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The end of an era?—The conservation status of redwoods and other members of the former Taxodiaceae in the 21st century

Abstract The nine genera and thirteen species that were formerly included in the family Taxodiaceae represent a unique and fascinating group of conifers. Throughout much of their Cretaceous and Tertiary history many were significant components of the mid- to high-latitude Northern Hemisphere forests and grew under a range of ecological, environmental, and climatic conditions. Global cooling and increasing aridity following the Eocene-Oligocene boundary led to a hemisphere-wide contraction of their overall distribution. Increased climatic instability during the Plio-Pleistocene intensified this process and by the start of the Holocene most species were restricted to small areas in eastern Asia and southern and western North America. The Holocene has been characterized by wide ranging changes associated with the development and expansion of human civilizations, especially over the last two centuries. The rapid expansion of agriculture, industrialization, and urbanization has severely impacted almost all species. Nine are currently listed as critically endangered, endangered, or vulnerable on the International Union for Conservation of Nature and Natural Resources' (IUCN's) *Redlist of Threatened Species*. This paper reviews the current conservation status of all thirteen species and discusses their prospects for the immediate future. There is a special focus on *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch.

Introduction

The nine genera and thirteen species that were formerly included in the family Taxodiaceae (now subsumed within the Cupressaceae) represent a unique and fascinating group of conifers. The majority have fossil records that date back to at least the Early Cretaceous, and several genera have shown relatively little morphological change since their first appearance (LePage et al., 2005; LePage, 2007, 2009; Kunzmann et al., 2009). Combined morphological and genetic analyses indicates that these genera represent basal lineages in the widespread, ecologically and economically important family Cupressaceae (Gadek et al., 2000). Throughout much of their Late Mesozoic and Cenozoic history, many genera were significant components of the mid- to high-latitude Northern Hemisphere forests and grew under a wide range of ecological, environmental, and climatic conditions. Global cooling and increasing aridity beginning at the Eocene-Oligocene boundary led to global contraction in their overall distribution. Increased climatic instability during the Plio-Pleistocene intensified this process. By the start of the Holocene, *Cryptomeria* D. Don., *Cunninghamia* R. Brown in L.C. Richard., *Glyptostrobus* Endlicher, *Metasequoia* Hu et Cheng, and *Taiwania* Hayata were restricted to small areas in eastern Asia with *Sequoia* Endlicher and *Sequoiadendron* Buchholz in western North America, and *Athrotaxis* D. Don to Tasmania. *Taxodium* Richard has the most widespread distribution extending from Mexico to southern Illinois in the United States.

The Holocene is characterized by wide ranging changes associated with the development and expansion of human civilization. The rapid and unabated expansion of agriculture, pastoralism, industrialization, and urbanization, especially over the last two centuries, has severely impacted natural habitats and the remaining populations. Intense exploitation for timber has significantly reduced the number of mature individuals in many populations, while large-scale habitat conversion for agriculture and forestry has reduced and fragmented natural ranges. In China, *Cunninghamia* and *Glyptostrobus* have been cultivated to such an extent and over such a long period of time, that their origi-

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nal distributions are now unclear. Overall, nine of the thirteen species are currently listed as critically endangered, endangered, or vulnerable on the International Union for Conservation of Nature and Natural Resources' (IUCN) *Redlist of Threatened Species* (IUCN, 2010; www.iucnredlist.org/apps/redlist/search). The aim of this paper is first, to review their current global conservation status and second, to discuss the possibility that we may witness the final extinction of several species within the next century.

IUCN categories

Before discussing individual species and genera it is useful to outline the nature and scope of the IUCN categories and criteria that are used to determine their global conservation status. The IUCN conservation assessments are exclusively focused on wild populations of species, subspecies, or varieties. As the IUCN is not a taxonomic organization, it relies on checklists, monographs, and floras to determine which taxa are assessed. For conifers, the IUCN uses the *World Checklist of Conifers* compiled by Aljos Farjon and first published in 1998 (Farjon, 1998). An annually updated version of the World Checklist is available online from the Catalogue of Life website (http://www.catalogueoflife.org/). Under this classification, the family Taxodiaceae is merged with the Cupressaceae. Three species are recognized in *Athrotaxis*, while *Cunninghamia* and *Taxodium* each have two closely related species. The other six genera are monotypic.

The IUCN conservation assessments are based on five criteria:

A. Declining population (past, present, and/or projected). Under this criterion, past and future declines are limited to a period three generations with a maximum time period of one hundred years;

B. Geographic range, plus fragmentation, decline, or fluctuations;

C. Small population size plus fragmentation, decline, or fluctuations;

D. Very small population or very restricted distribution; and

E. Quantitative analysis of extinction risk (e.g., Population Viability Analysis). In practice, quantitative analysis is rarely used.

