Comment: "Great oak workshop, BTW. While Nowacki made a good case for oaks being evolved to fire, as I thought about it, I am not sure I agree. Fire was very common on the landscape only over the past 10,000 years in North America. While some landscape fire occurs without humans, frequent landscape fire is a distinctly human thing. But oaks evolved over a much longer time period, in the absence of humans and frequent fire. I think an equally strong argument could be made for oaks as mastodon adapted. Elephants today are ecosystem engineers. Elephants today create savannas. And mastodons were a common animal in North America (prior to humans.) It struck me that telling a skidder operator never to follow the same track in order to "flatten" oak and non-oak regen (or dragging "big spiked balls" through the forest to "tear things up") certainly sounds like elephant disturbance. Maybe oaks systems still exist only because Native American fires mimicked mastodon disturbance closely enough to allow oaks to continue to thrive".

GJN Response: Well, leave it up to a wildlife biologist to take on this perspective—quite intriguing! Here's some additional information for clarification and consideration.

Fire has a very long history on Earth, with fossil charcoal evidence dating back to the Silurian (416-444 million years ago (Mya); Glasspool et al. 2004). By the Carboniferous (299-359 Mya) charcoal was common and, ever since, wildfire has been a key evolutionary force shaping global ecosystems (Scott 2000, Pausas and Keeley 2009, Bowman et al. 2009). Natural ignitions, in the form of lightning (principally), volcanoes, rock falls, and meteorite strikes, prevailed until human acquisition of fire. Although it is difficult to ascertain exactly when hominids mastered fire and became important ignitors (this subject is wrought with controversy; see James et al. 1989), there is conclusive evidence of fire use by 1 Mya (Berna et al. 2012). From that time forward, humans have increasingly used fire to modify their environments (Bowman et al. 2011), with over 70 documented uses (Lewis 1993)!

Only natural ignitions existed on the North American continent until the relatively late arrival of humans at the end of the Pleistocene at least 14-15 thousand years ago (Kya) (Erlandson 2013, Amick 2016). At that time, vegetation zones (biomes) were compressed along the southern portions of the continent that have no modern analogue (Overpeck et al. 1992, Williams et al. 2004). During the Last Glacial Maximum, roughly 21 Kya, oak was largely confined to the Coastal Plain from east Texas to the Carolinas (Jackson et al. 2000). Over time, the range of oak expanded northward, stabilizing after 12 Kya and reaching modern-day abundances in east-central U.S. during the mid-Holocene roughly 9 Kya (Williams et al. 2004, Abrams 2002, Lorimer and White 2003).

Based on various ecophysiological characteristics, oak is a disturbance-based genus that seemingly benefits most from recurrent fire. However, other disturbance agents may have historically played an important role in fostering oak. Indeed, prior to human arrival and their pyrotechnic activities, disturbance by Pleistocene megafauna may have filled this niche to various degrees through grazing, browsing, trampling, and soil churning. Surely, one would think that oak would benefit from the open landscapes maintained by megafaunal disturbance. However, the dependency of oak ecosystems on megafaunal activities is tenuous as oaks did not develop megaherbivore defenses to ensure or improve survival under intense browsing pressure, such as stout thorns found on honey locust (*Gleditsia*), hawthorns (*Crataequs*), mesquite (*Prosopis*) and Osage-orange (*Maclura*) (Nowacki et al. 2012). Moreover, acorns are not reliant on megaherbivores for seed scarification and dispersal like anachronistic trees, including Kentucky coffee tree (Gymnocladus), honey locust, Osage-orange, pawpaw (Asimina), and persimmon (Diospyrus), all of which declined after megafaunal extinction (Janzen and Martin 1982, Barlow 2001). Multiproxy studies of pollen (vegetation), charcoal (fire), and dungspore fungus Sporormiella (megafauna presence) have shown positive oak responses more closely associated with fire; fires that either increased simultaneously with local megafaunal extinction (Binnewater Pond, NY; Robinson et al. 2005) or lagged by several thousand years (Pawelski Farm and Otisville, NY, Robinson et al. 2005; Appleman Lake, IN, Gill et al. 2009; Silver Lake, OH, Gill et al. 2012). In any event, the termination of megafaunal herbivory probably enhanced fire regimes through fuel loading and reduced landscape heterogeneity that would have facilitated fire frequency and spread (Gill 2014).

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