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Deep Time Lags: Lessons from Pleistocene Ecology

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Scientists involved in Gaian research—also known as geophysiology, Earth systems science, or whole-Earth science—as a matter of course provision their global climate and chemical cycling models with their best understandings of time lags inherent in Earth's thermal and chemical reservoirs. For example, how long will it take the carbonic acid content of the world's oceans to equilibrate with today's (and tomorrow's) elevated concentrations of carbon dioxide in the atmosphere?

Time lags are just as important to understand for biodiversity preservation. New forms of population modeling help conservation biologists estimate the probabilities that a particular population (of any given size) of plant or animal will "wink out" owing to fluctuations in natural conditions—even if the population seems to be self-maintaining in the present. Such models have served as wake-up calls to conservationists that even stabilized populations of threatened species may be doomed to extirpation unless their numbers can be increased or corridors established to facilitate cross migration with neighboring populations.

Another kind of time lag also impinges on biodiversity preservation. This time lag has come to the attention of conservation biologists, thanks to the work of those who specialize in Pleistocene ecology. In the late 1970s ecologist Dan Janzen, working in Costa Rica, began to suspect that his studies of seed dispersal in the large-seeded, fruit-bearing plants had gone awry. The studies were flawed by the then-unexamined (and universal) assumption that dispersal candidates could include only those fruit- or seed-eating mammals that *currently* were native to the plant's home range—or that had likely been there just prior to the arrival of Europeans in the Western Hemisphere. Janzen had previously concluded that several large-seeded tropical plants were dispersed by rodents who extracted and buried the seeds for later consumption. But when he noticed the same seeds protruding from the dung of domestic horses, he realized it was time to invite Pleistocene ecologist Paul Martin to join his studies.

Martin advised Janzen that not only were horses native to North America until the close of the last episode of glacial advance (about 13,000 years ago), but there were lots of other now-extinct mammals that might also have coevolved with the plants in question: notably, giant ground sloths and elephant-like gomphotheres (Martin 1990). Janzen and Martin coauthored a now-classic paper in evolutionary ecology; published in *Science* in 1982, they titled it "Neotropical anachronisms: The fruits the gomphotheres ate."

I spent three years examining the genesis of that paper and exploring how its "deep-time" perspective has inspired subsequent research projects in evolutionary ecology and conservation biology. I worked my findings into a popular book, *The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms* (2001). One section of the book used the deep-time perspective to re-examine the circumstances of perhaps the world's most endangered species of conifer tree: the Florida torreya (*Torreya taxifolia*). It occurred to me that torreya's desperate plight owed to its failure to migrate north (perhaps for want of a seed disperser) from its Ice Age refuge in the Florida panhandle to habitat better suited to the tree's needs in peak interglacial times. That better habitat would likely have been the core of torreya's range during previous interglacials: the southern and central Appalachian Mountains.

As it turns out, I was not the first to make this suggestion. Bill Alexander, forest historian at the Biltmore Gardens of Asheville, North Carolina (in the central Appalachian Mountains), observed his garden's own grove of Florida torreya, and concluded that North Carolina seemed more conducive to the well-being of this conifer than was northern Florida (personal communication). In a 1990 article, botanist Rob Nicholson speculated, "Is *Torreya* an early victim of global warming and a precursor of a new wave of inexplicable extinctions?" How prescient he was! Thanks to a host of recent scientific papers (e.g., Barlow and Martin 2005; McLachlan et al. 2007; Hoegh-Guldberg 2008) and popular articles (e.g., Fox 2007; Nijhuis 2008; Marris 2008), Florida torreya has become a "poster plant" for alerting the public and scientists alike to the lurking dangers of global warming and to the consequent need for what has come to be known as *assisted migration*. Assisted migration must not, of course, be promoted as an alternative to reducing greenhouse gas emissions. But it is decidedly unrealistic to assume that climatic change and its challenges to biotic diversity will vanish in the next decade or two. Again, time lags (melting polar and glacial ice) will take a long time to equilibrate even if the concentration of atmospheric CO_2 could politically and economically be stabilized at today's levels.

Assisted Migration in a Time of Global Warming

It is easy to grasp that rapid and profound climate change will exacerbate the biodiversity crisis, especially in those regions where biological preserves are no more than islands of biotic richness encircled by a sea of civilization. As climate shifts regionally (and globally), where might threatened species be encouraged to go, and how will they get there? Conservation biologists are thus now supplementing discussion of geographic corridors for connectivity with talk of assisted migration—that is, direct human involvement in choosing individuals to serve as founders for new populations deliberately transplanted to locations where that species does not currently exist (McLachlan et al. 2007; Hoegh-Guldberg 2008).

Assisted migration is, of course, a less than ideal way for societies to ensure the continued existence of wild populations of plants and animals. The human mark on the future of biotic expression and evolution is already so overwhelmingly in the negative that we yearn for conservation practices that would allow nature itself to direct the recovery process. Yet in some instances, and increasingly so, massive human intervention will be essential for biodiversity preservation. We humans will deliberately choose the would-be immigrants (worse-case scenario: the stricken refugees) and provide the vessel for rapid and safe passage to the promised land. And it is we who will decide where that land is to be found.