Each criterion has a series of sub-criteria with quantitative thresholds that are used to determine the overall category of threat. For example, if a species' extent of occurrence (the area of its total distribution) is less than 100 km^2 or if its area of occupancy (actual habitat occupied within its extent of occurrence) is less than 10 km^2, and it is only known from a single location and is undergoing a continuing decline in terms of its overall distribution, the number of mature individuals, or the quality of its habitat, it could then be assessed as Critically Endangered under Criterion B. If its total distribution was between 100 and 500 km^2, there were five or less locations known, or the population is severely fragmented, and there was a decline in terms of its overall distribution, the number of mature individuals, or the quality of its habitat, then under Criterion B, it could be assessed as Endangered (IUCN & Natural Resources Standards and Petitions Subcommittee, 2010).

The IUCN assessments are updated periodically to reflect changes in the conservation status of each species as well as any changes to the categories and criteria used to assess them. All conifers were assessed in 1998 and are now being reviewed through the IUCN's Conifer Redlisting Authority and the Conifer Specialist Group. While any individual or organization can submit an assessment, each one needs to be evaluated and validated by the Red List Authority before it can be officially included on the IUCN's *Redlist*. The majority of current IUCN assessments reflect the extent and impact of past or current activities although future declines based on factors such as current rates of exploitation or deforestation. Integrating the predicted effects of complex processes such as climate change is much more difficult as the predicted effects may vary depending on the model used (IUCN & Natural Resources Standards and Petitions Subcommittee, 2010).

Current global conservation status

Athrotaxis

Athrotaxis is restricted to the montane and sub-montane areas of central and southwest Tasmania. *Athrotaxis selaginoides* D. Don often occurs as an emergent tree in rainforest at altitudes between 600 and 1100 m above sea level (asl). The species usually requires some form of disturbance for regeneration, although it does have some shade tolerance. The second species, *Athrotaxis cupressoides* D. Don, has a more restricted distribution in the sub-alpine zones at altitudes ranging from 900 to 1300 m asl. It has a range of regeneration strategies including vegetative regeneration through the production of root suckers. The third species, *Athrotaxis laxifolia* Hooker, is only found where the distributions of the first two species overlap or have overlapped in the past (Cullen, 1987; Cullen & Kirkpatrick, 1988a, b). Many Australian botanists regard this taxon as a natural hybrid due to its intermediate morphological characters (Hill, 1998; Jordan et al., 2004).

Table 1 International Union for Conservation of Nature and Natural Resources status of taxodiaceous conifers

Name of taxon	IUCN status	Likelihood for extinction within 100 years
Athrotaxis cupressoides D. Don	Vulnerable	Possibly
Athrotaxis laxifolia Hooker	Vulnerable	Possibly
Athrotaxis selaginoides D. Don	Vulnerable	Possibly
Cryptomeria japonica (Thunberg ex L.f.) D. Don	Near threatened	Not Likely
Cunninghamia lanceolata (Lambert) Hooker	Not threatened	Not Likely
Cunninghamia konishii Hayata	Vulnerable	Possibly
Glyptostrobus pensilis (Staunton ex D. Don) K. Koch	Endangered	Yes
Metasequoia glyptostroboides Hu et Cheng	Critically endangered	Yes
Sequoia sempervirens (D. Don) Endlicher	Vulnerable	Possibly
Sequoiadendron giganteum (Lindley) Buchholz	Vulnerable	Possibly
Taiwania cryptomerioides Hayata	Vulnerable	Possibly
Taxodium distichum (L.) Richard	Not threatened	Not Likely
Taxodium mucronatum Tenore	Not threatened	Not Likely

All species are slow growing, long lived, and very susceptible to fire (Pyrke & Smedley, 2005). Fire has been a major problem in the recent past; more than one third of *A. selaginoides* habitat has been lost in the last century (Cullen, 1987). Other threats include fungal diseases such as *Phytophthora* Bary and a lack of regeneration associated with overgrazing and introduced animals such as rabbits. Currently the majority of stands are located in World Heritage Areas, national parks, or forest reserves where they have some protection from fire and where sheep and cattle are either excluded or managed (Balmer et al., 2004). All three species are currently listed as Vulnerable (Table 1), either as a result of past reductions or due to their restricted distributions.

The Tasmanian alpine and sub-alpine areas are predicted to be extremely sensitive to climate change with changes in rainfall patterns, drying of wetland areas, reduced snow cover, increased average temperatures, and an increased risk of wildfire (Dunlop & Brown, 2008). It is expected that species currently restricted by lower temperature could migrate to higher areas and that those species currently occupying the sub-alpine and alpine zones would become further restricted in their distribution. While *A. selaginoides* may not be significantly impacted by such changes due to its larger altitudinal and ecological amplitude, the other two species are very likely to be vulnerable. It is uncertain whether their dispersal capabilities are sufficient to keep pace with the changes to their current habitat or if there will be sufficient suitable habitat available at higher elevations.

