

Is the current range of *Torreya taxifolia* its true native range?

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Introduction

In the spring of 1875, distinguished Harvard botanist Asa Gray embarked upon a trip to the panhandle of Florida, to “make a pious pilgrimage to the secluded native haunts of that rarest of trees, the *Torreya taxifolia*” (Gray, 1875; Dupree, 1968). A member of the yew family (Taxaceae), *Torreya taxifolia* historically grew in small groves in northwest Florida and adjacent southwest Georgia, most notably along a 65-kilometer stretch on the eastern bank of the Apalachicola River and its tributaries from Chattahoochee south to the present-day location of Torreya State Park in northern Liberty County, Florida (Chapman, 1885; James, 1961; Schwartz and Hermann, 1993). The trees observed by Gray grew up to a meter in circumference and were as much as 20 meters tall (Godfrey, 1988). They were known by local residents as “stinking cedar” because of the strong odor exuded by their thickly furrowed, yellow-brown bark when cut for fence posts or fuel wood for steamboats (Gray, 1875).

Torreya taxifolia was first collected for scientific description in 1838 by Mr. Hardy Croom while traveling between his properties in Quincy and Mariana, Florida. Asa Gray was a student of the renowned plant taxonomist, John Torrey, when Croom brought specimens of the unusual conifer, along with an equally curious flowering herb that grew beneath the canopy of stinking cedars, to New York for identification (Dupree,

1968). “Mr. Croom, upon ascertaining that he was the fortunate discoverer of an entirely new type of coniferous tree, desired that it should bear Dr. Torrey’s name; and the genus *Torreya* was accordingly so named and characterized by the Scotch botanist, Arnott” (Gray, 1875; Arnott, 1838). The delicate-flowered herb that grew in association with *Torreya taxifolia* was also a member of a new genus, which Torrey proposed to be named *Croomia pauciflora* in honor of its discoverer. Croom assumed that the two genera had a very limited mutual distribution tied to the special environment of the Apalachicola River bluffs. Gray, however, observed (Gray, 1875) that “[*Croomia*] is not, as Mr. Croom then supposed, exclusively so found; for it grows also in the central and upper portions of Alabama and Georgia, where *Torreya* is unknown, but where I fancy it once must have flourished.”

So began the quandary conservationists continue to ponder more than 125 years after Gray’s pilgrimage: What is the true potential native range of *Torreya taxifolia*, the rarest of rare North American conifers? What historical and environmental factors have been responsible for its rarity in late historic times? And how can we use our knowledge of its growth requirements to anticipate its optimal future niche in order to be proactive in its conservation?

To answer our first question, we must first address the second, aided by evidence from the fossil record as well as studies of the recent effects of introduced pathogens. The answer to the last question can be based in part on application of knowledge of the history of *Torreya*, in part on studies of anticipated environmental changes with near-

future global warming, and in part on ethical and practical considerations pertaining to the efficacy of *ex situ* conservation.

Torreya taxifolia: a rare, endemic species in decline

When first discovered in the 19th century, *Torreya taxifolia* was found growing vigorously in groves beneath the overstory of late-successional forests dominated by American beech (*Fagus grandifolia*), southern magnolia (*Magnolia grandiflora*), and other mesic southern hardwoods (Harper, 1914; Delcourt and Delcourt, 1977; Schwartz and Hermann, 1993). It was listed as one of the most common trees of northern Florida by Harper (1914). In the 1930s, however, *Torreya taxifolia* became diseased, apparently through introduction of fungal pathogens, and suffered a catastrophic decline in population during the late 1950s, with adults of all known naturally occurring populations killed by the time the decline was first documented (Godfrey and Kurz, 1962; Schwartz and Hermann, 1993). Recent changes in climate and fire frequency also may have contributed to the decline (Schwartz and Hermann, 1993). By 1992, the largest recorded *Torreya taxifolia* trees in remaining natural populations were only a little over three meters tall, with most stems less than a meter high and less than ten years old. The current estimated total population is between 800 and 1500 individuals, with no known reproductive adult female trees remaining in natural populations in northern Florida (Schwartz and Hermann, 1993).

