GEOPHYSICAL RESEARCH LETTERS, VOL. 37, L15703, doi:10.1029/2010GL043985, 2010

Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming?

Christopher E. Doughty,[1] Adam Wolf,[1] and Christopher B. Field[1]

Received 13 May 2010; revised 17 June 2010; accepted 21 June 2010; published 7 August 2010.

[1] A large increase in *Betula* during a narrow 1000 year window, ~13,800 years before present (YBP) in Alaska and Yukon corresponded in time with the extinction of mammoths and the arrival of humans. Pollen data indicate the increase in *Betula* during this time was widespread across Siberia and Beringia. We hypothesize that *Betula* increased due to a combination of a warming climate and reduced herbivory following the extinction of the Pleistocene mega herbivores. The rapid increase in *Betula* modified land surface albedo which climate-model simulations indicate would cause an average net warming of ~0.021°C per percent increase in high latitude (53–73°N) *Betula* cover. We hypothesize that the extinction of mammoths increased *Betula* cover, which would have warmed Siberia and Beringia by on average 0.2°C, but regionally by up to 1°C. If humans were partially responsible for the extinction of the mammoths, then human influences on global climate predate the origin of agriculture.

Citation: Doughty, C. E., A. Wolf, and C. B. Field (2010), Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming?, *Geophys. Res. Lett.*, *37*, L15703, doi:10.1029/2010GL043985.

1. Introduction

[2] Megafauna (defined as animals >44kg) experienced a global extinction with 97 of 150 genera going extinct by ~10,000 YBP [*Barnosky et al.*, 2004]. These extinctions, including such keystone taxa as mammoths, may have been driven by human over-hunting, climate change, or a combination of the two [*Barnosky et al.*, 2004].

[3] An excavation of a Paleolithic site in Siberia containing points, scrapers and "vast quantities of Pleistocene bones, especially mammoth bones" [*Pitulko et al.*, 2004], indicates hunting of Pleistocene megafauna by humans. Under certain assumptions, such kill sites are common for mammoths [*Barnosky et al.*, 2004]. In Eurasia, many cold-adapted species, including mammoths, went extinct between 14,000 and 10,000 YBP [*Barnosky et al.*, 2004], during a period of increasing population sizes of *Homo sapiens sapiens* [*Bar-Yosef*, 2002; *Barnosky et al.*, 2004]. The evidence that humans had a role in the extinction of mammoths is stronger than for other Pleistocene megafauna [*Guthrie*, 2006].

[4] Changing climate may also have caused the extinction of the Pleistocene megafauna [*Barnosky et al.*, 2004; *Guthrie*, 2003]. For instance, *Guthrie* [2003] suggested that the declining body size and eventual extinction of horses in Alaska occurred because vegetation changes caused by a warming climate decreased access to optimal foods [*Guthrie*, 2003]. Vegetation changed drastically in Alaska [*Guthrie*, 2006] and in the Eastern US [*Gill et al.*, 2009] as the megafauna went extinct. This drastic change in vegetation can alternatively be explained by reductions in megafauna populations leading to vegetation changes.

[5] In the past, it has been difficult to determine whether the vegetation change took place before or after the Pleistocene megafauna went extinct. The difficulty was compounded because megafauna remains are rare, especially in the lakes that generally archive late Quaternary pollen records. However, *Sporormiella* spores follow the end-Pleistocene megafauna population decline: they are abundant in late-glacial sediments, rare through the Holocene, and increase in abundance with the historic introduction of domestic grazers [*Davis and Shafer*, 2006]. A recent study used these spores to show that vegetation change followed the extinction of the Pleistocene megafauna in North America versus preceded it as had been previously thought [*Gill et al.*, 2009].

[6] This is not unexpected because living megafauna play a dominant role in the maintenance of grasslands against the expansion of trees in savannas [*Caughley*, 1976; *Owens-Smith*, 1988]. Woody cover increased ~9% over ~36 years when fauna (>5kg) were excluded from a large African savanna [*Asner et al.*, 2009]. The maintenance of low woody cover is mainly driven by elephants, which uproot up to 1500 trees per elephant per year [*Duffy et al.*, 1999]. The biogeochemistry of the mammoth steppe of the Pleistocene may have functioned like current grazing systems in Africa [*Owens-Smith*, 1988], with abundant herbivores maintaining productivity by enhancing the rate of nutrient cycling through more labile biomass pools [*Zimov et al.*, 1995]. Mammoth diets may have been similar to the diet of African elephants as excavated guts of frozen mammoths contain grass and a variety of common Pleistocene tree species such as willow, birch, larch and alder [*Lister and Bahn*, 2007]. With the demise of mammoths and other herbivores, forests would tend to thicken and/or expand [*Lister and Bahn*, 2007].

[7] During the warming that led to the Holocene, vegetation changed rapidly in the high latitudes of Eurasia and North America [*Binney et al.*, 2009; *Williams et al.*, 2004]. This increase in tree cover has important positive biophysical feedbacks as the replacement of boreal grasses by forests can decrease the surface albedo by 0.25, increasing the absorption of solar radiation, and causing local warming of up to 6°C [*Bala et al.*, 2007; *Foley et al.*, 1994].

[8] Was the disappearance of the mammoths a significant driver of changes in climate through the following scenario? Climate change and hunting reduced mammoth populations, which allowed the rapid expansion of dwarf deciduous trees at high latitudes (Figure 1). Additional dwarf tree growth decreased surface albedo, which accelerated climate change

---

[1] Department of Global Ecology, Carnegie Institution for Science, Stanford, California, USA.

