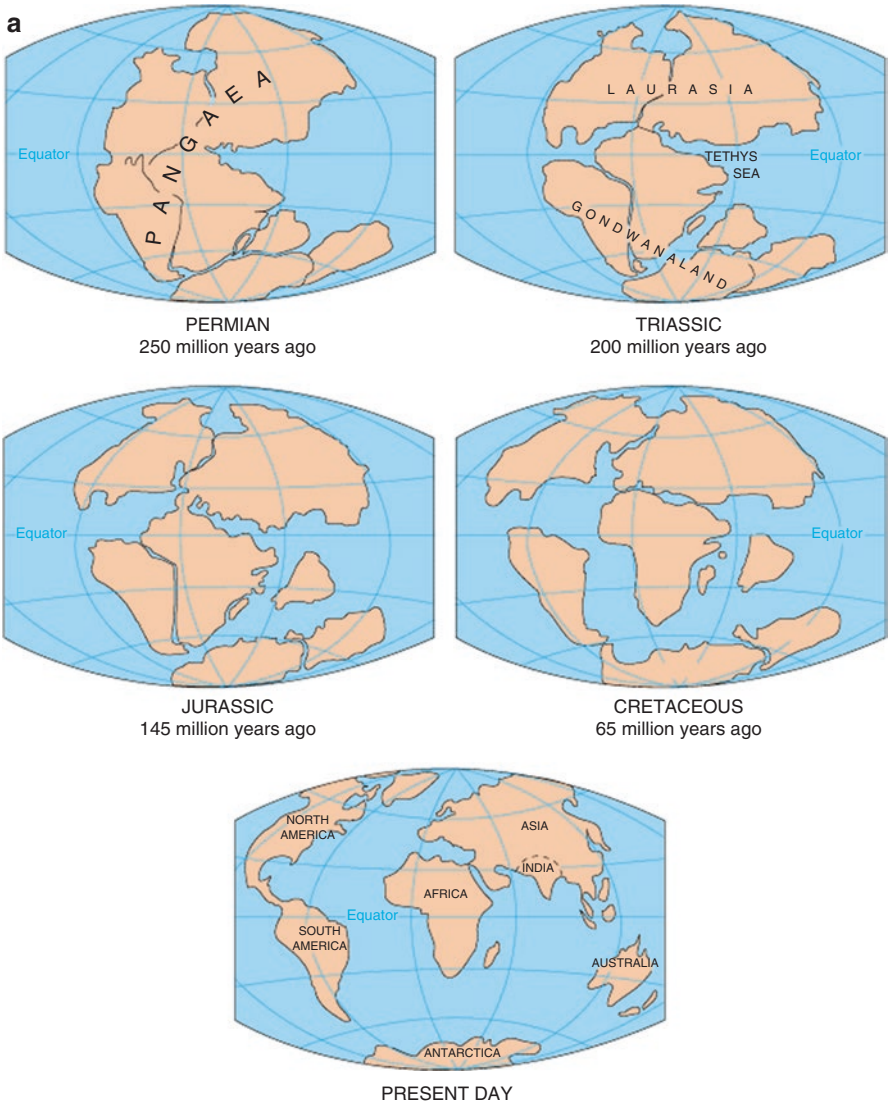
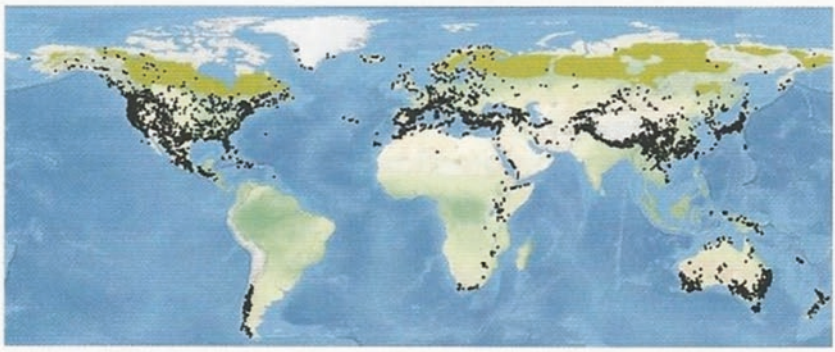
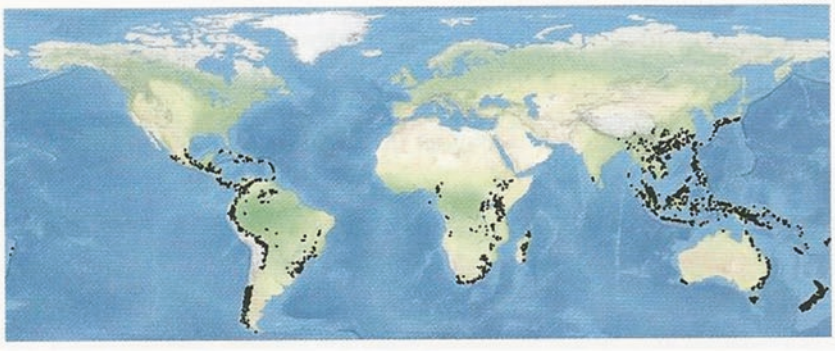