Biology and fossil history of the genus Torreya

Torreya taxifolia is a classic example of a narrowly endemic plant, long considered by botanists to be a relict of geologic history, surviving for millions of years in a specialized “island-like” habitat (Thorne, 1946; Braun, 1950; Hubbell *et al.*, 1956; James, 1961). The genus is a member of the ancient gymnosperm family Taxaceae, whose ancestors were evolutionarily distinct from other conifers by the Jurassic Period (Thomas and Spicer, 1987). *Torreya* trees have whorled branches with flattened, pungent, needle-like, evergreen leaves. The plants are dioecious, with female trees developing ovules in spring in arillate structures. Male trees bear globular cones with four pollen sacs on each scale. The exposed ovules exude pollen drops that trap the pollen grains after they are released in clouds. By the end of the second year after pollination, the fertilized ovule becomes a single, nearly globose, gray-blue fruit about 2 to 4 cm in diameter (Stalter, 2003). Seed predators including small dinosaurs, tortoises, and primitive microtuberculid mammals may have been the first dispersers of ancient *Torreya* fruits; in recent decades, squirrels have been observed to disperse seeds of cultivated *Torreya taxifolia* (Barlow, 2000).

The genus *Torreya* includes three living species in addition to *Torreya taxifolia*. *Torreya californica*, California nutmeg, is native to the Santa Cruz and Sierra Nevada Mountains. *Torreya nucifera* grows in the mountains of Japan, and *Torreya grandis* is found in the mountains of northern China. In North America, the fossil record of the genus *Torreya* extends back to the Cretaceous Period. *Torreya gracillima* has been described from Upper Cretaceous deposits along the Yukon River in Alaska (Hollick and Martin, 1930). Chaney (1925) described two unnamed species of *Torreya* from Lower

Eocene (Tertiary Period) deposits of the John Day Basin, Oregon. Dorf (1933) considered remains of *Torreya* as common in the Oligocene (Tertiary Period) flora of California. In southeastern North America, Berry (1908, 1914, 1919) described *Torreya caroliniana* from Mid- to Upper Cretaceous deposits of North Carolina and Georgia on the basis of leaf and seed characters. *Torreya antiqua*, possibly conspecific with *T. caroliniana* and ancestral to *T. taxifolia*, has been described from Upper Cretaceous deposits near Fayetteville, North Carolina, based on secondary wood (Boeshore and Gray, 1936).

Climate and paleogeography of the Cretaceous world

Sixty-five million years ago, during the Cretaceous Period, North America and EurAsia were united by a North Atlantic land bridge between 40° and 60° N latitude (Dietz and Holden, 1970). The former supercontinent of Laurasia was breaking up along the mid-Atlantic rift zone, at the same time moving toward the North Pole. Once-contiguous populations of redwoods and other northern-hemisphere temperate conifers were destined by the process of plate tectonics to become isolated from one another, not only because of the breakup of the continents, but because of mountain building in the Rockies, the Alps, and the Himalayas, as well as the gradually cooling global climate.

During the Early Cretaceous, the climate of Laurasia was more uniform than today, with a less steep latitudinal gradient in temperature, and with an ice-free polar region (Thomas and Spicer, 1987). The vegetation was dominated by gymnosperms, ferns, lycopods, and mosses. Angiosperms evolved in semi-arid, marginal environments along coastal rivers at mid-latitudes. Flowering plants underwent rapid adaptive radiation

during the Early to Mid-Cretaceous, as evidenced in deposits of the Potomac group of Virginia and Maryland (Doyle and Hickey, 1976). Angiosperms subsequently migrated northward following riparian corridors (Thomas and Spicer, 1987).

