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ELEGANCE VERSUS SPEED: EXAMINING THE COMPETITION BETWEEN CONIFER AND ANGIOSPERM TREES

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Angiosperm radiation in the Cretaceous is thought to have profoundly diminished the success of the conifers, the other major woody plant group present at the time. However, today the conifers persist and often thrive despite their supposed inferiority in vegetative and reproductive function. By exploring this apparent conflict for global tree dominance, we seek here to reveal patterns that explain not only how the allegedly inferior conifers persist among angiosperms but also why some conifer groups became extinct in the Cretaceous. We find that despite the profound contrast between the dominant conifer families in the Southern and Northern Hemispheres, all conifers can be characterized by a common set of functional attributes that allow them to exist in an important group of niches, from high latitudes to the equator. In these environments, conifers are often highly efficient at outcompeting, outliving, or outsurviving angiosperms. Hence, we conclude that conifer success cannot be dismissed as being uniquely associated with habitats that are unfavorable for angiosperms.

Keywords: conifer, angiosperm, evolution.

Introduction

Gymnosperms and angiosperms are often depicted as arch-rivals in the competition for space in forest canopies. This adversarial image derives from paleoecological reconstructions that suggest angiosperm radiation during the Cretaceous occurred at the expense of gymnosperm diversity and abundance (Lidgard and Crane 1988). Such evidence of a major transition in plant diversity toward the end of the Cretaceous has led evolutionary ecologists to propose an array of theories to account for angiosperm dominance over conifers in both historical and contemporary contexts. In terms of diversity, gymnosperms are manifestly outgunned by angiosperms, which have a superior capacity to diversify due to relatively high reproductive efficiency, self-incompatibility, and reduced generation time (Crepet and Niklas 2009). This angiospermous reproductive advantage probably stems from floral evolution; however, diversity and ecological dominance are not synonymous, and explanations for the apparent displacement of gymnosperms from their ecologically dominant role in the canopy of Early Cretaceous forests have largely focused on vegetative characteristics (Carlquist 1975; Bond 1989; Berendse and Scheffer 2009; Brodribb and Feild 2010). This latter category of ecological dominance is the focus of our discussion.

One gymnosperm group, the conifers, remain as a major contender for canopy dominance across the globe. In this review, we determine whether generalizations about the ecology, physiology, and biogeography of this key gymnosperm

clade can explain their continued success in the face of over 100 million years of angiosperm competition. Of particular interest is the stimulating hypothesis of Bond (1989) that conifer persistence can be explained by vegetative competition in the seedling phase. By portraying conifer seedlings as slow “tortoise” regenerators compared with the fast-growing angiosperm “hare” seedlings, Bond suggested that conifers compete where angiosperms are unable to realize their maximum growth potential because of environmental limitations on photosynthesis and growth. Abiotic stress thus reduces the growth of angiosperm seedlings to similar rates as those of conifers, which are intrinsically constrained by inferior water transport in wood and leaves. Here we explore the evolutionary history of conifers, highlighting the distinct nature of Podocarpaceae and Pinaceae in the Southern and Northern Hemispheres, respectively. The contrasting history and ecology of these key conifer families raises questions about the concept of a predictable rule for conifer–angiosperm competition. In an attempt to reconcile the observed diversity in conifer biogeography with the functional characterization of conifers, we reexamine key aspects of conifer physiological and trait evolution, seeking general principles that may be used to define global conifer ecology. We conclude that, although many conifer species have conservative traits that enable persistence in stressed environments, others are successful pioneers of disturbed habitats. This allows modern conifers to escape head-on competition for light with broad-leaved angiosperms and to occupy a much broader range of habitats than is included in Bond’s hypothesis. We emphasize that different lineages of conifers (specifically the Cupressaceae, Podocarpaceae, and Pinaceae) are distinct in the environmental stressors they tolerate, giving rise to distinct biogeographic distributions of these clades.

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History and Biogeography of Conifer–Angiosperm Competition

Traditionally, the evolution of angiosperms has been portrayed as a dire competitive challenge for many Mesozoic plant groups, including conifers (Krassilov 1978; Knoll 1984). However, the degree to which angiosperm radiation resulted in conifer extinction and displacement is a matter of debate. Here we examine the three largest living conifer families to determine whether the ecology of extant conifers supports a general functional limitation argument whereby conifers are disadvantaged relative to angiosperms (Bond 1989). As a pre-text to this discussion, it is important to note that the general concept of angiosperm superiority over conifers is not borne out by an examination of contemporary forest cover worldwide. The living conifers are a very successful group, and few angiosperm families could compete with the largest conifer families for biomass or productivity. The only woody plant biome that appears to be generally hostile to conifers is lowland equatorial rain forest, where very high productivity and competition for light creates a bias for large and highly photosynthetic leaves with low leaf mass per unit area (Brodribb and Hill 1997), characteristics that are absent from any conifer taxon (Wright et al. 2004). Forests at higher latitudes and altitudes typically contain mixtures of conifers and angiosperms, and the division of conifer taxa among these regions is well structured, providing useful information about the history of evolutionary competition between these two groups.

Perhaps the most challenging aspect in characterizing conifer–angiosperm competition is the highly distinct nature of the two most successful conifer families, Podocarpaceae and Pinaceae. The result of this familial differentiation on the global biogeography of conifers is profound because it produces a taxonomic and ecological split between the Northern and Southern Hemispheres. Conifers in the Northern Hemisphere are highly successful in regions subject to seasonal freezing, while in the milder oceanic Southern Hemisphere, freezing conditions are less prevalent and conifers are much patchier in distribution but reach their highest diversity in wet tropical forests. This pattern derives largely from the contrasting distributions and ecologies of the two largest conifer families, Pinaceae and Podocarpaceae, but similar biases are evident in Araucariaceae and Taxaceae. In fact, Cupressaceae is the only family that is evenly distributed between the hemispheres (fig. 1). Biogeographical zonation seems to have characterized the distribution of several conifer families as far back as the Mesozoic, with Pinaceae (Millar 1998) and Podocarpaceae (Hill and Brodribb 1999) fossils almost always being restricted to within the extant range of the families and the extinct Cheirolepidiaceae inhabiting low latitudes (Alvin 1982). Other conifer families appear to have been more cosmopolitan in the past, with Araucariaceae distributed globally (Stockey 1994) and Northern Hemisphere Cupressaceae such as *Sequoia* found in the early Cenozoic in Australia (Peters and Christophel 1978).

Pinaceae Domination of the Northern Hemisphere

Pinaceae are the most successful of all conifers; curiously, however, this success is restricted (with the exception of one species) to the Northern Hemisphere. The northern bias of

the family is repeated in the fossil record, with no fossil Pinaceae having ever been identified south of the equator. Analysis of fossil deposits throughout the Northern Hemisphere (Mirov 1967; Rothwell et al. 2012) and molecular evidence (He et al. 2012) suggest an Early to Middle Mesozoic origin of Pinaceae at high northern latitudes and of *Pinus* at middle northern latitudes (Millar 1998). Although extant Pinaceae forests extend from the Arctic Circle to the tropics, the diversity of Pinaceae today remains highest at the middle latitudes. The strongest climatic correlate is the distribution of most modern Pinaceae species in habitats subject to freezing (Farjon 2010). Not only is the association between the distribution of Pinaceae and cool temperatures strong in extant species, there is evidence that this may have been a feature of the family throughout its evolution. Indeed, the fluctuating fortunes of Pinaceae appear to have been much better correlated with temperature than other phenomena throughout the past 100 million years, including the radiation of angiosperms. Fossils of *Pinus* are rare or globally absent during warm periods in the Paleocene and Eocene, while cooler periods are characterized by an abundance of *Pinus* fossils at middle latitudes (Millar 1993). Migration of pines between high and middle latitudes is a recurrent theme during the climate oscillations of the Neogene, with Pinaceae apparently contracting toward the Arctic during warm periods and moving southward under cooler conditions (Mirov 1967; Millar 1998).

As discussed in detail below, the wood of conifers is well suited to freezing because the small size of its conduits prevents freeze-thaw embolism. This, combined with a photosynthetic physiology that is well adapted to downregulation during freezing (Ottander and Öquist 1991), raises the possibility that Pinaceae have always occupied forests prone to freezing. It is therefore conceivable that angiosperm evolution may have had little effect on the Pinaceae niche and this conifer family has maintained or increased its importance as freezing climates extended to lower latitudes during the latter half of the Cenozoic. It is difficult to directly assess the impact of angiosperm evolution on Pinaceae, because angiosperms radiated at a time when temperature and humidity at middle latitudes were high and hence the distribution of Pinaceae was minimal (Millar 1998). However, the paradigm of angiosperm domination does not really apply to contemporary forest cover in most of the land masses of the Northern Hemisphere. Indeed, it seems that since the inception of Pleistocene glacial cycles, the Pinaceae have been aggressive competitors capable of dominating entire regions such as the boreal zone, often to the exclusion of angiosperm trees. Two factors appear to be closely linked to the success of Pinaceae. First, their tracheid-bearing vascular system is highly resistant to freeze-thaw embolism (see below). Second, in *Pinus* in particular, photosynthetically efficient needle leaves can produce maximum photosynthetic rates that are equivalent to or greater than those of associated angiosperm trees (Turnbull et al. 1998; Brodribb and Feild 2008), and low wood density enables fast-volume growth rates under high-light conditions (Becker 2000). In this way, the classic *Pinus* pioneer ecology largely seems to defy the analogy of Bond (1989) that conifer seedling growth was tortoise-like compared with that of the hare-like angiosperms. Indeed, considering the rapid dispersal of Pinaceae into postglacial landscapes across the Northern