Fig. 1.6 (**a**) Hypothetical pattern of continental shifting following the breakup of the supercontinent Pangea (from http://www.rocksinmyheadtoo.com/Pangea.htm), and global distribution of (**b**) the Cupressaceae (map GTC-5, Farjon and Filer 2013, p. 14), (**c**) the Pinaceae (map GTC-6, Farjon and Filer 2013, p. 14), and (**d**) the Podocarpaceae (map GTC-10, Farjon and Filer 2013, p. 15)



Map GTC-5. The global distribution of Cupressaceae.

Map GTC-6. The global distribution of Pinaceae.



Map GTC-10. The global distribution of Podocarpaceae.

Fig. 1.6 (continued)

Fig. 1.7 Conifers are the dominant plants on expansive areas of (**a**) boreal and (**b**) high-elevation temperate ecosystems in the Northern Hemisphere

Ecological Tolerance

Conifers have adapted to and successfully competed with angiosperms in most (17 of 21) major vegetation types in which vascular plants occur (Farjon 2008, p. 36–37). They tolerate extremes of temperature and moisture, from arctic tundra to hot deserts, and from less than 250 mm/year to well over 5000 mm/year of precipitation. Conifers are dominant across the vast boreal forests (Fig. 1.7) of the North American and Eurasian continents where they thrive under short growing seasons, extreme cold, heavy winter snow loads and, frequently, what otherwise might be considered desert conditions (precipitation less than 375 mm/year). At these high latitudes, low evapotranspiration demands do not inhibit the development of closed stands. The modest number of species that survive in these conditions possess many physiological and morphological adaptions that contribute to their success. All have relatively

tall, narrow crowns that both shed snow in the winter and capture low-angle sunlight at the end of the growing season. Evergreen crowns (*Abies, Pinus*, and *Picea*) require less energy to produce and maintain than annually replacing the entire leaf surface and permit photosynthetic activity as soon or as late as conditions permit. *Larix* species avoid cold damage to foliage by dropping needles annually. All species have deep dormancy capacity and the biochemistry to tolerate extreme cold events that might otherwise damage or kill primary and secondary meristematic tissues (buds, cambium). Conifers that inhabit the higher elevations of the world's major mountain ranges share many of the same adaptations. Adaptation to winter cold in temperate and boreal trees involves an array of complex genetic, physiological, and developmental processes for which most conifers in these environments exhibit remarkable diversity (Howe et al. 2003).

Elsewhere, in the Northern Hemisphere, conifers often grow in areas with high evaporative stress (Gernandt et al. 2011) and may be considered as xerophytes (Mirov 1967). In large part, members of the Pinaceae and Cupressaceae possess an array of traits that confer drought tolerance, like thick cuticles and epicuticular wax layers on needles, the ability to shut down stomata under unfavorable conditions, and mycorrhizal associations that can significantly enhance water uptake (Molina and Trappe 1984; Smith and Brewer 1994). By contrast, many of the Southern Hemisphere Podocarpaceae and Araucariaceae have evolved under more mild, wetter conditions (Leslie et al. 2012) and are generally less cold and drought hardy. Exceptions to this are common however. Though Podocarps have a pan-tropical distribution across continents, they are largely montane dwelling in Africa and South America where droughty conditions exist (Addie and Lawes 2011).

Though conifers do not typically tolerate saturated or flooded soils, here too exceptions exist such as New Zealand's Kahikatea swamp forests (with *Dacrycarpus dacrydioides*), the cypress swamps of the Southeastern United States (with *Taxodium disticum*), and the temperate rainforests of the Pacific Northwest (US), Canada, and Southeast Alaska. Conifers in temperate rainforests in both hemispheres adapt by establishing extensive, but shallow, spreading root systems close to the surface. Few if any conifers tolerate saline conditions (Farjon 2008).