In southeastern North America, Cretaceous upland environments were confined to the ancient Appalachian Mountains, including the Piedmont, Blue Ridge, Ridge and Valley, and Interior Low Plateaus physiographic regions. Fluctuating shorelines of ancient Cretaceous seas built sedimentary deposits that are now exposed and form much of the inner Coastal Plain, extending from Maryland and Virginia through the Carolinas, Georgia, Alabama, and Mississippi. With continued spreading of the continents, Laurasia became positioned near the North Pole and Antarctica moved over the South Pole, setting the stage for a change in circulation of both oceans and atmosphere that promoted the permanent accumulation of ice and snow at high latitudes. The Cretaceous/Tertiary boundary was significant for mass extinctions of dinosaurs and the subsequent rise of mammals; climate cooling through the Tertiary Period resulted in replacement of many conifers with herb-rich communities and temperate broad-leaved deciduous forest at mid-latitudes of the northern hemisphere (Thomas and Spicer, 1987; Delcourt and Delcourt, 1993, 2000). In southeastern North America, the outer Coastal Plain and Florida Peninsula formed in the late Tertiary and Quaternary periods of the past 3 to 5 million years.

Quaternary history of vegetation in southeastern North America

During the past two million years of the Quaternary Period, the driving mechanism for climate change associated with alternating glacial-interglacial conditions has been the dominance of “Milankovitch” cycles, named for the Serbian scientist who calculated the mathematical relationships between the amount of solar energy intercepted by the Earth at different latitudes through the year given systematic changes in the eccentricity of the Earth’s orbit about the sun along with changes in the wobble and tilt of the Earth’s axis through time (Imbrie and Imbrie, 1979). Relatively cold climate prevails at mid- and high latitudes for some 90% of each 100,000 year “Milankovitch” cycle, promoting expansion of both continental and alpine glaciers; only 10% of each glacial-interglacial cycle is characterized by warm interglacial conditions. The present interglacial interval, the Holocene, began 10,000 years ago and represents an anomalous time in Quaternary history. Further, great changes in seasonality of climate occurs between glacial and interglacial times – the last glacial maximum was characterized by cool but equable climate conditions over much of North America south of the great Cordilleran and Laurentide ice sheets, whereas interglacial times have been characterized by greater contrasts in temperatures between winter and summer. In southeastern North America, pronounced changes in climate thus have occurred during the Quaternary, not as a direct result of presence or absence of glacial ice, but of the way in which incoming solar radiation has been redistributed on a regional and global basis by changes in atmospheric and oceanic circulation patterns (Imbrie and Imbrie, 1979).

The twenty or more glacial-interglacial cycles of climate change that have occurred during the Quaternary Period represent a series of “natural experiments” during

which plant and animal communities have been repeatedly disassembled and reassembled (Delcourt, 2002; Delcourt and Delcourt, 2004), with each episode of glacial-age cooling more severe than the previous one. Whereas glacial-age cooling occurs gradually, over tens of thousands of years, the transition from glacial to interglacial conditions is relatively abrupt, over a few thousand years. In North America, the changeover from Pleistocene to Holocene climates between 15,000 and 10,000 years ago was marked by two distinctive differences from that of previous glacial-interglacial transitions: (1) the extinctions of megaherbivore mammals (>44 kg body weight); and (2) the presence of Paleoindians (Martin and Klein, 1984; Delcourt and Delcourt, 2004).

The effects of ice-age climate cooling on the biota of southeastern North America were profound (Delcourt and Delcourt, 1987). During the most recent glacial maximum, the Laurentide continental ice sheet advanced southward to nearly the confluence of the Ohio and Mississippi rivers. Tundra vegetation was confined to small pockets of cold-air drainage at the edge of the ice sheet and to high elevations in the Appalachian Mountains. Boreal-like forest was widespread south to about 34°N latitude and down to about 300 meters elevation in the southern Appalachian Mountains. Late-Pleistocene boreal forest included a now-extinct species of spruce tree, *Picea critchfieldii*, which was abundant on floodplains and bluffs along the lower Mississippi River valley as well as along the Flint-Chattahoochee-Appalachicola River system (Watts *et al.*, 1992; Jackson and Weng, 1999). Boreal jack pine (*Pinus banksiana*) grew as far south as northern Georgia and central South Carolina (Watts, 1983). Temperate deciduous trees were confined to small “pocket” refuges located along bluffs of major streams such as the Mississippi,