Cunninghamia

The genus *Cunninghamia* includes two closely related species, *C. lanceolata* (Lambert) Hooker and *C. konishii* Hayata. Both are fast growing when young, early maturing, disturbance dependent, and shade intolerant. *Cunninghamia lanceolata* is also capable of regenerating from basal sprouts (del Tredici, 2001), which not only increases its ability to withstand disturbance, but also makes it suitable for short rotation forestry (Li & Ritchie, 1999).

Cunninghamia lanceolata is widespread on mainland China. Its natural distribution is unclear, mainly due a very long history of cultivation that dates back at least 800, if not 1600, years (Li & Ritchie, 1999; Menzies, 1988). In many parts of its current range *C. lanceolata* has become established and is regenerating in secondary forests. Despite the uncertainty about its natural distribution it has been assessed as Not Threatened (Table 1).

Cunninghamia konishii is distinguished from *C. lanceolata* by possessing shorter narrower leaves and amphistomatic, rather than hypostomatic stomatal bands (Farjon, 2005). Until recently it was thought to be restricted to mixed conifer forests in the montane areas in central and northern Taiwan at altitudes ranging from and 1300 to 2000 m asl. In 1999, an isolated population was reported from Nghe An in Vietnam (Phan & Nguyen, 1999). Since then several more populations have been recorded along the Vietnam/Lao People's Democratic Republic (Lao PDR) border at altitudes ranging from 900 to 2000 m asl. In these areas it is usually only found on the steepest ridges and slopes, close to the summits (Nguyen et al., 2004;

Thomas et al., 2007).

Natural stands in Taiwan have been extensively exploited in the past although the majority of the remaining old growth stands are now located in national parks. In both Vietnam and Lao PDR almost all of the stands have been heavily exploited over the last 20 years. Recent changes in legislation and the establishment of new nature reserves and national parks in Vietnam have resulted in a few stands being protected (Nguyen et al., 2004), but exploitation continues in Lao PDR. The most recent global conservation status for *C. konishii* resulted in a listing of Vulnerable (Table 1) under criterion A, population reduction. This assessment, undertaken in 1998, did not include the Vietnamese or Lao PDR populations and therefore needs revising.

The potential impacts of climate change on the southeast mainland of Asia are likely to include greater seasonality in rainfall, longer dry seasons, and greater temperature extremes. These are likely to result in increased flooding in the low-lying deltaic areas, more frequent droughts, an increased frequency of fires, and possibly a general upward trend in the altitudinal range of major vegetation types (Christensen et al., 2007). In areas occupied by *C. konishii*, the species is already growing close to the summits, so there is little room for any further upward migration. The species may ultimately seek refuge on the cooler north-facing slopes. In Taiwan, *C. konishii* mainly occurs in mid-elevation forests, so that there is at least the potential for upward migration and re-establishment (Feng & Hsuan, 2007). Rising sea level may pose a more significant threat to the remaining mainland *C. konishii* populations if lowland human populations become displaced leading to an increased demand for land and resources in the upland areas.

Cryptomeria

On the IUCN Redlist, *Cryptomeria* is treated as a monotypic genus that is endemic to Japan. Naturalized Chinese populations are regarded as the result of ancient introductions from Japan (Farjon, 1999) and in that sense, are not considered to be 'wild'. In Japan, the remaining natural forests are widely distributed in the montane areas that extend from Aomori Prefecture in northern Honshu to Yakushima Island in the south. Populations range in size from one hectare to around 8000 ha. The current fragmented distribution is the result of past logging, past climate change, and localized volcanic activity. On Yakushima Island, many trees are estimated to be well in excess of 1000 years old (Takahashi et al., 2005). These remnant forests are well conserved and highly valued.

Cryptomeria japonica (Thunberg ex L.f.) D. Don is currently assessed as Near Threatened (Table 1). This category is used when a species is close to qualifying for a threatened category or is likely to do so in the near future. For *Cryptomeria*, the area of occupancy of the natural forests is more than 10 km^2, but less than 500 km^2. Although this is within the threshold for being classified as Endangered, there is little direct evidence of current decline. Without a continuing decline in the natural populations, it cannot be assessed as threatened under criterion B. However, the potential impact of predicted climate change could be severe. A recent study of the potential impacts on a suite of Japanese conifers indicated declines in suitable habitat of up to 60% by the year 2100 for species such as *Chamaecyparis pisifera* (Siebold et Zuccarini) Endlicher that have similar environmental requirements as *Cryptomeria* (Ogawa-Onishi et al., 2010). Earlier studies on the response of *Cryptomeria* plantations to changes in precipitation have also highlighted the susceptibility of *C. japonica* to drought (Matsumoto et al., 2006).