Florida torreya has attracted my attention (and increasingly that of others; e.g., Nijhuis 2008) for the simple reason that if there is any plant species for which assisted migration makes sense right now, it is surely America's most endangered conifer. Why? Because *Torreya taxifolia* has been struggling for half a century to persist in its current native range. Despite the best efforts by conservation scientists to nurture and coddle it in the wild, its numbers diminish each passing year. It is my contention that the combination of peak-interglacial climate conditions that the world is now in, elevated by human contributions to global warming, have for fifty years been urging this large-seeded (and charismatic) conifer tree to head north to cooler realms.

In the 1950s Florida torreya suffered a catastrophic decline, the ultimate cause of which is still unexplained. By the mid-1960s, no large adult specimens—which once measured more than a meter in circumference and were perhaps 20 meters tall—remained in the wild, felled by what seemed to be a variety of fungal pathogens. Today, the wild population persists as mere stump sprouts, cyclically dying back at the sapling stage, such that seeds are rarely, if ever, produced. *T. taxifolia* thus joins American chestnut in maintaining only a juvenile and diminishing presence in its present range.

Florida torreya is a yewlike conifer. Its large, single seed resembles that of a plum; it is encased in a fleshy packet (as is the seed of a yew). Historically, it has been found only along a short stretch of the Apalachicola River of northern Florida and the adjacent sliver of southern Georgia. It favors the cool and shady ravines that dissect the high bluffs of the river's eastern shore. Despite its current extreme endemism, the species was once a prominent mid- and understory member of its forest community, which even today includes an odd mix of northern and southern species: towering beech and hickory next to tall evergreen magnolia, and surrounded by stubby needle palm.

Prehistorically, the ancestral torreya species almost surely thrived as an understory tree on the slopes of the Appalachian mountains. As with its mountain-dwelling cousin to the west, California Torreya (*Torreya californica*), America's eastern torreya would have been shade-adapted, growing slowly while awaiting an opening in the canopy for the additional sunlight required to produce seed. The Appalachian torreya would have been similar to California Torreya in its supreme ability to re-sprout from rootstock after a fire, thus giving the plant a chance to mature and produce seeds (or pollen, as the genus is characterized by distinctively male or female trees), before the new recruits of rival species could shade it, once again, into a nonreproductive phase of survival.

Fundamentally, a deep-time perspective helps us see that the Apalachicola River of northern Florida is best understood as native habitat for eastern torreya only during a peak of glacial advance. After all, there is no dispute that the Apalachicola served as one of eastern North America's most important refugia during ice times (Delcourt 2002). There are still a few scattered beech trees lingering in the rich soils along that river, but the great bulk of the beech population long ago migrated and settled far to the north. A deep-time perspective thus opens up a new line of questioning: where would native range for species X have been during a peak interglacial—or during even more ancient times (species of genus *Torreya* coexisted with Cretaceous dinosaurs) when global climate was even warmer than it is today?

Assisted migration as a conservation tool is both fascinating and frightening for anyone focused on plants. It is fascinating because endangered plants can be planted by whomever so chooses, with no governmental oversight or prohibitions—provided that private seed stock is available and that one or more private landowners volunteer suitable acreage toward this end. This cheap-and-easy route for helping imperiled plants is in stark contrast to the high-profile, high-cost, and governmentally complicated range recovery programs for mobile animals, like gray wolf, lynx, and California condor.

Assisted migration frightens for precisely the same reasons it fascinates: anybody can do it, for good or ill, and with care or abandon. Its promotion could undermine decades of public education about the dangers of nonnative plants, as well as more recent efforts to promote the concept of wildlands corridors and connectivity. Still, in an age of deforestation, severe habitat fragmentation, and rapid global warming, assisted migration as a plant conservation tool should not be ignored. According to Peter Wharton, curator of the Asian Garden of the University of British Columbia Botanical Garden writes, the *Torreya* question is a door to immense issues relating to how we facilitate global "floraforming" of vegetational zones in a warming world. It represents another layer of responsibility for those of us who have a passion for forests and wish to promote the ecologically sensitive reforestation of so many degraded forest ecosystems worldwide (P. Wharton, personal communication).

The test case for assisted migration occurred in July 2008 when the citizen group I helped found (Torreya Guardians) undertook assisted migration for 31 seedlings of *Torreya taxifolia* purchased from a nursery in South Carolina. A handful of volunteers (and reporters documenting the action) gathered in the mountains near Waynesville, North Carolina, to spend a day planting the seedlings into wild forested settings on two parcels of private land. The Torreya Guardians' website documents that action.[1]

Deep-Time Lags and the Imperative for Rewilding

The plight of the endangered Florida torreya tree is an exemplar of deep-time lags in which a species seems to have gotten "stuck" (perhaps for lack of its seed disperser) in once-suitable habitat that is no longer capable of supporting its survival. A second example of deep-time lags that is already informing the leading edge of conservation thinking involves plant–animal interactions at the landscape level. This is the proposal for "Pleistocene rewilding" (Donlan et al. 2005, 2006).