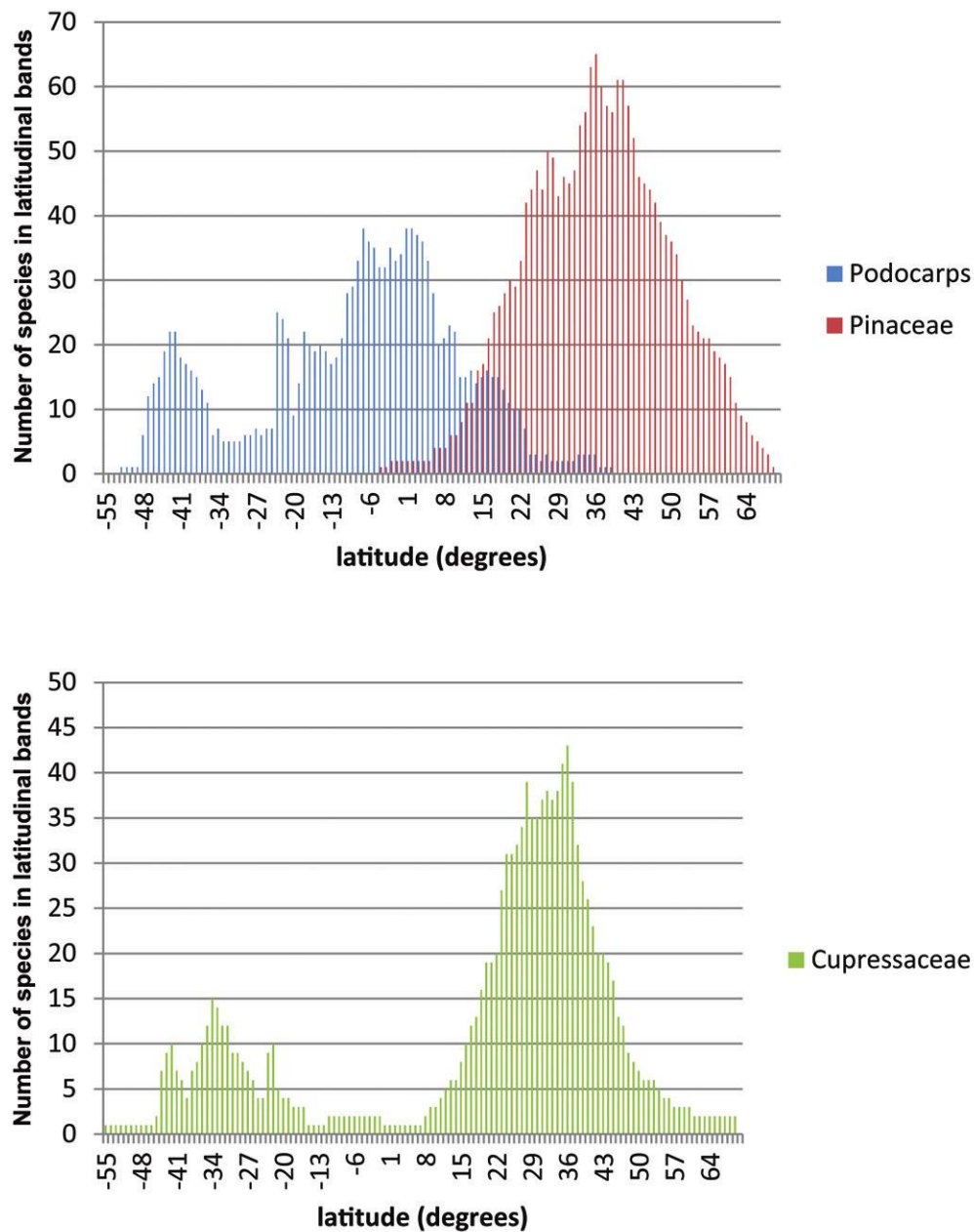


Fig. 1 Frequency distribution plots of the three major conifer families from Arctic to Antarctic latitudes. Podocarps and Pinaceae show strong latitudinal differentiation, while Cupressaceae are successful in both hemispheres. The peak diversity of Podocarpaceae at equatorial latitudes contrasts strongly with the pattern in both Cupressaceae and Pinaceae.

Hemisphere, conifers do seem to be more deserving of the “hare” title (Gear and Huntley 1991).

Within the broad environmental envelope established by winter cold, local abundance of Pinaceae is strongly influenced by nutrient cycling. Pinaceae dominate boreal and montane regions of the Northern Hemisphere, where low temperatures and slow decomposition hamper recycling of organic nitrogen by the soil microbial community. Pines in cool and warm temperate regions often attain the greatest abundance on sandy or shallow soils (Richardson and Run-

del 1998), although the link between soil type and conifer abundance may be blurred by disturbance history, which also has strong influences on local abundance patterns (Becker 2000). Pinaceae are associated with poor soils because their needles live longer than the leaves of co-occurring angiosperm trees, reducing the flux of nutrients to the decomposer community via litterfall and increasing the trees’ nutrient use efficiency. Deciduousness is effective in preventing damage to temperate angiosperm trees over the cold winter months, but at higher latitudes where winter conditions are much harsher

it is evergreen conifers that dominate; this indicates the critical role of mineral nutrition alongside winter cold in giving conifers a competitive advantage in boreal regions.

Pinaceae diversity reaches a maximum at temperate latitudes, although it is also significant in the northern tropics, including in China and Mexico, where this family is common at altitudes subject to freezing or fire (Agee 1998; Farjon 1996). With a few exceptions (*Pinus canariensis* and *Pinus caribaea*), Pinaceae are not capable of growing at low altitudes in the tropics; their diversity drops very quickly when moving from the Tropic of Cancer to the equator, with only one species (*Pinus merkusii* in Sumatra) recorded in natural forest in the Southern Hemisphere. The rapid decline in the success of Pinaceae at low latitudes has been attributed to the absence of freezing habitats and high rainfall close to the equator. Without fire disturbances to open the canopy, Pinaceae needles are ineffective at tolerating the deep shade cast by angiosperms (Brodribb and Feild 2008). Leaves of Pinaceae are characteristically needle shaped and hence rather inefficient at harvesting light of low intensity because of both their relatively high leaf mass per unit area (Reich et al. 2007) and self-shading (Leverenz and Hinckley 1990). Hence, the Pinaceae needle leaf morphology is not likely to be competitive with the fast-growing angiosperms producing large, thin leaves in the tropics. In this respect, it is interesting to note that of the few Pinaceae species living close to the equator in Vietnam, several (e.g., *Keteleeria* and *Pinus krempfii*) have flattened leaves that enable them to grow in the understory of angiosperm-dominated forests (Brodribb and Feild 2008). However, the anatomical adaptations linked to leaf flattening in these species render these leaves less sophisticated and less efficient than the multivein leaves of angiosperms or the flattened leaves in many of the Podocarpaceae genera that inhabit the tropics (see below).

One common ecological attribute of modern Pinaceae, and of *Pinus* in particular, is the capacity to regenerate as pioneers after fires, which is related to their light-demanding needle leaf morphology. In sharp contrast, the Podocarpaceae are typically very fire sensitive, with the notable exception of *Podocarpus drouynianus* in Australia (Chalwell and Ladd 2005). Many species of Pinaceae develop thick bark that protects trees from low-intensity ground fires; *Pinus* species in particular appear to use fire as a means of escaping competition with angiosperms for long enough to complete their life cycles (see below). Given the apparent abundance of fire-prone vegetation in the Southern Hemisphere, the absence of Pinaceae here is rather enigmatic, particularly considering the successful northward movement of Podocarpaceae from the Southern Hemisphere into Asia and Central America (Morley 2011). It is possible that the absence of Pinaceae in the Southern Hemisphere is linked to the much more limited existence of conditions below the tree line where freezing is common. Climatic differences between hemispheres are borne out by much lower minimum temperatures at the tree line in the Northern Hemisphere compared with the south. These differences are highly significant, because evergreen angiosperms often dominate the tree line in mountains in the Southern Hemisphere, where they possess small-diameter xylem vessels that are resistant to moderate, low-frequency freezing events (Feild and Brodribb 2001). By contrast, even at sea

level in the middle to high latitudes of the Northern Hemisphere, plants are exposed to a high frequency of cold events that are sufficiently harsh to freeze xylem sap in tree trunks. This provides a significant advantage to Pinaceae with their small, freeze-thaw-resistant tracheids (Sperry et al. 1994). It is noteworthy that Pinaceae species have become invasive above the tree line in some parts of South America and New Zealand (Wardle 1985). This suggests that there exists potential for Pinaceae to colonize some alpine zones in the Southern Hemisphere, although climate analysis suggests that there is only a narrow “vacant altitudinal belt” for introduced Pinaceae (Jobbagy and Jackson 2000).

It is unclear why Pinaceae species have not been able to disperse through Central America and Southeast Asia into the Southern Hemisphere alpine zone over the past 5 million years, when Northern and Southern Hemisphere landmasses came into contact. However, there is evidence that the Cenozoic proliferation of angiosperms in the equatorial zone led to the creation of a highly productive and deeply shaded rain forest belt (Boyce et al. 2010) that is hostile to typical needle-leaved, shade-intolerant Pinaceae. Given the relatively recent connections between northern and southern landmasses in the Americas and Southeast Asia, it is possible that Cenozoic development of an angiosperm equatorial forest created a barrier to Pinaceae penetration into the Southern Hemisphere (Brodribb and Feild 2008). Another possible limitation for southward-bound Pinaceae is the absence of suitable fungal symbionts in the Southern Hemisphere. Many species of Pinaceae have become invasive in temperate regions of the Southern Hemisphere (Richardson and Rejmánek 2004), having spread from forestry block, but plantations were unsuccessful until suitable ectomycorrhizal fungi were introduced from these species’ home ranges (Pringle et al. 2009). Indeed, the mycorrhizal fungi associated with invasive *Pinus contorta* in New Zealand are all nonnative or cosmopolitan species, with no evidence of novel associations with native mutualists (Dickie et al. 2010), emphasizing the reliance of pines on coinvasion by mutualists.

Podocarpaceae Evolution in the Tropics

Podocarps are diverse and widespread in the Southern Hemisphere but, despite being the most successful conifer family there, they are rarely dominant at a regional level in the way Pinaceae forests are in the Northern Hemisphere. Podocarps exhibit an enormous morphological diversity, but ecologically they are almost always restricted to rain forest communities, where they coexist with angiosperms. Despite a wood density that is relatively high for conifers (Pittermann et al. 2006a), the water transport system of podocarps is vulnerable to water stress-induced embolism, causing a family-wide drought sensitivity (see above). As a result, podocarps are absent from the type of dry forest communities in which Pinaceae and Cupressaceae often thrive. However, a combination of significant shade tolerance and longevity appears to allow podocarps to compete successfully with angiosperms, particularly where low temperatures or nutrients restrict angiosperm productivity. In total, about three-quarters of all podocarp species predominate on soils that are either shallow, waterlogged, sandy, high altitude, or derived from ultramafic rocks rich in plant-toxic ele-

ments (Coomes and Bellingham 2011). Efficient nutrient use in podocarps is evidenced by typically long leaf life spans compared with those of angiosperm associates in temperate rain forests (Lusk 2001; Coomes and Bellingham 2011).