Metasequoia

Metasequoia glyptostroboides Hu et Cheng has the distinction of being the only extant conifer to be described as a member of a genus that had previously only included fossil species (see Miki, 1941). It is also one of the few conifers that grow in areas where no primary forests remain. Since its discovery, *Metasequoia* has become one of the world's most iconic trees and the focus of considerable efforts to ensure its conservation both in its original location in China and in cultivation. Initially, the in situ efforts were focused on maintaining individual 'Original Natural Mother Trees' within the mainly agricultural landscape. More recently, this has shifted towards a population and ecosystem approach in an effort to mitigate the impacts of human activities at the landscape level and to encourage natural regeneration. The most recent census indicated that the total population is over 5000 individuals spread over an area of about 600 km^2 (Wang et al., 2006; Wang & Guo, 2009).

Metasequoia is currently listed as Critically Endangered on the IUCN Redlist (Table 1). The assessment, undertaken in 1996, was based on an estimated past decline of 80% over its last three generations and a declining current population of less than 250 mature individuals with no more than 50 individuals in any one sub-population. The most recent national assessment listed *M. glyptostroboides* as Endangered with an estimated population reduction of 50% over the last century, an area of occupancy (the total number of 4 km^2 grid cells in which *Metasequoia* occurs) less than 500 km^2, sub-populations severely fragmented, and a decline in the quality of its habitat (Wang & Xie, 2004). This second assessment is probably more accurate than the first as it incorporates data published since the initial assessment.

Sequoia and *Sequoiadendron*

Sequoia sempervirens (D. Don) Endlicher and *Sequoiadendron giganteum* (Lindley) Buchholz are possibly the most well known members of the Taxodiaceae, partly because they are the tallest, largest, and amongst the oldest conifers known to exist. Both have narrow distributions with *S. sempervirens* occupying a narrow band along the central and northern coast of California, while *S. giganteum* is restricted to a few groves on the western slopes of the California Sierra Nevada (Piirto & Rogers, 2002). Since their discovery during the 19th century both species have played a significant role in the economic and social development of California and the United States. Initially both were heavily exploited for their valuable timber. The devastation that ensued eventually led to the formation of preservation organizations such as the Save the Redwoods League who lobbied for an end to the destruction and for the long term preservation of the old-growth forests. Despite considerable opposition from lumber companies and people who were focused on the economic development of the state, several protected areas were established from 1890 onwards. Popularization of these protected areas also led to the development of a significant tourist industry, which, as it became more economically significant, led to the establishment of more protected areas. Providing public access necessitated the construction of roads, hotels, and other facilities in the forests—in extreme cases some trees were hollowed out to allow for cars and buses. Fire suppression policies were also instigated, partly to ensure public safety, but also to try and ensure that the forests would remain as they were at the time that the parks were established. Unfortunately this had unintended consequences, especially for the *S. giganteum* forests that require regular low-intensity fires for regeneration. In the absence of fire, the increase in associated species not only prevented new regeneration of the giant redwood, but increased the chances of catastrophic crown fires (Elliott-Fisk et al., 1997; Piirto & Rogers, 2002). Over the last few decades, increased understanding of the ecology of these forests has led to the gradual introduction of controlled burns to try and promote regeneration of the giant redwoods (Tweed, 1994). Overall, the struggle to ensure the conservation of the remaining, fragmented old growth *Sequoia* forests and groves of *Sequoiadendron* has been relatively successful compared to many of the other taxodiaceous species. Currently *Sequoia* and *Sequoiadendron* are both listed by the IUCN as Vulnerable on the basis of declines over the last century (Table 1).

Their future conservation may be less assured as a range of climate change scenarios predict changes in fire frequency, fire intensity, temperature, and precipitation along with changes in the distribution of major vegetation types (Lenihan et al., 2003). While both species have been able to survive and adapt to significant climatic changes during the Holocene (Millar, 2006), their survival has been in the context of longer time scales and within a landscape that was not significantly modified by humans as it is today. The *S. sempervirens* forests may be particularly vulnerable given their climatic sensitivity, need for moisture (e.g., fog), and the degree of population fragmentation (Westerling et al., 2006; Chennel et al., 2009).

Taxodium

On the IUCN *Redlist* two species of *Taxodium* are recognized. *Taxodium mucronatum* Tenore has a scattered distribution along water courses in Mexico and Guatemala at altitudes above 200 m asl (Stahle et al., 2005). It has a long history of cultivation extending back for at least 2000 years (Marcus & Flannery, 2004). Some parts of its distribution may be the result of naturalization. In the southeastern and central United States *Taxodium distichum* (L.) Richard occurs across a wide area in a range of lowland wetland habitats, including near-coastal swamps. As a result of their extensive geographic distributions, and despite extensive logging (Stahle et al., 2005), neither species is currently listed as threatened on the IUCN Redlist (Table 1).