While most conifers grow exceptionally well on good soils, such as the deep, uplifted marine sediments of the coastal northwestern United States, they are more typically found on nutrient-poor, often shallow soils in upland and mountainous regions where angiosperms compete less well (Fig. 1.7). Their success on poor soils has been attributed, in large part, to the near-universal association and coevolution (Brundrett 2008) between conifers and mycorrhizae, a symbiotic plant–fungus relationship that enhances nutrient and moisture uptake, provides plant hormones to facilitate root growth, and functions to reduce some soil toxins and protect against other deleterious fungi (Malloch et al. 1980; Molina and Trappe 1984). Mycorrhizae are classified by how they physically associate with plant roots. Ectomycorrhizae, which form extensive mycelia mats or mantles among the tree's fine root tips (extracellular), are found in association with members of the Pinaceae, while vascular–arbuscular (VA) mycorrhizae, which form intercellular associations, are associated with all other conifer families (summarized by Brundrett 2008; see also Malloch et al. 1980; Molina and Trappe 1984).

Soils play a significant role in the distribution of conifers worldwide and can influence both species composition and successional status of conifer forests. While this often is manifest in a tree's tolerance to drought or moisture, it may also result from adaptation to unusual soil chemistries. To illustrate, three examples are drawn from the diverse forests of western North America. The short-lived, pioneering *Pinus contorta* ssp. *contorta*, common from coastal muskeg to upland sites, may become an edaphic climax species on deep, excessively drained sand and gravel soils along the Pacific Coast of western North America, where other temperate rain forest species simply cannot compete or survive. At mid-elevations, in the Klamath Mountains of northern California and southern Oregon, ultramafic soils (serpentine soils) support unique plant assemblages including some conifers, like *Pinus jeffreyi*, that tolerate the heavy metal concentrations in such soils, often without competition from other conifers (Sawyer 2006; Kauffmann 2012). And lastly, the Great Basin bristlecone pine (*Pinus longaeva*), known for specimens of remarkable age, grows almost exclusively on limestone soils at elevations more than 2800 meters in the western United States, virtually to the exclusion of other species. *Pinus longaeva* has combined adaptive tolerances to cold, drought, intense solar radiation, and soil chemistry challenges, and in so doing, largely avoids physical challenges from disease and insect pests that cannot survive in these rarified conditions.

Light and fire represent the remaining abiotic factors that contribute to the success or failure of conifer establishment and survival. Most conifers are early successional or pioneering species, occupying newly disturbed sites with full-sunlight conditions and exposed mineral soil. Such species are shade intolerant. Disturbance is key to conifer succession (Peattie 1953; Daubenmire 1968). Primary succession, on newly created sites, results following land shaping events like glacial retreat, floods, lava flows, and avalanches. More commonly, secondary succession of conifers follows existing stand disturbance caused by factors such as fire, wind-throw, timber harvest, or pestilence. At least in the Northern Hemisphere, fire has played, by far, the greatest single role in shaping conifer stand dynamics and evolution, and has been doing so for a very long time (Muir and Lotan 1985; Keeley and Zedler 1998; Pausas and Keeley 2009; Keeley 2012). Conifers have evolved an array of fire-adapted traits, the origins of which date at least to the Cretaceous period (65–145 mya, He et al. 2012a). Such traits include bark thickness, pyriscence (a special case of serotiny), branch shedding, the presence of a grass stage, and re-sprouting capacity (Keeley and Zedler 1998; Keeley et al. 2011; He et al. 2012a). Fire-adapted traits are most pronounced in the Pinaceae, particularly in the genus *Pinus*, and to a lesser extent the Cupressaceae. Pyriscence refers to the habit of retaining seed in cones that are sealed by a resinous coating and are triggered to open when heated by fire. The trait, common in the genus *Pinus*, subsections Contortae, Oocarpae, and Sylvestris, can result in large crown-borne seed banks and the release of millions of seeds per hectare following fire (Wheeler and Critchfield 1985; Stevenson 1991). Extreme examples of regeneration success following fire in *Pinus contorta* stands in northern British Columbia, Canada exceed 20,000 stems per hectare (Wheeler, personal observation, 1975; Fig. 1.8).