Podocarps and Pinaceae express different nutrient associations, with the former often associated with old lowland soils with a phosphorus deficit while Pinaceae are very successful in the nitrogen-limited soils of high altitudes and latitudes. This distinction may be linked to differing mycorrhizal associations. Pinaceae tend to be ectomycorrhizal, with fungal symbionts capable of extracting nitrogen directly from organic matter, whereas Podocarpaceae are arbuscular mycorrhizal, with fungi associates from a basal group, Glomales, that lack the capacity to break down organic matter but that are effective at capturing phosphate from soils (Brundrett 2002; Smith and Read 2008). Thus, it may well be that Southern Hemisphere conifer species are better suited to growing on phosphorus-depleted soils. In New Zealand, for instance, tall podocarps are prevalent in lowland rain forests, while ectomycorrhizal angiosperms (in Nothofagaceae) dominate over much of the Southern Alps (Wardle 1984). Interestingly, the ectomycorrhizal Douglas fir is starting to invade *Nothofagus* forests in the mountains of New Zealand and is showing signs of becoming a formidable competitor against the dominant native tree (Dickie et al. 2010). The types of mycorrhizal fungi that are prevalent in a region depend on whether the nitrogen or the phosphorus supply is most threatening plant fitness (Read and Perez-Moreno 2003). There is virtually no nitrogen in mineral soil, so the supply of this element to roots is dictated by rates of litter decomposition and nitrogen fixation by microbes. Decomposition of organic matter is slow in regions with low mean annual temperatures, resulting in limited nitrogen supply for plants growing in tundra, taiga, and boreal ecosystems and in tropical and temperate mountains (Aerts and Chapin 2000). Under these conditions, ectomycorrhizal (alongside ericoid) associations often dominate, because the fungi are physiologically capable of extracting nitrogen directly from organic matter in the litter and upper soil layers. Many ectomycorrhizal fungi produce extracellular enzymes capable of degrading structural materials within detritus, enabling them to attack nutrient-containing polymers with diffusible proteinase enzymes (Read et al. 1989). The hyphae take up short-chain organic nitrogen produced by proteinases as well as NH_4^+ mineralized by generalist saprotrophs. The situation in lowland temperate and tropical rain forests is quite different: detritus is decomposed rapidly, releasing nitrogen to plants in the process, while phosphorus is bound in aluminium sesquioxide complexes and leached from soils by heavy rainfall. Arbuscular mycorrhizal fungi dominate in most tropical rain forests.

The most striking contrast between Pinaceae and Podocarpaceae emerges in the tropics, where podocarp diversity reaches a maximum and can occur anywhere from sea level up to the tree line. Their abundance in tropical regions means that podocarps compete directly with angiosperms in tropical rain forests (fig. 2), and there is strong evidence that a history of competition with broad-leaf angiosperms has had a major impact on the adaptive morphology and function of podocarps. Reconstructions of the morphological evolution of podocarp shoots show that, coincident with the angiosperm

radiation of the Late Cretaceous–Early Cenozoic period, there was a rise in the diversification rate of Podocarpaceae with broadly flattened leaves and shoots (Biffin et al. 2012). These multiple independent origins of shoot flattening are generally associated with the development of water-conducting tracheids lying outside the midrib xylem that provide radial water transport from the midrib to the leaf margin (Griffith 1957; Brodribb and Holbrook 2005). This efficient alternative to the angiosperm reticulate-vein leaf enables single-veined podocarp “needles” to achieve widths of >30 mm (fig. 2), which greatly enhances the efficiency of light harvesting and shade tolerance in these topical podocarps (Brodribb and Hill 1999). During angiosperm diversification, the rate of speciation of imbricate podocarp species with lower light-use efficiency declined (Biffin et al. 2012), and this supports the idea that shoot flattening in podocarps was a response to angiosperm competition for light. One interpretation of these observations is that the invasion of broad-leaf angiosperms into the tropics caused a change in the ecology and climate of the equatorial belt (Boyce et al. 2010), increasing rainfall and hence the competition for light in the understory. As a result, narrow- and imbricate-leaved conifers seem to have been subsequently replaced by podocarps with large, flat photosynthetic structures capable of efficient light harvesting. Other conifers such as Taxaceae (*Amentotaxus*, *Austrotaxus*, and *Cephalotaxus*) and Araucariaceae have also enjoyed some success competing with broad-leaf angiosperms by producing large, flattened leaves. However, no tropical conifer group comes close to the diversity of flattened morphologies or the competitive success of tropical Podocarpaceae.

An ability to coexist with angiosperms in evergreen broad-leaf forest enables Podocarpaceae to extend into the northern tropics, but similar to Pinaceae at the equator, Podocarpaceae success drops off rapidly north of the Tropic of Cancer. Reasons for this northward limit may include a combination of declining rain forest environments due to reduced rainfall north of 20°N latitude and a rapid increase in freezing exposure, to which Pinaceae appear to be better adapted (Sakai and Wardle 1978). Possibly because of the specialized leaf anatomy in podocarps (an abundance of sclereids; Brodribb 2011) or a sensitivity to drought (also significant under freezing conditions), Pinaceae are likely to outcompete podocarps in environments where freezing creates opportunities for Pinaceae to succeed. Dispersal rates could also limit the success of transhemispheric colonization of both Pinaceae and Podocarpaceae. However, in the light of evidence demonstrating very rapid dispersal in Pinaceae (Huntley and Webb 1989) and long-distance dispersal of podocarps between Pacific islands, it seems that an ecological rather than vicariance explanation is more likely to account for latitudinal distributional limits of both conifer families.

Global Cupressaceae

The third-largest conifer family, Cupressaceae, provides an interesting comparison with Pinaceae and Podocarpaceae because it exhibits a panglobal distribution. In the Northern Hemisphere, Cupressaceae show a similar latitudinal distribution to Pinaceae, with maximum diversity between 30° and 40°N and a rapid decline to only a few species in equa-



Fig. 2 Podocarps *Phyllocladus hypophyllus* in Papua New Guinea (*top*) and *Podocarpus dispersis* in tropical northern Australia (*bottom*). Both compete successfully with broad-leaf angiosperms in the understories of tropical rain forests, and both have divergent mechanisms for leaf and shoot flattening that lead to the production of broad photosynthetic structures reminiscent of angiosperm leaves.

torial regions. South of the equator, diversity rises again to a peak at a latitude of $\sim 35^{\circ}\text{S}$, equivalent to that in the dry latitudes, where podocarp diversity falls to its lowest level in this hemisphere. In both hemispheres, Cupressaceae adopt a similar strategy whereby they coexist with Pinaceae or

Podocarpaceae in cool, wet environments but also have the capacity to survive in very dry areas, where the efficient water transport capacity of angiosperms is limited by regular exposure to extreme water stress (Willson et al. 2008; Brodribb et al. 2010; Pittermann et al. 2010). Cupressaceae

exhibit an extremely large range of xylem tolerance to water tension, from swamp-dwelling species that are highly vulnerable (e.g., *Taxodium*) to arid-zone species with the most water-stress-resistant xylem yet measured, *Juniperus* in the Northern Hemisphere (Willson et al. 2008) and *Callitris* in the Southern Hemisphere (Brodrribb et al. 2010). Diversity in xylem cavitation resistance appears to be an important adaptive tool for Cupressaceae, and one that is likely to have contributed to the success of the family in both hemispheres. It should be noted that there are distinct north–south divisions in the phylogeny of Cupressaceae after the divergence of the old Taxodiaceae groups (Gadek et al. 2000). Interestingly, within both of these subdivisions (Callitroideae in the Southern Hemisphere and Cupressoideae in the Northern Hemisphere) there are multiple origins of extreme drought tolerance, indicating that this capacity has favored diversification of these clades but that extreme drought tolerance is not the ancestral condition (Pittermann et al. 2012). Presumably, the higher cost associated with producing cavitation-resistant wood in angiosperms (see above) prevents this group from competing effectively with conifers in dry habitats, particularly where dryness and cold are combined. The resultant domination of dry habitats by *Juniperus* and *Cupressus* in the Northern Hemisphere and *Callitris* and *Widdringtonia* in the Southern Hemisphere is tempered only by intense fire, which greatly impedes the success of these species in most cases.

The preceding discussion paints a rather diverse picture of conifer evolution, with major families following relatively distinct evolutionary pathways. This apparent functional diversity seems to defy a reductionist principle for predicting the outcome of conifer–angiosperm competition, such as that proposed by Bond (1989). However, an examination of the general physiology of conifers suggests that the functional amplitude of conifers is small compared with that of angiosperms and that there is potential to explain the familial diversity of interactions between conifers and angiosperms in terms of generalities. In the following section, we review key aspects of conifer function, including water transport.

General Functional Attributes of Conifers

William Bond was the first to link conifer and angiosperm biogeography and evolutionary strategy with xylem function, and his ideas have had a profound influence on comparative plant ecophysiology. When commenting on the dominance of angiosperms in the tropics and conifers in the Northern Hemisphere, many have argued that enhanced transport efficiency, courtesy of large vessels and complex venation patterns, equipped the angiosperms with a physiological supremacy that is reflected in their rapid growth rates, particularly at the establishment stage, during which the less vascularized conifer seedlings simply cannot compete (Carlquist 1975; Bond 1989; Brodrribb et al. 2005a). The following section reviews recent progress in our understanding of water transport, nutrient acquisition, and photosynthesis in conifers and angiosperms, first by discussing key anatomical differences between these plant types and the climatic drivers that have acted to favor one vascular strategy over another across the world's biomes.

Hydraulic Efficiency in Conifers and Angiosperms

The main goal of xylem function is to move water from root to shoot with low resistance, thus minimizing the pressure drop associated with gravity and friction (Sperry 2003; McCulloh et al. 2010). A secondary requirement is canopy support. Hence, the combined needs of transport efficiency and support selected for a variety of secondary growth patterns, of which only the tracheid-based conifer and vessel-fiber-based angiosperm models remain common (Spicer and Groover 2010). Conifers move water by means of xylem composed entirely of tracheids: dead, hollow, overlapping single cells rarely exceeding 2 mm in length. By contrast, the more derived angiosperm xylem relies on vessels: multicellular tubes composed of dead and hollow vessel elements stacked to create pipes that can reach several meters in length and up to 500 μm in width. Vessels can be distributed in a ring or a diffuse-porous pattern and are embedded in a matrix of fibers, making them less abundant per unit area than tracheids (Ewers et al. 1989; Isnard and Silk 2009; McCulloh et al. 2010).

Vessels that are wide and long are considered to be the pinnacle of hydraulic efficiency; in comparison, conifer xylem, with its narrow tracheids, should be doomed to extinction. Indeed, as early as in the Devonian, the need for low-resistance xylem selected for a 17-fold increase in tracheid diameter, from the narrow 8- μm -wide conduits of *Cooksonia* to the 140- μm -wide tracheids of the fern relative *Stenomylon* (Niklas 1985). Today, the largest conifer tracheids rarely exceed 40 μm in diameter, even in riparian species such as *Taxodium* (Pittermann et al. 2006b), and yet conduit size is critical to transport. This is because the hydraulic conductance (K ; volume flow rate standardized for the pressure gradient driving flow) of a conduit scales to the fourth power of the lumen radius, so even marginal gains in size translate to major gains in flow (Zimmermann and Tyree 2002).

Despite the size limitations imposed on tracheids, some of the tallest and oldest plants in the world, such as the coast redwood (*Sequoia sempervirens*) and the bristlecone pine (*Pinus longaeva*), are conifers. Vast regions in the Northern Hemisphere are dominated by Pinaceae, while conifers such as *Agathis*, *Fitzroya*, and *Dacrycarpus* are the largest and longest-lived species south of the equator (Enright and Hill 1995). Clearly, selection has acted on conifer xylem in a manner that compensated for its unicellular composition. In recent years, the ultrastructure of tracheids and vessels has come under close scrutiny, revealing that the movement of water from one conduit to another through interconduit pit membranes is just as important as its travel within tracheid and vessel lumens.