In the United States climate change impacts are predicted to include decreased precipitation, higher temperatures and rates of evapotranspiration, and more frequent salt-water intrusions into freshwater coastal swamps in response to higher sea levels and storm surge. The restriction of *T. distichum* to wetland habitats, particularly in the low elevation coastal floodplain forests and swamps, heightens its susceptibility in this regard (Middleton, 2006).

Taiwania

Taiwania is a monotypic genus whose largest extant populations are found in Taiwan and along the border of Yunnan and Myanmar. Individual trees may grow to 40 m and reach ages in excess of 1600 years (Hu, 1950). *Taiwania cryptomerioides* Hayata was first discovered in Taiwan in 1906 and then in western Yunnan in 1916. Almost 100 years later, in 2002, a small, remnant population of about 100 trees was discovered in the Hoang Lien Mountains of northern Vietnam (Nguyen et al., 2002). These mountains represent the southernmost extension of the Himalayas.

Despite the distance between these areas, there are many climatic and ecological similarities between the localities in Taiwan, Vietnam, and Yunnan. Each population occurs at altitudes ranging from 1800 to 2500 m asl, usually on steep slopes in moist evergreen forests. Annual precipitation may be as high as 4000 mm, while the mean annual temperature varies from 9°C to 15°C (Liu & Su, 1983; Nguyen et al., 2004; Lai et al., 2006; Li et al., 2008).

The majority of extant *Taiwania* populations are generally small and found in isolated patches (Farjon & Thomas, 2007). In the Yunnan/Myanmar border area, this reflects a recent history of exploitation for its valuable timber (Kermode, 1939, 1945; Kingdon-Ward, 1956, 1960) that has led to its near eradication from the southern part of its range and restriction to almost inaccessible areas in the north. The Vietnamese population is the remnant of a larger population that has been reduced by swidden agriculture over the last several decades (Nguyen et al., 2002). The Taiwanese populations have also been fragmented and reduced through exploitation; although in 2002, a large undisturbed forest with more than 10,000 mature individuals was discovered in southeastern Taiwan (Wang, 2002).

Taiwania is currently assessed as globally Vulnerable (Table 1) by the IUCN with regional assessments of either Critically Endangered in Vietnam (Nguyen, 2007), or Endangered in Taiwan and Yunnan (Wang & Xie, 2004; Farjon & Thomas, 2007). In Taiwan and Yunnan, the remaining populations are located in large, strictly protected areas. In Vietnam, an intensive in situ conservation program was initiated soon after the discovery of the species in 2002. This involves a stewardship program with individual trees being adopted by local families and also includes a reforestation program using seed collected from the few remnant trees (Morris & Hieu, 2008).

On mainland China, small populations of *T. cryptomerioides* are also recorded from several localities in Guizhou, Hubei, and Fujian Provinces. These populations are potentially highly significant from both a biogeographic and conservation point of view. In each of these localities, *Taiwania* occurs in secondary forests at altitudes ranging from 750–1200 m asl, while precipitation ranges from 500–1200 mm (Liu & Su, 1983; Fu & Jin, 1992). Large, old trees and natural regeneration are absent. Associated conifers include various fast growing pines and *Cunninghamia lanceolata* (Liao et al., 2004; Yang et al., 2006, 2009; Li et al., 2008).

The contrast in ecological profiles and their proximity to human settlements has led to some debate about their origin and to an assertion that they are the result of historic human introductions (Farjon & Thomas, 2007). However, while other members of the former Taxodiacaeae such as *Cunninghamia* and *Glyptostrobus* have a long history of cultivation in China that is documented in early floras and other ancient manuscripts (Li, 1979; Li & Ritchie, 1999; Li et al., 2004; Li & Tan, 2009), *Taiwania* does not appear to have such a record. Additionally, some of the populations, although geographically close to major settlements, are located in topographically isolated areas that have only recently been settled (Liao et al., 2004; Yang et al., 2006, 2009; Li et al., 2008). The status of these populations is the subject of ongoing research (Chou et al., in press).

The future conservation status of *Taiwania* is uncertain. While the largest populations in Yunnan and Taiwan are located within protected areas that are potentially large enough to mitigate any impacts from climate change, other populations are already either so small or degraded that their long term survival is doubtful at best and certainly bleak without significant continued intervention.