Apalachicola, and Savannah (Delcourt and Delcourt, 1987), as well as to steep-sided watersheds of sinkhole ponds in northern Florida (Watts *et al.*, 1992). Much of the remainder of the southeastern coastal plain and peninsular Florida was arid (Watts, 1983).

Implications for Torreya taxifolia

No record of *Torreya taxifolia* pollen, seeds, leaves, or wood exists from Quaternary deposits in southeastern North America. The closest Quaternary fossil site to present-day stands of this species is Camel Lake, located near Bristol in Liberty County, Florida, at the western edge of the Apalachicola National Forest 6 km east of the Apalachicola River (Watts *et al.*, 1992). Camel Lake has a fossil record extending back 40,000 radiocarbon years before present (yr BP). Before 12,000 yr BP, pine (unidentified species of *Pinus*) dominated the vegetation; after that date oak (*Quercus*) became important until the final rise of southern pine (probably including *Pinus palustris*, *Pinus taeda*, and *Pinus elliottii*) 7800 yr BP. The Camel Lake record is similar to that from Goshen Springs in south-central Alabama (Delcourt, 1980), with fluctuating representation of pine and oak and with nearly continuous representation of pollen of warm-temperate tree taxa such as hickory (*Carya*), bald cypress (*Taxodium distichum*), elm (*Ulmus*), planer tree (*Planera aquatica*), sycamore (*Platanus occidentalis*), hackberry (*Celtis*), sweetgum (*Liquidambar styraciflua*), hornbeam (*Ostrya virginiana* and *Carpinus caroliniana*), American chestnut or chinquapin (*Castanea*), American beech (*Fagus grandifolia*), tupelo gum (*Nyssa aquatica*), and titi (*Cyrilla*) over the past

40,000 years suggesting persistence of a mix of warm-temperate evergreen and deciduous tree taxa (Watts *et al.*, 1992).

It is likely that during the Tertiary Period the range of *Torreya taxifolia* contracted from its evolutionary homeland in and around the southern Appalachian Mountains to a number of more restricted habitats scattered across the southeastern coastal plain. It is also probable that *Torreya taxifolia* has persisted through the Quaternary Period in small pocket refuges throughout the southeastern coastal plain; its restriction to the Apalachicola River Bluffs would therefore have been a result of local extinctions in many of those refugial patches during the changeover from Pleistocene to Holocene conditions between 15,000 and 10,000 years ago. A series of cascading environmental and biotic events, including changes in seasonality of climate, loss of seed dispersers through end-of-Pleistocene extinctions, and changes in fire regime caused by activities of late Paleoindian and Archaic hunter-foragers probably led to the present-day distributional range of *Torreya taxifolia* that we think of as narrowly endemic. The habitat occupied by *Torreya taxifolia* today thus is a relict one but is not representative of the true potential range it occupied at previous times in Earth history. Our dilemma now becomes: What is the most appropriate time-line to consider as the “true” climate/environment zone to which *Torreya taxifolia* is best adapted? Does a present-day and near-future climate/environment zone exist that will be favorable for this species in any part of its former range?