Pit membranes are permeable, partially digested regions of the primary conduit cell wall that are composed of cellulose and pectin polysaccharides (for details, see review by Choat et al. [2008]). In angiosperm vessels, pit membranes resemble a tightly woven fabric of microfibers with variable porosity and thickness but otherwise exhibit little structural variation (fig. 3; Jansen et al. 2009; Lens et al. 2011). By contrast, the presence of the torus and margo regions readily distinguish the conifer pit membrane from the angiosperm type. The margo is the porous, netlike region of the membrane that allows water flow between tracheids, and it supports the

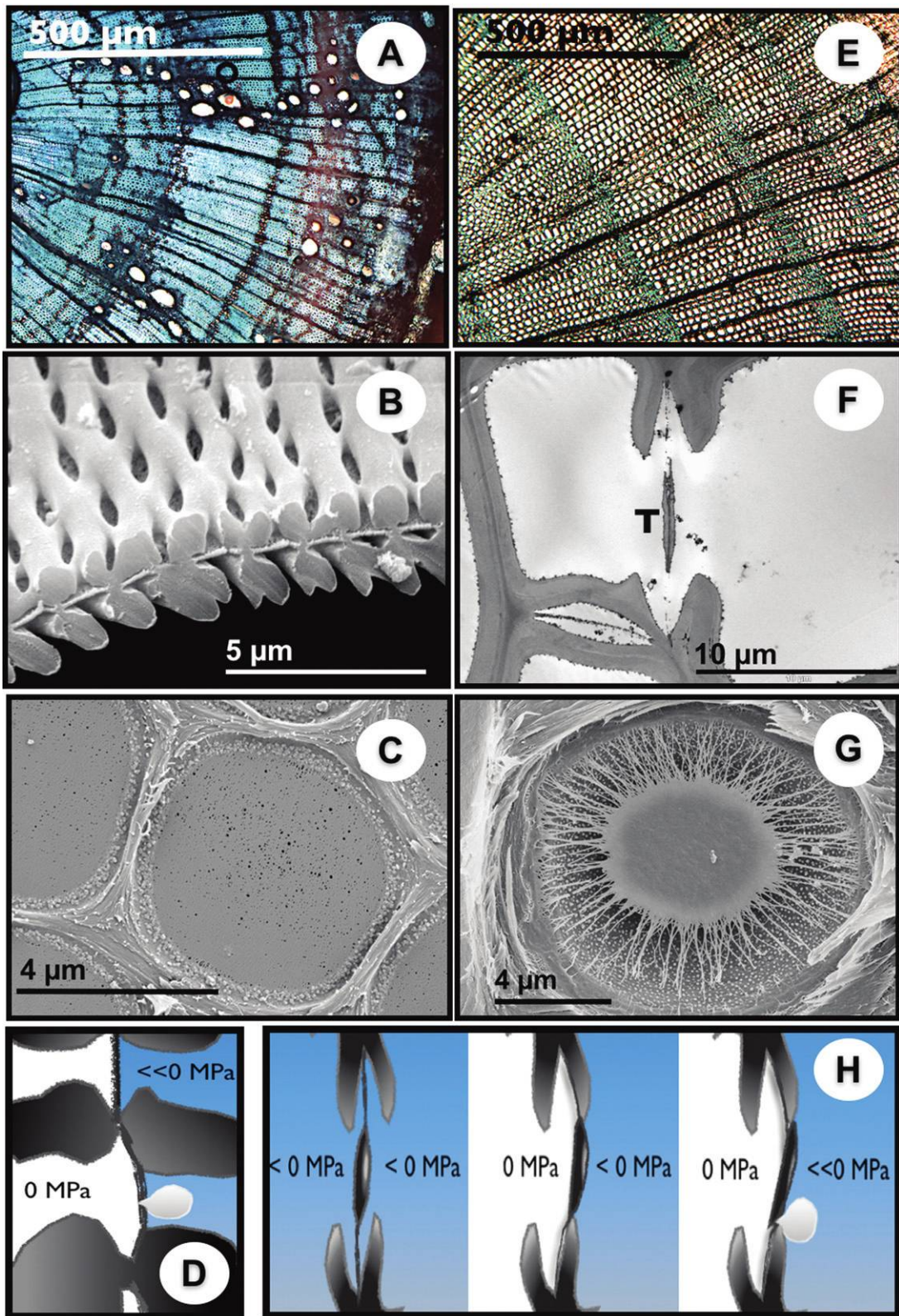


Fig. 3 Comparative anatomy of conifer and angiosperm xylem. *A*, Cross section of *Quercus agrifolia* wood stained with toluidine blue, showing large, clear vessels surrounded by thick-walled fibers. *B*, SEM micrograph of a cross section of *Betula nigra* vessel wall showing pit membranes connecting the two vessels. *C*, SEM micrograph of an exposed *Acer negundo* pit membrane with visible membrane pores (image courtesy of B. Choat). *D*, Air seeding in angiosperms (see text). *E*, Cross section of *Sequoia sempervirens* xylem stained with toluidine blue. *F*,

centrally located torus: a dense, impermeable structure that seals an air-filled tracheid from a functional, water-filled one (see below; Hacke and Jansen 2009; Delzon et al. 2010; Pittermann et al. 2010).

What explains the dimorphism of angiosperm and torus-margo pit membranes? The answer lies in the hydraulic resistance conferred by these structures and its effect on xylem sap flow in unicellular versus vessel-based xylem. On a pit area basis, the resistance (inverse of conductance) of the torus-margo pit membrane is on average $5.7 \pm 1.3 \text{ MPa s m}^{-1}$, nearly one-sixtieth that of the angiosperm pit membrane ($336 \pm 81 \text{ MPa s m}^{-1}$; Pittermann et al. 2005). On a sapwood area basis, this means that conifers and angiosperms with equivalent mean conduit diameters can exhibit comparable hydraulic conductivity because the low hydraulic resistance offered by the porous margo region of the conifer pit membrane compensates for the shorter length of the conifer tracheids and the more frequent tracheid-to-tracheid crossings (Pittermann et al. 2005; Sperry et al. 2006). Indeed, in the absence of torus-margo pitting, tracheid-based xylem resistivity is predicted to increase 38-fold, on account of passage through the much less porous, homogenous pit membranes.

The torus-margo pit membrane thus confers a tremendous hydraulic advantage to long-distance transport in an otherwise ancestral, tracheid-based vascular system that may have constrained the physiological development of ferns, basal angiosperms, and cycads as well as extinct tracheid-based flora with secondary xylem (Sperry 2003; Pittermann 2010; Wilson and Knoll 2010; Pittermann et al. 2011). Given the high frictional resistance associated with both short conduits and homogenous pit membranes, it is unlikely that conifers could compete with angiosperms in northern temperate habitats or reach their spectacular heights without torus and margo pitting (Koch et al. 2004; Pittermann et al. 2005; Burgess et al. 2006; Domec et al. 2008).

Research over the past decade has shown that the gap in hydraulic aptitude between conifers and angiosperms has narrowed, but it is important to emphasize that not even high pit membrane conductance can compensate for the developmental and hydraulic limits imposed on conifer tracheid dimensions. Indeed, the evolution of long and wide vessels allowed the angiosperms to explore peaks in hydraulic conductivities that are unmatched by conifers. For example, lianas and vines are regarded as paragons of hydraulic efficiency by virtue of their exceptionally large vessels, which allow these climbers to transport water over 100 times more efficiently than gymnosperms (Zimmermann and Tyree 2002). By relying on plants and other external structures for support, climbing angiosperms minimize investment in nonconductive xylem tissue such as fibers and thus maximize transport with large conduits that are structurally irrelevant though hydraulically

efficient (see below). Presumably, it is the canalized developmental pattern of homoxylous wood that precluded the evolution of viny conifers (with broad, innervated leaves) and thus set a low upper limit on the hydraulic capacity of conifer xylem. Gnetales, a vessel-bearing gymnosperm lineage, is the exception that proves the rule, because several species in the genus *Gnetum* have evolved lianescence (Feild and Balun 2008). However, the hydraulic capacity of these plants is, on average, one-fifth that of angiosperm vines.

Trade-Offs Associated with Drought Stress Resistance in Conifer and Angiosperm Xylem

Depending on their habitat, terrestrial plants may experience water deficit on a daily basis. Drought stress can cause air to enter the xylem; if a large proportion of xylem conduits contain air rather than water, hydraulic transport is significantly impeded. Not surprisingly, plants have evolved ways to increase the drought-stress tolerance of their xylem tissue, but such resilience typically requires a sacrifice in the economy or efficiency of other vascular traits. The following section examines the hydraulic and construction costs associated with cavitation resistance, focusing on these trade-offs first at the pit membrane level and then the xylem tissue level in both conifers and angiosperms.

Aside from facilitating water transport throughout the xylem, pit membranes function to isolate functional, water-filled conduits from those that are filled with air (fig. 3). Because water moves through a plant in a state of negative potential or tension, the water column is vulnerable to the entry of air (cavitation). Air-filled or embolized conduits cannot conduct water and so, unless the conduits are repaired, extensive embolism causes stomatal closure or plant death (Hubbard et al. 2001; McDowell et al. 2008). Plants may contend with drought-induced embolism on a seasonal or even a daily basis (Aranda et al. 2005; Li et al. 2007), and there is consensus that during drought stress it is the pit membranes that are the primary sites of air entry (Choat et al. 2008; Christman et al. 2009; but see Jacobsen et al. 2005 for alternative hypotheses).

In angiosperms, cavitation occurs when the pressure difference between an air-filled vessel and an adjacent water-filled vessel (ΔP_x) exceeds the meniscal strength of the largest pore in the pit membrane (ΔP_x^*) as described by the Young-Laplace equation:

$$\Delta P_x^* = \frac{2t}{r},$$

where t is the surface tension of water and r is the radius of the largest membrane pore (Cochard et al. 1992; Choat et al. 2008; Christman et al. 2009). A simple prediction would

TEM micrograph of a cross section of an *S. sempervirens* torus-margo pit membrane, where T indicates the torus. The thin strands of the margo are not visible. (Image courtesy of S. Jansen.) G, Face view of a *Sequoiadendron giganteum* torus-margo pit membrane. Water moves from one tracheid to another through the margo strands that support the torus. (Image courtesy of B. Choat.) H, The function of the torus-margo pit membrane. When tracheids on both sides of the membrane are water filled, the pit membrane remains in a neutral position (*left*). Should one tracheid become air filled, the pit membrane is pulled against the pit aperture in the direction of the functional conduit (*center*). Air seeding occurs when the xylem pressure in the water-filled conduit exceeds the mechanical strength of the pit membrane and the torus slips from its sealing position, allowing air to enter the functional conduit and creating an embolism.

be that angiosperms with larger membrane pore diameters should be more vulnerable to cavitation by air seeding; yet, this idea has received mixed empirical support depending on the species examined and the experimental approach used. The “rare pore” or “pit area” hypothesis first proposed by Wheeler et al. (2005) argued that the probability of air seeding increases with pit area, because a greater pit area is more likely to give rise to a large pore: the weak link that renders the xylem vulnerable to air seeding. Support for this has been found across a broad sampling of angiosperms (Hacke et al. 2006, 2007; Hacke and Jansen 2009). However, more targeted work on *Acer* species with variable cavitation resistance has revealed that vulnerability to air seeding is closely related to pit membrane thickness and porosity rather than pit membrane quantity (Christman et al. 2009; Lens et al. 2011; see also Hacke and Jansen 2009; Jansen et al. 2009). In general, it appears that both pit membrane anatomy and abundance contribute to cavitation resistance in angiosperms, although the relative importance of these traits across different angiosperm lineages remains unclear.