Glyptostrobus

Glyptostrobus, like many other members of the former Taxodiaceae, was formerly much more widely distributed across the Northern Hemisphere, but became more restricted due to increasing aridity, cooling, and probably increased competition for space and resources (LePage, 2007). Throughout its history it has mainly been associated with wetlands and river deltas in lowland areas where it was commonly associated with *Metasequoia* and *Taxodium*. As with *Metasequoia*, its most recent macrofossil records are from Pliocene deposits in Japan (LePage, 2007). Unlike *Metasequoia*, *G. pensilis* (Staunton ex D. Don) K. Koch is now known to have had a wider distribution during the Holocene that includes southeastern China, central Vietnam, and Lao PDR. This wide latitudinal distribution, between 25°N and 13°N almost parallels that of *Taxodium* in the United States and Mexico.

Glyptostrobus in China

In southeastern China *G. pensilis* is widely cultivated along paddy fields, in temples, and around villages. Its popularity is partly due to its Feng-Shui associations —planting trees in temples, around villages, and especially along levee banks is thought to bring good luck and prosperity (Metcalf, 1937; Li et al., 2001, 2004). As a result of its wide cultivation, its current natural distribution is difficult to determine. Late Holocene sub-fossil records and ancient Chinese texts indicate that *Glyptostrobus* was common in the lowland river deltas, especially in Guangdong Province (Li, 1979; Li et al., 2001; Ding et al., 2009). Climate change, the expansion of wetland rice cultivation and a rapid expansion in the rural and urban populations may have led to their gradual demise (Weng, 2000; Li et al., 2001; Ding et al., 2009; Li & Tan 2009). Today there are few, if any, wild populations remaining in primary habitats (Fu et al., 1999; Li & Xia, 2004, 2005).

Glyptostrobus in Vietnam

In Vietnam *Glyptostrobus* is currently only known from a small area of Dac Lac Province at the southern end of the Tay Nguyen Plateau in central Vietnam at altitudes between 500 and 700 m asl. This plateau extends for almost 450 km from the north to the south and about 150 km from the east to the west at its widest point. It is fringed by mountains in the north, west, and south, while the eastern side forms a steep escarpment that descends to a narrow coastal plain. The plateau's topography consists of a series of undulating hills criss-crossed by numerous rivers and streams that flow both east and west. Swampy depressions are common. The area has a monsoon tropical climate with a mean annual temperature of 20°C–23°C, an annual rainfall of 1300–1800 mm, and a pronounced dry season. The original vegetation of this area consisted mainly of closed semi-deciduous and dry evergreen lowland forests dominated by representatives of the families Dipterocarpaceae and Lythraceae (Averyanov et al., 2009). Since the end of the war in the early 1970s, extensive areas of the plateau have been cleared for coffee and pepper production, and there has been a considerable expansion of the human population.

The most recent survey of *Glyptostrobus* in Dac Lac (Averyanov et al., 2009) identified five localities, three of which consist of ten or fewer trees. One site is located in a village, while the other four are located in broad, seasonally inundated depressions surrounded by coffee plantations. In one area, recently cut stumps were observed. Ring counts of some of these stumps indicated the trees had reached an age of up to 400 years. The two largest stands, at Trap Kso and Earal, have 34 and 200–500 trees, respectively. Although both of these areas have been deemed Provincial Nature Reserves since 1987 and 1994, they have been repeatedly burnt. They have also been affected by changes in hydrology relating to the establishment of plantations, villages, and towns. In 1985 the construction of a small dam led to the permanent inundation and subsequent die back of a large part of the main stand at Earal. At Trap Kso, the construction of irrigation and drinking water wells around the periphery of the swamp have caused a lowering of the water table leading to a gradual drying of the swamp and increasing the vulnerability of *Glyptostrobus* as well as the forest community to fire. In the remaining localities, regeneration is absent; many trees do not produce seed cones. Seeds collected from the few trees that do produce seed cones are undeveloped. Various forms of vegetative propagation have been attempted, but only with limited success. The current conditions within the swamps, their small size, and the continuing demand for water to support the surrounding plantations make it unlikely that restoration programs in these areas will be successful (Averyanov et al., 2009).

Glyptostrobus in Lao PDR

In May 2007, wetland ecologists undertaking a survey on the Nakai Plateau in central Lao PDR reported a stand of *Taxodium*-like trees. Photographs and specimens were sent to the Royal Botanic Garden, Edinburgh (RBGE) and were subsequently identified as *Glyptostrobus*. This was the first confirmed discovery of *Glyptostrobus* in Lao PDR. Earlier reports by Vietnamese foresters involved in logging on the plateau in the early 1990s (Nguyen, 2000) had never been confirmed.