Near-future climate change: global warming

Because of anthropogenically caused increases in carbon dioxide and other greenhouse gases, climate modelers project that in the next one hundred years, global temperatures will be higher than at any previous time in the Holocene interglacial; in the next several centuries, continued global warming could create an Earth's atmosphere as warm as that of Cretaceous times (Kim and Crowley, 1994). The effect of modern industrial humans in all probability will override the Milankovitch climate forcing for as long as ten to fifty thousand years (Kim and Crowley, 1994; Loutre and Berger, 2000). In such a future "greenhouse world," species such as redwoods and their relatives that originated in Cretaceous times may be expected to be favored over more cold-tolerant boreal and tundra species that evolved under much cooler Tertiary and Quaternary environmental conditions. In the southern Appalachian Mountains, boreal-like spruce-fir forest may be expected to become locally extinct, replaced by warm-temperate mixed deciduous-evergreen forests that will include many species that have been characteristic of coastal plain environments during the Quaternary (Iverson *et al.*, 1999). Therefore, the current "potential planting range" for *Torreya taxifolia* identified as the southeastern coastal plain by the Florida Cooperative Extension Service (Gilman and Watson, 1994) may contain little overlap with its potential future range defined by shifting cold hardiness zones with greenhouse warming (Iverson and Prasad, 1999).

The case for ex situ conservation of Torreya taxifolia

The primary reason that Asa Gray wrote up a summary of his pilgrimage to *Torreya* was to promote cultivation of *Torreya taxifolia* as a horticulturally interesting

specimen tree. From its earliest collection, *Torreya taxifolia* was placed in cultivation in a variety of arboreta in the eastern United States; it has been found, however, not to be cold-hardy north of the latitude of Virginia (Bailo *et al.*, 1998). At the turn of the 20th century, *Torreya taxifolia*, *T. californica*, and *T. nucifera* were all in cultivation at the Biltmore Estate near Asheville, North Carolina. *Torreya taxifolia* still thrives there today, with several female trees of reproductive age that bear seed (Alexander, ???).

The most recent attempt at *ex situ* conservation of this species is an ongoing experiment conducted between the Botanic Garden of Smith College, Massachusetts, and the Atlanta Botanical Garden, Georgia, based upon vegetative propagation of rooted cuttings (Barnes, 1985; Bailo *et al.*, 1998). The goal of this attempt at propagation is to preserve the genetic diversity of the species and to produce a large number of rooted cuttings for distribution to additional botanic gardens, agricultural stations, colleges, nature reserves, and state parks in Georgia with the eventual goal of restocking the “native range” of *Torreya taxifolia* in southern Georgia and northern Florida with healthy plants (Schwartz and Hermann, 1993; Bailo *et al.*, 1998).

We propose an even more extensive replanting program to restore *Torreya taxifolia* to its rightful native range in southeastern North America. Given that near-future climate warming may produce environments roughly analogous to those of the Cretaceous across this region, there is every expectation that many coastal plain species will spread northward and replace populations of more-northern species whose tolerances will soon be exceeded. *Torreya*, however, is not likely to expand its range on its own

until there is a successful reintroduction program in the Apalachicola River bluff habitat that includes maturation of both male and female trees that produce viable propagules, and unless there are suitable seed dispersers such as tortoises also reintroduced into that habitat, coupled with establishment of a contiguous corridor of acceptable habitat for migration. These several conditions may not be attained within the time frame necessary for survival of the species. It may therefore be reasonable to contemplate developing a form of “assisted migration” to establish this species in localities to which it is preadapted and in which it will be likely to flourish in the future. Based on the fossil record and prospects of future climate warming, we suggest that mid-elevation slopes of the southern Blue Ridge Mountains may offer the appropriate habitats for such introductions, whether by planting seeds or rooted cuttings.

One potential uncertainty in establishing *Torreya taxifolia* within its potential natural range in the southern Appalachian Mountains concerns its functional role in the plant community (Soule *et al.*, 2003). Having evolved in a Cretaceous world along with other gymnosperms and lycopods, this taxon has long since been largely replaced ecologically by more aggressive angiosperm competitors. Whereas specimen trees growing in a protected arboretum environment may grow vigorously, seedlings planted within an existing forest community may languish unless the functional niche and successional strategy of the species is understood, including responses to various forms of disturbance. Experimental work remains to be done to understand the true potential role of *Torreya taxifolia* in a future greenhouse world.

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