The conifer pit membrane also protects against the spread of air, but it functions differently. A water-filled tracheid is isolated from an embolized one by an aspirated pit membrane, whereby the torus seals over the pit aperture, thereby preventing the spread of air (Sperry and Tyree 1990; Choat et al. 2008; Cochard et al. 2009). The bulk of the evidence suggests that cavitation occurs when the torus is displaced from its sealing position because of negative xylem pressure (Sperry and Tyree 1990; Delzon et al. 2010). Consistent with this hypothesis, pit membranes in cavitation-resistant conifer xylem exhibit a high degree of torus–aperture overlap, a trend driven primarily by a reduction in pit aperture diameter in Cupressaceae and Pinaceae (Domec et al. 2008; Hacke and Jansen 2009; Pittermann et al. 2010). Interestingly, torus thickness increases with greater cavitation resistance in Cupressaceae but not in Pinaceae, which suggests that torus flexibility may also contribute to effective sealing (Hacke and Jansen 2009; Pittermann et al. 2010). Pit membranes in other important families such as Podocarpaceae and Araucariaceae have not been scrutinized to the same level of anatomical detail, but a broad survey by Delzon et al. (2010) suggests that the presence of greater torus–aperture overlap in cavitation-resistant conifers is a conserved trait.

Broadly speaking, can we say that the torus-margo membrane is superior to the angiosperm type? Cavitation resistance is under strong selection in woody plants, and on the whole, conifers and angiosperms show an equivalent range of cavitation resistance, indicating that homogenous and torus-margo pit membranes are equally functional in preventing air seeding (Pittermann et al. 2005). Angiosperm pit membranes persist despite their high hydraulic resistance, which suggests that they may confer important although less obvious functional advantages. For example, homogenous pit membranes may be an asset in angiosperms that routinely refill their embolized vessels, such as grapevine (Sperry et al. 1987; Brodersen et al. 2010), bay laurel, and rice (Hacke and Sperry 2003; Salleo et al. 2004; Stiller et al. 2005). These membranes potentially resist mechanical damage caused by air seeding (cavitation fatigue) and simultaneously serve to isolate conduits undergoing active refilling from those that are functional

and under tension (Hacke et al. 2001; Zwieniecki and Holbrook 2009). By contrast, it appears that once the conifer torus-margo pit membrane is aspirated and displaced from the aperture, stretching and mechanical damage of the margo strands cannot be repaired and the associated tracheids remain dysfunctional (Sperry and Tyree 1990). Recent evidence indicates that when they are exposed to mildly negative pressures, conifer tracheids may exhibit a mechanism for embolism repair (McCulloh et al. 2010), suggesting that membranes stretched within their elastic limits may spring back to their original functional position, not unlike the “strong and flexible” membranes first described by Hacke et al. (2004).

Characterizing the carbon investment and hydraulic costs associated with cavitation resistance at the xylem tissue level is straightforward in conifers but less so in angiosperms. Hence, a basic comparison of xylem-level structural differences between these wood types is a useful starting point. Angiosperms exploit a larger range of life-history strategies and have evolved more complex xylem structures associated, for example, with the climbing habit and ring- and diffuse-porous wood. At a minimum, it is the fiber- and vessel-based structure of angiosperm xylem that represents a derived and highly adaptive departure from the ancestral unicellular, tracheid-based xylem of conifers. This is because the two different cell types allow for a division of labor whereby fibers serve in a biomechanical capacity, supporting the shoot, whereas vessels evolved to function solely for the purpose of water transport. By contrast, conifer tracheids perform tasks of water transport as well as canopy support. Because angiosperm fibers are single celled and narrow and occupy a higher fraction of the xylem than vessels, they represent a substantially greater carbon investment relative to the conifers’ tracheid-based xylem. Indeed, average wood densities in northern temperate angiosperms can be over 40% greater in angiosperms (hardwoods) than in conifers (Hacke et al. 2001). It is not unlikely that the “cheaper” xylem of conifers, in combination with their evergreen habit, may explain why conifers succeed in habitats with low resource availability, where selection favors more economically conservative life-history strategies (Bond 1989; Hacke et al. 2001; Wright et al. 2004; Coomes et al. 2005). The degree to which cavitation resistance reinforces these structural costs is a function of a species’s habitat.

In conifers and angiosperms, drought-induced cavitation resistance is correlated with minimum seasonal water potential or rainfall (Brodribb and Hill 1998; Pockman and Sperry 2000; Blackman et al. 2010), meaning that woody plants are only as resistant as they need to be. This is because drought resistance is associated with xylem-level costs, which arise from the need for conduits to be sufficiently fortified to transport water under varying degrees of negative pressure; without this fortification, conduits collapse under tension (Cochard et al. 2004; Brodribb and Holbrook 2005). Specifically, xylem conduits must withstand implosion from the tension-induced bending stresses imposed on cell walls. This implosion resistance is characterized by the ratio of conduit double-wall thickness to lumen diameter $(t/D)_h^2$, with cavitation-resistant species exhibiting conduits with higher thickness-to-diameter ratios (Hacke et al. 2001; Jacobsen et al. 2007; Hacke and Jansen 2009).

In cavitation-resistant conifers, increased $(t/D)_h^2$ ratios are a function of reduced tracheid diameter (D) rather than a dramatic thickening of tracheid secondary walls (Pittermann et al. 2006a; Sperry et al. 2006). Functionally, this reduction in conduit size increases redundancy and pathway potential during drought stress (McCulloh et al. 2010), but it also translates to lower transport rates in drought-resistant conifers, an important cost of cavitation resistance (Pittermann et al. 2006a). Finally, these tracheid-level adjustments also mean that drought-resistant conifers exhibit a higher fraction of wall material relative to mesic species, and so cavitation resistance in northern temperate conifers is necessarily associated with higher wood densities (Hacke et al. 2001; Pittermann et al. 2006a; McCulloh et al. 2010).

Cavitation-resistant angiosperm xylem also exhibits greater wood density and thickness-to-span ratios, as well as reduced hydraulic efficiency, but the functional links between conduit-scale adjustments are more complex here than in conifers (Hacke et al. 2001, 2006; Jacobsen et al. 2007). For example, drought-resistant angiosperms typically exhibit reduced vessel lengths and diameters (Hargrave et al. 1994; Hacke et al. 2006; Jacobsen et al. 2007), probably because smaller conduit size is coupled with a reduced total pit area and thus an increased cavitation safety (Wheeler et al. 2005; Hacke et al. 2006; Hacke and Jansen 2009). Second, embolism is better contained in xylem composed of smaller, redundant vessels, such that transport is less impeded by the loss of several small conduits than a few large ones (Comstock and Sperry 2000; Zimmermann and Tyree 2002; Loepfe et al. 2007). Finally, the degree to which vessels cluster and contact one another relates to cavitation resistance, because conduit arrangement can directly affect air propagation through the xylem network (Zanne et al. 2006; Loepfe et al. 2007; Schenk et al. 2008; Lens et al. 2011). These structural variables are responsible for the tremendous adaptability of angiosperms with respect to water availability, but they introduce challenges to generating a simple trade-off model, as in the conifers. Additionally, it is worth noting that the fibers of drought-resistant angiosperms also exhibit adjustments in $(t/D)_h^2$ ratios, and variation in tissue composition may further affect trade-offs with respect to xylem safety and efficiency (Jacobsen et al. 2005; Poorter et al. 2010; Zanne et al. 2010).

The anatomical diversity of their xylem has allowed angiosperms to exploit a suite of life-history strategies and habitats that are significantly more diverse than those of the conifers. Indeed, hydraulic flexibility may trump hydraulic capacity if we wish to understand the evolutionary and biogeographical implications of differences in the physiology, morphology, and ecology of conifers and angiosperms. For example, highly diverse angiosperm leaf venation patterns that improve leaf conductance as well as safety in the form of redundancy further reinforce the idea that hydraulic flexibility, combined with a surge in photosynthetic capacity, growth rates, and diversification, gave the angiosperms a tremendous competitive advantage (Sack et al. 2008; Brodrribb and Feild 2010). By contrast, leaf and needle architecture in conifers is canalized, even in large-leaved members of *Agathis* and *Podocarpus* (Brodrribb et al. 2007, 2008). In the absence of developmental potential to evolve complex xylem traits and variable structural arrangements, conifers cannot exploit the physiological capacity of angiosperms and are

thus relegated to stressful habitats where angiosperms pay a competitive penalty for their more expensive xylem strategy.

The discussion above centers on safety versus efficiency trade-offs characterized in northern temperate woody plants, but Podocarpaceae and Araucariaceae conifers are an interesting exception to these so-called rules. In contrast to northern temperate Pinaceae and Cupressaceae, the stem xylem of Southern Hemisphere conifers exhibit on average 30% higher wood densities, and these bear no relationship to species' cavitation resistance, suggesting that selection has acted differently on this xylem relative to that of the northern temperate species (Pittermann et al. 2006a). Surprisingly, the xylem of these trees appears to be excessively fortified, possessing narrow tracheids and low hydraulic efficiencies despite growing in mesic habitats where prolonged drought and frost are uncommon. Even at the pit level, no relationship was observed between pit conductivity cavitation resistance, in interesting contrast to the northern temperate conifer data (Pittermann et al. 2006a, 2010; Domec et al. 2008).

Several ideas have been proposed to explain the divergent xylem strategies of the Southern Hemisphere taxa, but perhaps the most plausible hypothesis is that these plants evolved to compete for light in emergent Cretaceous angiosperm canopies. Indeed, the leaves of several Podocarpaceae and Araucariaceae resemble those of angiosperms in both size and shape, reinforcing the idea that selection acted on leaf rather than xylem traits (Hill and Brodrribb 1999). That said, the relevance of wood density to xylem traits is not only related to transport and support functions; denser wood may also serve to reduce respiration costs in long-lived species and prevent decay by microbial and fungal agents, which may be abundant in the mesic to subtropical forests where these conifers grow (Augsburger and Kelly 1984). Alternatively, there may be a relatively small cost associated with dense wood in regions with limited seasonality and thus year-round growth.

In summary, the structural and functional trade-offs associated with drought-induced cavitation resistance are similar for both conifers and angiosperms, but the presence of fibers increases those costs in angiosperm xylem relative to that of conifers. This can explain the success of shrubby rather than arborescent angiosperms in habitats with seasonal and intense water deficits, such as the Great Basin high deserts and the coastal and Mojave scrublands of Southern California (Hacke et al. 2000; Jacobsen et al. 2008). Interestingly, many such habitats also experience freezing temperatures, and the conduit features that explain resistance to drought-induced cavitation can confer traits that resist cavitation brought about by freeze-thaw cycles.