The Nakai Plateau lies on the western slopes of the main Annamite Mountains and extends for almost 100 miles from the northwest to the southeast, with a maximum width of about 50 miles. It has some similarities to the Tay Nguyen Plateau, located about 300 miles to the south in central Vietnam, in that it is bounded to three sides by mountains. To the west, a steep escarpment descends 400 m to the Mekong Valley. The plateau is dominated by the Nam Theun River and its various tributaries. This river meanders across the plateau and eventually makes a sharp descent and discharges into the Mekong River. Climate on the plateau is strongly influenced by the southwest monsoon; almost 88% of the rainfall occurs between May and September. Average annual precipitation is around 2500 mm. Rain may occur on the surrounding mountains throughout the year so that there is an almost constant supply of water into the tributaries that feed the Nam Theun River. Most of the plateau is level varying in altitude from 500 to 650 m asl. Although low lying, seasonally inundated areas are relatively frequent, they usually only cover an area of 1–2 ha. Temperatures range from about 19°C to 30°C (Environmental Assessment and Management Plan, 2004).

The topography and hydrology of the area make it an ideal site for hydroelectric projects and over the years, various schemes have been proposed. In the late 1990's, after much controversy, the World Bank agreed to finance the development of the Nam Theun II hydroelectric scheme. This would involve flooding more than 450 km^2 of the plateau, including most of the area below 538 m asl. As part of the environmental mitigation strategy, the contractors had a legal obligation to ameliorate any negative effects on any rare or threatened plants or animals located within the projected reservoir area. This could involve translocation of trees to unaffected areas or the creation of suitable new habitats. In order to do this, extensive surveys were required to identify any potentially threatened species and to identify potential areas for restoring damaged habitats or creating new ones—especially wetlands. The focus of this work was primarily animals (Dersu and Associates, 2008).

It was in this context that the wetland ecologists were undertaking their surveys when they discovered a single stand of *G. pensilis* that consisted of 30–40 trees that were 25–40 m high and with diameter at breast heights (dbh) of up to 1 m. Within and around the stand, felled logs and stumps that were up to 1.5 m in diameter were also identified. The stand was located in a broad flat valley with several small streams running through it. The soils in which tree were growing were grey or gleyed clay (hydric), rather than peaty.

The elevation of this stand was originally recorded as 539 ± 10 m asl. There was some uncertainty about whether the stand would be impacted by the creation of a reservoir and therefore required some kind of action (Dersu and Associates, 2008). More accurate GPS data indicated that the altitude of the stand was closer to 532 m asl, so that when the reservoir becomes full, the trees would ultimately be inundated to a depth of approximately 5 m. The inundation started in June 2008 and was completed by June 2009. Various plans were proposed and at one stage they included the use of earthmoving equipment to physically remove some of the smaller trees and replant them above the maximum water level of the reservoir. Eventually a seed collection was organized and about 2 kg of seed was collected. Approximately 500 g of seed was sent to the RBGE for storage and to establish germination protocols. In Lao PDR, nursery space was allocated and potential planting sites were identified. The seed that was sent to the RBGE was sent to the United Kingdom Forestry Seed Testing Center for X-ray analysis to determine potential viability (D. Luscombe, Forestry Commission, 2008, unpublished data). The analysis revealed that all of these seeds lacked embryos and were not viable. The seed that was retained in Lao PDR was sown, but only six seedlings were produced—these are still located in the nursery and are reported to be growing well (pers. comm. Jim Johnson, Nam Theun Power Company, July 2009).

Further ecological surveys have been undertaken in an attempt to locate other stands. To date, five more small populations have been identified. The largest population contains about 40 trees that are up to 25 m high and appear to be in good health. All of the new stands are located outside of the inundation zone and beyond the perimeter of the protected area that was established in the watershed above the reservoir. The new stands are on land that had been allocated to villages for forestry or agriculture, and each stand has been impacted to various degrees by logging, construction of fish ponds, and clearing for food crops. None show any signs of regeneration although several trees in each stand have been producing cones. Additional surveys are planned to locate other stands.

In China, the national conservation status of *G. pensilis* is Vulnerable (Table 1; Wang & Xie, 2004). This assessment includes what are considered by the IUCN to be cultivated, semi-natural populations. If they were to be excluded, then a national assessment of Critically Endangered or possibly Extinct in the Wild would be appropriate. In Vietnam the species has been assessed as Critically Endangered (Nguyen et al., 2004). No official redlist exists for Lao PDR. If an assessment were to exist, then *Glyptostrobus* would probably qualify as being Critically Endangered. The overall current global status is Endangered although given the small population sizes in Vietnam and Lao PDR, along with the nature of the threats facing them, this may be an underassessment.

Conservation or extinction: Where do we go from here?