In 2005 a dozen leaders in conservation biology, led by Josh Donlan, coauthored a short advocacy piece (a "commentary") in *Nature* in which they contended that even the most biologically intact wilderness parks in America are missing key components of ecological interactivity. These components moreover had shaped American landscapes over millions of years. Notably, the zones of America too dry to support closed-canopy forests now lack the large mammalian plant browsers—as well as the large carnivores that had preyed upon those browsers—that had thrived in those areas throughout the Pleistocene epoch. Humans had brought back the large grazers (cattle and horses), but the browsers (camels, ground sloths, mammoths, and mastodons) were absent, and so were the large predators.

In consequence what ecologists had considered to be natural configurations of native vegetation were actually quite the contrary—at least from a deep-time perspective. Lacking capable carnivores and big browsers, much of the American west's grasslands, savannas, and deserts had been damaged by hoofed grazers, fostering soil erosion and selecting for the proliferation of shrubby plants (e.g., mesquite, creosotebush, and sagebrush). Cattle and horses eschew these shrubs—but such plants would have been eaten by big browsers native to North America during the ice times of the Pleistocene. Thus came the Pleistocene rewilding proposal to return close proxies of the lost browsers (Bactrian camels for America's extinct *Camelops*) and carnivores (the African lion for America's extinct lion) to carefully chosen test ranges of the American West.

In a longer paper published in 2006, the same set of authors elaborated on the half dozen reasons to undertake a test of the rewilding concept. One such reason is to offer Pleistocene ecologists a chance to witness and study how Pleistocene megafauna would likely have shaped the vegetational landscape of the arid and semiarid American west. Another is to provide the public with a chance to witness something similar to the pageant of American wildlife that would have greeted the first human immigrants to this continent (predecessors of the now native American peoples). What makes this radical proposal even possible is time lags. Communities of plant species have changed enormously since the end of the Pleistocene. But no once-dominant plant species of the savanna or grassland appears to have gone extinct (Delcourt 2002). Rather, it is the *patterning* of vegetation that is the character in question.

Unlike *Jurassic Park* fantasies of resurrecting the dinosaurs, the proposal to jump-start one or more Pleistocene parks is not only within the realm of possibility but arguably an ethical imperative. Humans are not responsible for the death of the nonavian dinosaurs. Yet the majority opinion in science is that humans are at least partly culpable for the huge loss of megafaunal species at the end of the ice times. Earth's "sixth mass extinction" began some 50,000 years ago when spear-toting, fire-wielding humans made their way to the once-isolated continent of Australia, and eventually into the Americas and onward to the islands of Polynesia, Madagascar, and New Zealand.

Deep-time lag, because of which continental vegetation has not yet fully adjusted to the loss of browsers, is the reason rewilding is a scientifically responsible proposal—even 13,000 years after America's "extinction of the massive" (Martin 2005). A deep-time perspective, penetrating far into the future, invokes a felt urgency for humans to engage in repopulating this continent with megafaunal stock that may eventually re-evolve species truly *native* to this land. This is the ethical ground from which the rewilding proposal ultimately springs. Here is how the dozen scientists and conservationists proposing "Pleistocene rewilding" concluded their call to action:

> In the coming century, by default or design, we will constrain the breadth and future evolutionary complexity of life on Earth. The default scenario will surely include ever more pest-and-weed dominated landscapes, the extinction of most, if not all, large vertebrates, and a continuing struggle to slow the loss of biodiversity. Pleistocene re-wilding is an optimistic alternative.
>
> We ask of those who find the objections compelling, are you content with the negative slant of current conservation philosophy? Will you settle for an American wilderness emptier than it was just 100 centuries ago? Will you risk the extinction of the world's megafauna should economic, political, and climate change prove catastrophic for those populations remaining in Asia and Africa? The obstacles are substantial and the risks are not trivial, but we can no longer accept a hands-off approach to wilderness preservation. Instead, we want to reinvigorate wild places, as widely and rapidly as is prudently possible. (Donlan et al. 2005: 914)

In conclusion, the deep-time perspective that comes naturally to those who work in the realm of geophysiology can now become the lens through which conservation biologists and other biodiversity activists go about their work. Specifically, the deep-time perspective encourages conservationists to revise the parameters we use for judging which species are native to a region. It also encourages us to be mindful of time lags in biological adjustments to shifts in climate, and thus in how we read the past and how we prepare for the future.

Note

1. The Torreya Guardians' website has a page dedicated to providing citations and links to the classic and current scientific papers and news reports on the assisted migration debate and actions: www.TorreyaGuardians.org/assisted-migration.html.

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