Trade-Offs Associated with Freeze-Thaw Stress in Conifers and Angiosperms

For conifers and angiosperms growing in temperate climates, freeze-thaw cycles can cause severe impediment of hydraulic function. Bond (1989) commented that freeze-thaw cavitation resistance may be related to the conifers' success at high-latitude/high-altitude habitats, but the mechanism, as well as the conifer and angiosperm strategies to cope with it, has received only modest attention when compared with the efforts aimed at understanding the drought response. It is clear that

conifers have a distinct advantage over angiosperms in their tolerance of freezing temperatures, as evidenced by their predominance in alpine and boreal ecosystems. Why evergreen angiosperms occupy cold habitats less successfully than conifers do has not been explored, but there is no a priori reason for their diminished distributions at higher elevations and higher latitudes. It may be that short growing seasons in these regions constrain total carbon uptake and wood production to a degree that selects against more costly angiosperm wood. The following discussion explores the mechanism of freeze-thaw cavitation and how resistance to freeze-thaw stress constrains transport efficiency in woody plants.

In both conifers and angiosperms, vulnerability to freeze-thaw cavitation is directly related to conduit diameter, rendering species with large conduits, such as ring-porous angiosperms and riparian conifers, vulnerable to freeze-thaw cavitation (Sperry and Sullivan 1992; Sperry et al. 1994; Davis et al. 1999; Cochard et al. 2001; Stuart et al. 2007). The classical “thaw-expansion” mechanism of freeze-thaw cavitation explains this phenomenon as follows: when xylem sap freezes, the movement of the ice crystal lattice in a centripetal direction forces gases out of solution and into a bubble that is typically located in the center of the conduit. As the conduit diameter increases, so too does the volume of air that coalesces into a bubble (Sperry and Sullivan 1992; Davis et al. 1999; Pittermann and Sperry 2006). Whether the bubble redissolves back into the sap during the thaw or expands to create an embolism depends on both the size of the bubble and the negative xylem pressure, whereby:

$$P_x^* = \frac{2t}{r} + P_b.$$

This modification of the Young-Laplace equation for spherical surfaces states that a bubble of radius r and surface tension t will expand and nucleate cavitation if the value of P_x is more negative than the value of P_x^* , the critical xylem pressure (Davis et al. 1999; Mayr and Sperry 2010). For simplicity, it is assumed that the internal pressure of the bubble (P_b) is atmospheric (or 0 MPa in relative terms). Functionally, this means that large-diameter conduits will produce larger bubbles during freezing, and these larger bubbles will nucleate cavitation at less negative P_x values as the xylem thaws.

Empirical data collected on both conifer and angiosperm xylem are consistent with this theory. They indicate that it is conduit diameter rather than volume that dictates vulnerability to freeze-thaw cavitation, and that this is in spite of any variation in conduit and pit membrane anatomy, which was previously proposed to explain conifer resistance to this stress (Davis et al. 1999; Sperry and Robson 2001; Pittermann and Sperry 2003, 2006). Specifically, species with mean conduit diameters greater than 30 μm are vulnerable even at a moderate P_x value of -0.5 MPa during thawing (Davis et al. 1999). As xylem tensions increase in magnitude during the thaw, these critical conduit diameters have been shown to decrease (Pittermann and Sperry 2006). Hence, the biophysics of freeze-thaw embolism are consistent with the dominance of conifers in high-latitude and alpine environments, where the narrow tracheids found in stems and shallow roots are resistant to freeze-thaw stress (Sperry and Sullivan 1992; Sperry et al. 1994; Feild and Brodribb 2001; Pittermann and Sperry 2003).

Hydraulic dysfunction over the winter season may also be attributed to the co-occurring effects of drought and freeze-thaw cavitation, although it is difficult to resolve how these stress events interact in situ. Indeed, almost complete losses of transport capacity have been observed in several *Pinus* species by the end of a winter season, and this cannot easily be explained on the basis of freeze-thaw cavitation alone (Mayr et al. 2003; Mayr and Charra-Vaskou 2007). Frozen soils combined with cuticular water loss can reduce P_x values such that conduits narrower than 30 μm can suffer hydraulic losses from freeze-thaw cavitation, but drought stress may also occur when some parts of the plant remain frozen while others transpire (Hadley and Smith 1983; Grace 1990; Mayr et al. 2003). Despite extensive embolism over the winter season, conifers do recover full hydraulic conductivity in spring, but the mechanism by which they refill their xylem remains unknown (Sperry and Robson 2001). Because pit-mediated air seeding does not occur during freeze-thaw cavitation, it is possible that the membranes avoid so-called cavitation fatigue, making refilling possible.

Reduced hydraulic efficiency is the key trade-off associated with resistance to freeze-thaw cavitation in both conifers and angiosperms, because conduit diameter is intimately linked to both vulnerability to freeze-thaw stress and hydraulic efficiency. Invariably, freeze-thaw-resistant species exhibit narrow conduit diameters and lower conductivities (Davis et al. 1999; Feild and Brodribb 2001; Feild et al. 2002; Pittermann and Sperry 2003). Recent work on high-elevation angiosperms has demonstrated that the hydraulic limitations imposed by narrow vessel diameters constrain leaf-level processes such that freeze-thaw-resistant species exhibit reduced rates of gas exchange during the growing season (Choat et al. 2011). The degree to which freezing stress affects productivity and competition has not been studied explicitly, but several studies show that the hydraulic limitations imposed by selection for freeze-thaw resistance constrain species distributions and may be a barrier to competition with seasonally deciduous taxa (Cavender-Bares and Holbrook 2001; Stuart et al. 2007). Wang et al. (1992) effectively argue that it is resistance to freeze-thaw cavitation that governs the phenology of coniferous, diffuse-porous, and ring-porous species, such that ring-porous plants (e.g., oak and walnut) exhibit the most delayed seasonal leaf flush to avoid the possibility of a late-season freezing event. In high-elevation/high-latitude regions, the frost-free growing season may be too short to support the carbon investment required by the arborescent angiosperm xylem strategy, thus giving conifers a distinct advantage.

Longevity

One of the key unifying traits of conifers is the longevity of the whole plant (table 1), including leaves and possibly roots (Coomes and Bellingham 2011). Many species of conifers are capable of exceeding an age of 1000 years, and although very long-lived species are more common in Pinaceae and Cupressaceae, other major families (Podocarpaceae, Araucariaceae, and Taxaceae) have species capable of attaining >1000 years of growth (Ogden and Stewart 1995). The capacity for great longevity in conifers has been attributed to decay resistance in conifer wood (Savory 1954; Takahashi and Nishimoto 1973),

Table 1
Summary of Some Key Functional Differences between Conifers and Angiosperms

	Conifers	Woody angiosperms
Species diversity (no.)	600–630	>250,000
Families (no.)	7	460
Individual longevity (no. years)	20–4800	<1–2300
Origins	Triassic	Early Cretaceous
Leaf life span (years)	3–26	<1–5
Mean leaf mass per area (g cm ⁻²)	227	106
Maximum photosynthesis (C3; ambient CO ₂ ; μmol m ⁻² s ⁻¹)	16	30
Maximum stomatal conductance (mol m ⁻² s ⁻¹)	.5	>1
Leaf venation	Single or a few parallel veins	Reticulate veins
Maximum leaf size (cm ²)	>100	750,000
Phloem type	Sieve cells, Strasburger cells	Sieve elements/tubes, companion cells
Root mycorrhizae	Pinaceae: ectomycorrhizae; Podocarpaceae: arbuscular	Ectomycorrhizae and arbuscular mycorrhizae
Conduit type	Tracheids: unicellular	Vessels: multicellular
Maximum conduit lumen diameter (μm)	~80	~500
Maximum conduit length	.0057 mm	10–11 m
Maximum hydraulic conductivity (kg m ⁻¹ MPa ⁻¹ s ⁻¹)	4.7	>10
Drought-induced cavitation resistance, P ₅₀ (mPa)	–2.1 to –14.1	–2 to <–10
Vulnerability to freeze-thaw cavitation	Typically quite low in shoots, may be higher in roots with larger tracheid diameters	Dependent on vessel size and thus variable, with deciduous species showing highest vulnerability
Pit membrane type	Torus-margo	Homogenous, with very few species bearing torus-margo pitting
Mean ± SD pit membrane resistance (MPa s m ⁻¹)	5.7 ± 1.3	336 ± 81
Mean ± SD stem wood density (g cm ⁻³)	Northern temperate conifers: .526 ± .134; Southern Hemisphere conifers: .65 ± .138	.613 ± .184 (min: .23, max: 1.9)

and all conifers possess a system of resin canals that bathe the wood and leaves in a terpene-rich sap, which guards them against insect and fungal attacks. It has been suggested that other adaptations at the chromosomal level contribute to conifer longevity (Flanary and Kletetschka 2005), although these adaptations are unlikely to be specific to the conifer clade. Long-lived trees can be relatively fast-growing pioneer species such as *Sequoiadendron* (maximum verified age, 3266 years) or slow-growing rain forest trees such as *Lagarostrobos* in Tasmania (maximum age, 2500 years). Furthermore, climate seems to exert little influence on the existence of long-lived conifers, with dry forest (*Juniperus* and *Pinus*), temperate rain forest (*Sequoidendron*, *Fitzroya*, and *Lagarostrobos*), and tropical species (*Agathis vitiensis*) all being capable of at least 600 years of growth. The almost ubiquitous presence of long-lived species in conifer clades indicates that this trait is a deeply embedded feature of the group.

Conifer leaves are also often very long lived, with the Chilean *Araucaria araucana* holding the record, with leaf life spans of ~25 years (Lusk 2001). In temperate rain forests the conifers have longer-lived leaves than most of the angiosperms (Lusk 2001; Coomes and Bellingham 2011), and in northern temperate forests the conifers retain leaves for two or more years while the majority of angiosperms are deciduous. Whether conifers have longer root life spans than angiosperms remains almost entirely unexplored because of the immense challenges involved in measuring this attribute. In a comparison of 11 North American species, root life span was found to be negatively correlated with root nitrogen-to-

carbon ratios, but conifer and angiosperm species were indistinguishable (Withington et al. 2006). In contrast, species found on soils with low nitrogen availability tend to have longer root life spans (Eissenstat and Yanai 1997); given that conifers are often associated with poor soils, this suggests that conifer roots are long lived.