The evolutionary history of the Taxodiaceae is impressive with many representatives having fossil records that in some cases extend 100 million years to the Early Cretaceous (Aulenback & LePage, 1998; LePage et al., 2005; LePage, 2007, 2009). The ability of some genera in the past to occupy and adapt to a wide range of environments and climatic regimes throughout the Northern Hemisphere from latitudes as far south as 33°N to as high as 80°N attest to their physiological adaptability, plasticity, and resiliency. Biogeographic studies of *Metasequoia* and *Glyptostrobus* demonstrate extensive forests dominated by one or both of these genera throughout the mid- to high-latitude regions of the Northern Hemisphere, especially during parts of the Tertiary (LePage et al., 2005; LePage, 2007; Momohara, 2005). Population contraction and range restriction that began at the Eocene-Oligocene boundary (about 35 Ma) is coincident with increased global aridity and global cooling. Continued global cooling and aridification during the Miocene, as well as competition for space and resources by representatives of the Pinaceae further restricted their distribution (LePage, 2003), so that by the start of the Holocene, the remaining species were restricted to areas in eastern Asia, North America, and Tasmania. For several genera such as *Metasequoia*, *Taiwania*, *Cunninghamia*, and *Glyptostrobus*, the extent of their distribution and abundance at this time is unclear. Since the mid-Holocene, and especially over the last three centuries, the rapid expansion of human civilization has had a considerable and generally detrimental impact on the surviving members of the Taxodiaceae. So then, the obvious question is what is the fate of these thirteen species over the next hundred years?

The development of rice-based agriculture in eastern Asia transformed many of the lowland and wetlands habitats where *Metasequoia* and *Glyptostrobus* had persisted and led to a reduction in their range and decrease in abundance. The increase in human populations and their gradual concentration into more urban areas that were supported by an increase in agricultural, pastoral, and forestry lands, coupled with the development of more complex societies and religions impacted populations of *Cunninghamia*, *Cryptomeria*, *Glyptostrobus*, and *Taiwania* in a variety of different, almost contradictory ways. Primarily, these factors led to the depletion and fragmentation of the wild populations and their eventual restriction to geographically more remote and inaccessible areas. At the same time, it also ensured the survival of some species through introduction to cultivation either through plantations (*Cunninghamia*) or in temples, villages, and sacred forests (*Cryptomeria* and *Glyptostrobus*).

In North America and Tasmania human impacts have been most marked over the last three centuries following the colonization of what are now the United States and Australia by European settlers. Prior to this period, indigenous people and their practices had comparatively little detrimental impact on the existing redwood populations (Norman, 2007), at least compared to that of the European settlers. Rapid economic and social development in the 18th and 19th centuries led to an initial depletion of natural populations either through direct exploitation (*Sequoia*, *Sequoiadendron*, and *Taxodium*) or, more indirectly, through the conversion of forests to pastoralism and the associated changes in fire regimes coupled with the impact of introduced species such as rabbits and sheep (*Athrotaxis*). During approximately the same period, exploitation was accompanied by the development of conservation movements that resulted in the preservation of considerable areas of natural forests. At least part of the motivation for this conservation was the recognition of the special scientific and aesthetic attributes of the Taxodiaceae within those areas (Tweed, 1994; Elliot-Fisk et al., 1997; Balmer et al., 2004). Such recognition has also been instrumental in the more recent conservation efforts for redwoods such as *Metasequoia* and *Taiwania* in eastern Asia.

The cumulative impacts of human civilizations, particularly over the last three centuries, has not only been the principal driver behind the reduction in distribution and abundance for the majority of the remaining redwoods during the Holocene, but is also likely to determine their future particularly within the context of predicted changes associated with climate change. For taxa such as *Glyptostrobus pensilis* and *Metasequoia glyptostroboides*, where habitat loss is likely to continue unabated, their extinction, at least in natural habitats is imminent, if it has not already occurred (Table 1). However in both cases these taxa are likely to persist in cultivation due to their iconic status or their cultural associations. For several others such as *Cryptomeria japonica, Cunninghamia konishii, Taiwani cryptomeroides,* and species of *Athrotaxis* and *Taxodium*, and possibly *Sequoia sempervirens* and *Sequoiadendron giganteum* we are at the tipping point (Table 1). Their future depends initially on the political will to maintain protected areas of sufficient size to allow them the opportunity to adapt to future environmental, climatic, and other anthropogenic changes. In all cases constant monitoring and possibly direct intervention through habitat management and even assisted migrations will be necessary to ensure their survival. *Cunninghamia lanceolata* appears to be the one species of least concern due to its utility as a plantation species, its range of regeneration strategies, and relatively wide ecological amplitude. One final thought for the future—over the last 100 million years the redwoods have survived and even thrived under a range of climates and in habitats that have been absent during the Holocene. There is a chance that if some of the predicted climate changes occur, then the climatic and environmental conditions that prevailed when the redwoods were largely dominant could return. Under such a scenario could it be possible to see a resurgence of the redwoods, especially in areas of the world such as the polar regions that are currently devoid of forest?

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