Adaptations to Poor Soils

Species associated with nutrient-poor soils often have long-lived leaves (Grime 1977; Chapin 1980), because a long life span reduces the annual rate of mineral nutrient loss via abscission (Monk 1966; Small 1972; Givnish 2002). Plants salvage only ~50% of nitrogen and 60% of phosphorus from leaves during abscission (Aerts and Chapin 2000); the rest is lost to the ground in leaf litter and must be recaptured in the face of strong competition with neighboring plants (Coomes and Grubb 2000). Thus, a long leaf life span is advantageous (Berendse et al. 1987; Aerts 1995) on poor soils, but this adaptation comes at the cost of photosynthetic rate. Associated with long leaf life span are high leaf construction costs and relatively low maximum rates of photosynthesis (Wright et al. 2004); conifer needles have even lower photosynthetic rates than the leaves of angiosperms with comparable leaf life spans (Lusk et al. 2003). Fine root traits have an even greater influence on soil nutrient availability than leaf litter (Parton et al. 2007), but not enough is known about root longevity to comment on its influences in relation to soil nutrients.

There is also evidence that conifers are “ecosystem engineers” that alter habitats to their own favor: the tough, fibrous leaves of conifers are slow to decompose (Wardle et al. 2008; Hoorens et al. 2010), resulting in the accumulation of organic matter within soils, which increases soil C:P and N:P ratios and affects the community structure of soil microflora (Wardle et al. 2008). Nutrients are sequestered within the recalcitrant organic matter. Locking up nutrients in this way is an effective means of competing for nutrients if competitors are relatively intolerant of extreme nutrient shortage or less able to access organic nutrients. The roots of conifers also have slow decomposition rates relative to those of angiosperms (Silver and Miya 2001), because they contain relatively low concentrations of Ca and N and have high C:N and lignin:N ratios. In effect, conifers may engineer their local belowground environments to their own advantage. Berendse and Scheffer (2009) proposed that an acceleration of nutrient cycling by angiosperms may have contributed to their rise to dominance, but Mueller et al. (2010) questioned the evidence for this.

Conifers form symbiotic relationships with mycorrhizal fungi, providing the decomposers with sugars such that they are no longer carbon limited. In return, the conifers gain access to otherwise inaccessible forms of N and P. The figures are remarkable: a single gram of soil beneath a pine forest may contain 200 m of hyphae, exceeding root length by a factor of 200,000 (Read 1998). Fungal production, as estimated in a boreal pine forest study, corresponded to 14%–15% of carbon assimilation (Finlay and Söderström 1992). Carbon fixed by autotrophs is transported to roots and fungi within hours, as has been demonstrated vividly by monitoring soil respiration before and after severing phloem connections between leaves and roots (girdling experiments; Högberg et al. 2001). Symbioses with pines allow ectomycorrhizal fungi to monopolize decomposer communities on nutrient-poor soils and suppress nutrient immobilization by generalist saprotrophs (Högberg et al. 2001). Increasingly, such studies challenge the traditional view that plants depend on the mineralizing activities of microbial generalists to supply them with N and P, because ectomycorrhizal fungi are capable of mobilizing and capturing these mineral nutrients directly from organic matter. Whether conifers are more successful at exploiting mycorrhizal symbioses than angiosperms is largely unresolved. For instance, angiosperm species in podocarp-dominated forests are also heavily infected with arbuscular mycorrhizae and so can be similarly effective at acquiring nutrients via their fungal partners (Hurst et al. 2002; Dickie and Holdaway 2011). Two studies provide tantalizing evidence that conifer mycorrhizae may be particularly effective. Soil respiration rates were 10% lower in coniferous forests than in broad-leaf forests growing on equivalent soils in temperate North America (six paired comparisons; Raich et al. 2000), suggesting that conifers meet their nutrient requirements at a relatively low cost. Podocarps growing along a soil chronosequence in New Zealand had lower foliar N:P ratios than ferns or angiosperms on the phosphorus-impoverished soils, which suggested that they were better able to extract soil phosphorus (Richardson et al. 2004). More work is required to understand the implications of fungal symbiosis for competition between conifers and angiosperms.

Responses to Disturbance: Early Successional Adaptations

Many conifers escape head-on competition with angiosperms by responding differentially to disturbance. Disturbance can be defined as a discrete, punctuated killing of or damage to one or more individuals, resulting in an alteration of the niche opportunities available to the species in a system by removing biomass and freeing up resources for other organisms to use (adapted from Sousa 1984 and Shea et al. 2004). As Svensson (2010) pointed out, this definition distinguishes disturbance from stress, which is defined as the external constraints that limit the rate of dry-matter production of all or part of the vegetation (Grime 1977) and cause changes in performance, as opposed to mortality, by reducing conversion efficiency or increasing metabolic costs (Wootton 1998).

Fire is the most thoroughly investigated of all disturbance agents. Intense crown fires consume virtually all aboveground biomass as well as the humus layer of soil. Pines and other members of Pinaceae have evolved alongside fire and have greatly expanded within their ranges since humans started lighting fires, at least 400,000 years ago in Europe and 30,000 years ago in the Americas (Richardson and Bond 1991; Agee 1998). Many pines produce serotinous cones, which are held on the tree for at least 1 yr and open rapidly when fire melts the resin sealing the cone scales, releasing seeds into the ash. *Pinus halepensis*, a widespread pine on poor soils in the Mediterranean region, produces serotinous cones from an early age (~7 yr). Given that the maximum fire return interval in the region is 30–50 yr, precocious seed production allows the species to accumulate large numbers of serotinous cones before fire next strikes and to disperse many seeds into freshly burned sites. However, passage from seedling to mature tree is far from assured: pine seedlings grow slowly at first, reaching a height of only 1 m after 10 yr, and competition with herbs and resprouting shrubs is intense, particularly because angiosperms respond strongly to 3–10-fold increases in available N, P, and K in soils following fire (Agee 1998). However, enough seedlings usually survive to overtop shrubs and create a new tree layer. Like most pines, *P. halepensis* is light demanding and would be replaced by angiosperms if protected from fire for ~100 yr (Naveh and Whittaker 1980), but this never occurs in the Mediterranean.

Pines occupy a remarkable range of habitats across temperate North America, from woodlands bordering semideserts to mesic broad-leaf forests, but in all cases they require catastrophic disturbance (most usually fire) to gain respite from angiosperms via a colonization advantage. The life-history traits of species map out in regional differences in fire intensity and frequency (Agee 1998; Keeley and Zedler 1998). One of the most challenging habitats for pines is mesic forests that experience infrequent fires: *Pinus strobus* in eastern forests is more shade tolerant than most pines, which allows it to regenerate in small gap environments within these deeply shaded areas, although it still takes advantage of occasional fires and hurricanes.

Three species of shade-tolerant podocarps that dominate the alluvial floodplain forests of New Zealand are excellent colonizers of catastrophically disturbed sites. The slow-growing podocarp *Dacrycarpus dacrydioides* on poorly drained soils and *Podocarpus totara* and *Prumnopitys taxifolia* on better-

drained soils are incapable of regenerating beneath mature forest canopies and seldom succeed in small gaps, which become clogged with fast-growing woody angiosperms, ferns, and herbaceous plants (Coomes et al. 2005, 2009; Ulrich et al. 2005). Their dominance of floodplain forests is due to their ability to successfully regenerate after catastrophic disturbances, such as those resulting from debris triggered by major movements of faults in the Southern Alps and associated floods (Wells et al. 2001; Cullen et al. 2003). The long life spans of these podocarps (up to 3000 yr) allow them to persist from one rare catastrophic disturbance to the next (Enright and Ogden 1995; Lusk and Smith 1998). Floodplain podocarps grow well in bare mineral soil (Wardle 1974) and presumably benefit from reduced competition with angiosperms on fresh alluvium. Birds feed on the pseudoarils of podocarps and disperse the seeds into seral communities (Wardle 1991); podocarp seedlings grow up beneath the open-crowned bushes and trees and eventually overtop them (Beveridge 1973). This unusual regeneration strategy is also observed in podocarps of Tasmania and mainland Australia (Barker 1991; Gibson and Brown 1991).

Response to Disturbance: Persistent Species

As has already been discussed, many conifers are long lived; by definition, they survive disturbance events that kill other trees around them. Many conifers in Pinaceae and Cupressaceae develop thick bark that protects them from low-intensity ground fires, at least when the trees become tall enough to avoid these ground fires spreading into their crowns. Because of this protection, fire is less damaging to thick-barked conifers than it is to competitors. Many pines are favored by frequent fire because seeds retained within serotinous cones on tree branches are dispersed immediately and in copious amounts into freshly burned areas and rapidly establish in the ash (Agee 1998). *Pinus palustris* is one of the most remarkable pines, growing in nutrient-poor sandy soils of the coastal plains of the southeastern United States (Keeley and Zedler 1998) and benefiting from frequent low-intensity fires. In early life stages, internode development is slow, with the seedling looking much like a bunchgrass; the needles protect the meristem against fire and starch is accumulated in lignotubers. After 5–20 yr of development, the stem elongates rapidly at a rate of 50 cm/yr and, although it is initially susceptible to fire damage, the bark soon thickens. Lower branches self-prune, which leads to fire-resistant trees after a few more decades. Without the occurrence of fires, oaks and other angiosperms soon crowd out the pines (Keeley and Zedler 1998). Where fire intensity increases, *P. palustris* gives way to equally remarkable pine species such as *Pinus echinata* that can resprout after fire from basal axillary buds or epicormical meristems (Keeley and Zedler 1998). Fires in mature forests of coast and Sierra redwood rarely damage mature trees, but they clear the understory of fire-sensitive species and promote seedling regeneration by removing the litter layer (Ramage et al. 2010).

Niches Occupied by Conifers

In this final section, we attempt to characterize the ecology of conifers and their coexistence with angiosperms in general

terms. We compare the general patterns observed among conifers with the concept of a single ecological theory of conifer–angiosperm competition proposed by Bond (1989). In figure 4, we provide four explanations for conifer occurrence across a wide range of habitats outside the lowland wet tropics.

Under Extreme Conditions because They Are Stress Tolerators

The proposition at the heart of Bond's theory, that conifers are archetypal stress tolerators that persist in stressful habitats by having conservative functional traits (Diaz et al. 2004), is indubitable. Numerous conifers survive in some of the most extreme environments on earth: *Pinus halepensis* and *Juniper turbinata* border the Sahara Desert in North Africa (Barbéro et al. 1998), *Pinus ponderosa* and *Juniperus occidentalis* inhabit the dry woodlands of the northwestern United States, *Pinus sylvestris* survives in ombrotrophic bogs, and *Podocarpus alpinus* and *Podocarpus nivalis* are found in the high-altitude shrublands of Tasmania and New Zealand. Such extreme environments lack fast-growing angiosperms capable of smothering slow-growing conifers, and facilitation rather than competition may predominate (Callaway 2007). In the xylem physiology section, we summarized recent research on the hydraulic conductivity of conifers compared with angiosperms, as well as conifer responses to abiotic stress arising from drought, freeze-thaw events, nutrient shortage, and shade. This section emphasizes that some species of conifers are adapted to stressful environments.

Under More Equable Conditions because They Are Not Necessarily Inferior Competitors

In some habitats, conifers may become strong competitors for resources when they become mature, suppressing the growth of neighboring angiosperms and stifling regeneration (fig. 4b). For instance, in the boreal region, statistical modeling of growth data provides compelling evidence that conifers are effective competitors for belowground resources, with adult trees suppressing angiosperms in their neighborhoods (Coates et al. 2009). Tilman (1988) defines this as R^* competition, which occurs when a population reduces resource availability in its neighborhood to such an extent that the growth and survival of other species are inhibited. It has also been recognized for many years that mature conifers can be effective belowground competitors and that trenching (i.e., cutting around the outside of a plot to sever conifer roots) results in sometimes spectacular colonization of patches by angiosperms (Coomes and Grubb 2000). Conifers of xeric habitats are able to extract water from soils at well below the wilting point of angiosperms (Ryan and Yoder 1997), and classic studies by Fricke (1904) and Korstian and Coile (1938) have shown that root trenching in dry *Pinus sylvestris* woodlands allowed trees that normally occur on moister soils to invade spontaneously. In the water transport physiology section of this article, we discussed why conifers can be as effective or more effective than angiosperms at acquiring resources in some habitats.

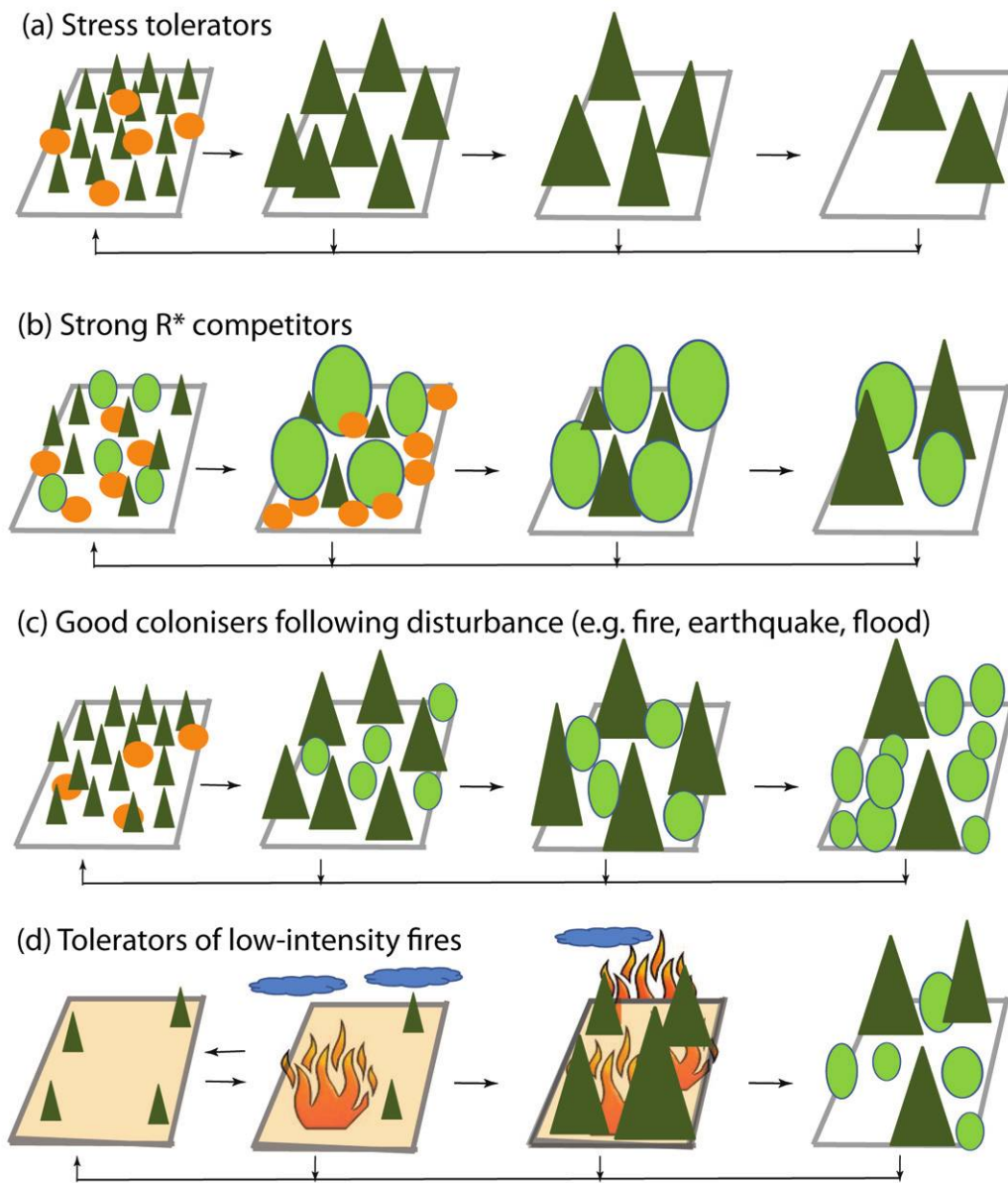


Fig. 4 Four explanations of why conifers have not been competitively excluded by angiosperms from every habitat on Earth. Each set of illustrations shows vegetation dynamics over time, with disturbances killing established vegetation and enabling regeneration from seed or resprouts. Triangles represent conifers, green circles represent angiosperm trees, and orange circles represent seral woody species. The four explanations are that (a) conifers have conservative traits, which enable them to persist in extreme environments (the Bond hypothesis); (b) conifers are ineffective competitors when small but strongly inhibit neighbors through resource competition when mature; (c) conifers are excellent colonizers of early successional habitats; and (d) conifers have traits associated with longevity, which enable them to persist after minor disturbances that kill their competitors. There is a great diversity of responses among the 800 or so species of conifer.

As we have already seen, whether a species is capable of tolerating shade and becoming the late-successional dominant depends critically on the shade cast by the forest canopy. Forests in dry regions and on nutrient-poor soils have open canopies (Coomes and Grubb 2000), which allow more light to penetrate to the understory. Under these conditions, conifers do not need broad, flattened needles in order to photosynthesize effectively. Indeed, many podocarps on poor soil have tiny, imbricated leaves and yet regenerate un-

der the forest canopy because it is so open (Coomes et al. 2009; Kunstler et al. 2009). English yew (*Taxus baccata*) regenerates most successfully in spiny shrublands of juniper (*Juniperus communis*) or hawthorn (*Crataegus monogyna*), which protect seedlings against herbivory by goats, deer, and domestic livestock (Myserud and Østbye 2004) and the drying effects of bright sunlight (García et al. 2000). Although this species is very shade tolerant, regeneration is rare within mature *T. baccata* woodlands in Europe (Thomas and Polwart

2003), and it seems that the trees are dependent on gaps created by the death of mature trees, in which shrubby communities can establish where yew seedlings can occur (Watt 1926).

After Catastrophic Disturbances because of Superior Colonization Ability

Many conifers are successful colonizers of disturbed sites, where they can buy themselves enough time to establish and grow in size before competition with angiosperms intensifies (fig. 4b). Fires, earthquakes, floods, volcanic ash deposition, and hurricanes all have the potential to disrupt the vicelike grip of angiosperm competition and provide opportunities for conifers to regenerate from seed (Ogden and Stewart 1995; Richardson and Rundel 1998; Wells et al. 2001; Richardson and Rejmánek 2004). Given enough time without catastrophic disturbance in an area, angiosperms may return to dominance (more details are provided in the section on response to disturbance above).

After Disturbance because They Are Able to Persist

Many conifer species are notoriously long lived, because they are better able to withstand disturbance events than angiosperms of the same region. We have provided examples of how some conifers develop thick bark, which protects them from low-intensity ground fires, at least when the trees become tall enough to escape ground fires spreading into their crowns. Because of this protection, fire is less damaging to thick-barked conifers than it is to competitors. More generally, the longevity of conifers means that they must regenerate only infrequently (even at intervals of several hundred years) to persist in forests (Ogden and Stewart 1995).

To summarize, conifer seedlings may often grow more slowly than those of angiosperms, but conifers are present in a wide range of habitats because many establish early in succession and persist for many hundreds or even thousands of years. They are thereby able to escape or tolerate intense competition for resources. In some circumstances, conifers are superior resource competitors to angiosperms, suppressing growth in their vicinity.

Synopsis

The evolution of angiosperms led to a significant reduction in conifer diversity and ecological success, but much of the impact may have been confined to extinct families (e.g., Cheirolepidiaceae) at low latitudes. When considering extant conifers, some generalizations are useful to account for the paucity of species in the most productive regions of the tropics; specifically, hydraulic limitations prevent gymnosperms from competing with large, superproductive angiosperm leaves (Bond 1989; Brodribb and Feild 2010). However, explaining the continuing success of contemporary conifers outside the lowland equatorial zone is complicated by the divergent ecology of the major conifer families. It may be that Pinaceae and Cupressaceae have been little

impacted by the evolution of angiosperms and they continue to occupy the same dry and/or cold niches they have occupied since the Mesozoic, protected by the fact that adapting to water stress or freezing is likely to be more costly for angiosperms than conifers, particularly in terms of wood properties. Economically cheap wood and highly photosynthetic needles enable Pinaceae to succeed as pioneer seedlings after fire, but other traits of adult plants such as serotiny, longevity, thick bark, and ectomycorrhizae allow them to avoid angiosperm competition in the Northern Hemisphere. Podocarpaceae, on the other hand, seem to have responded to angiosperm evolution by adapting to the angiosperm-modified tropical rain forest niche. They successfully compete with angiosperm trees, albeit often in sites of lower soil nutrition, by converging upon similar leaf and tree morphologies. Similar family-specific ecology of other conifers groups such as Araucariaceae and Taxaceae explain why concepts such as Bond's slow-seedling hypothesis (Bond 1989) encounter many exceptions with species found outside the equatorial zone (Becker 2000). Bond argues that conservative traits prevent conifers from growing rapidly as seedlings when resources are plentiful, leading to competitive exclusion from productive sites. This aspect of Bond's thinking resonates with the regeneration niche theory of Grubb (1977), which emphasizes the critical role of competition during the seedling stage in determining a species's fitness. However, we depart from Bond's perspective in one key respect. Whereas Bond's hypothesis regards competitive filtering during regeneration as the critical determinant of conifer abundance at the landscape level, evidence gathered over the past 20 yr lends support for the idea that conifers occupy a much broader range of habitats than predicted by the slow-seedling hypothesis because of various mechanisms that allow them to escape a more direct confrontation with their angiosperm competitors.

A more quantitative framework is required for specific theories to be tested. In the case of the tortoise and the hare (Bond 1989), it should be possible to define conifer seedling competitiveness as a function of maximum potential site productivity. Gradients in moisture, temperature, nutrients, and seasonality should therefore produce predictable gradients in conifer abundance. Given the discussion above, it seems unlikely that such a predictive test would support seedling competition as a unique predictor of conifer success. Conifers are more tenacious than they are often credited for. When taking together their efficient wood structure, longevity, diverse leaf morphology, and high physiological tolerances, conifers have access to a suite of traits that make them very effective competitors with angiosperms in all but the most highly productive environments.

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