0094-8276/10/2010GL043985

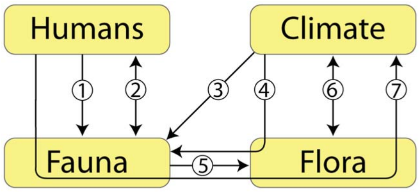

Figure 1. End-Pleistocene interactions between humans, flora, fauna, and climate. Arrow (1) is the "Overkill" hypothesis. *Alroy* [2001] expanded this hypothesis to include faunal control over human population density (2). A direct climate effect on Pleistocene fauna (3) is summarized by *Barnosky et al.* [2004]. (4) *Guthrie* [2003] suggests that climate impacted the health of Pleistocene fauna indirectly through flora. An alternative explanation is that changes in faunal population size and composition drove changes in North American floral assemblages (5), which is corroborated by *Gill et al.* [2009]. A separate set of literature [*Foley et al.*, 1994] examines climate-vegetation feedbacks in the Earth system (6). This study (7) examines a new mechanism for anthropogenic climate change via human impact on fauna, consequent change in vegetation, leading to carbon and albedo-driven changes in radiative forcing on climate.

and further stressed the remaining megafauna populations. This positive feedback accelerated global warming in a sensitive ecosystem.

[9] In this paper, we show pollen data that indicate a rapid increase for *Betula* in Siberia and Beringia close to the time of the extinction of the Pleistocene megafauna and hypothesize that this increase cannot be completely attributable to climate. We estimate what part of this increase was due to the extinction of the Pleistocene mega herbivores using an elephant-vegetation model [*Duffy et al.*, 1999] and what impact this would have on climate using a climate model (NCAR's CAM 3.0 coupled with the CLM 3.0 and a slab ocean model [*Collins et al.*, 2006]).

2. Methods

[10] We compiled pollen records from the Global Pollen Database (http://www.ncdc.noaa.gov/paleo/ftp-pollen.html) in Alaska, Siberia, and the Yukon Territory >15000 YBP between 53–73°N latitude focusing on 28 with the highest resolution (Table S1 of the auxiliary material).[1] We convert pollen data to estimated vegetation cover using the model REVEALS [*Sugita*, 2007] (further described in the auxiliary material). We used Alaskan mammoth and human archeological dates from the supporting material of *Guthrie* [2006]. We use the Fairbanks calibration curve [*Fairbanks et al.*, 2005] to convert radiocarbon years to calendar years. We used Greenland and EPICA ice core temperature and CO_2 proxies (http://www.ncdc.noaa.gov/paleo/icecore.html) to determine changes in global temperatures and atmospheric CO_2 concentrations.

[11] To simulate global climate, we used NCAR's CAM 3.0 [*Collins et al.*, 2006], coupled with the CLM 3.0 and a slab ocean model at a 20 minute time step with a resolution of 2° by 2.5° at the equator for 100 years at 280 ppm CO_2. We varied the percentage cold adapted boreal deciduous dwarf trees and grass cover in Eurasia and Beringia between 53–73°N latitude and 50°E–130°W by increasing dwarf tree cover 20–80% in 20% increments while decreasing percentage grass cover by the same amount [*Edwards et al.*, 2000]. We modeled dwarf trees (2m tree height) to reflect the diminutive stature of high latitude *Betula*. To evaluate the effect of changing CO_2 concentrations on local and global temperatures, we ran four climate simulations at 250, 260, 270 and 280 ppm with high latitude dwarf tree cover at 60% and grassland cover at 40%.

[12] We used a Lotka-Volterra predator-prey model, extended by *Caughley* [1976] and *Duffy et al.* [1999] to represent realistic elephant-vegetation interactions. We parameterized this model to estimate possible changes in vegetation cover by mammoth populations, using low vegetation growth ($a = 0.015$) because Siberia is colder than the African savannas, which will slow tree growth. There is a wide range of tree densities in Siberia and elephant behaviors towards trees. To account for this variation we used the Monte Carlo method to simulate 5000 tree mammoth interaction scenarios with realistic Siberian tree densities [*Usoltsev*, 2001]) and rates of dwarf tree elimination by mammoths (between 40–1200 trees per mammoth per year [*Duffy et al.*, 1999]) to estimate Siberian and Beringian dwarf tree cover into the Holocene with mammoths.

3. Results and Discussion

[13] There was a large, rapid increase in *Betula* pollen that roughly correspond in time with archeological evidence of people and the extinction of mammoths in Alaska (Figure 2a). This rapid increase in *Betula* appears widespread across Siberia, Alaska, and the Yukon, with *Betula* abundance increasing abruptly ($\geq 1\%$ century^{-1}) in 28 pollen records (Table S1). The percentage of the land surface covered by *Betula* increased on average by 26% (between 5% to 54%) over an average of 850 ± 570 years (between 350 and 2100 years) with the largest increase taking place on average 15200 ±1300 YBP. The average maximum rate of increase in *Betula* across all sites was ~0.4% decade^{-1}, comparable to the ~2.4% increase per decade in African megafauna exclusions [*Asner et al.*, 2009]. During the 850 year period of this rapid increase in dwarf tree cover, Antarctic ice core temperatures increased by ~2°C and atmospheric CO_2 concentrations increased by ~15ppm [*Augustin et al.*, 2004]. Greenland ice core temperatures showed more variability during this period with a 3°C max to min change but a linear trend of less than a degree [*Alley*, 2000].

[14] The climate was rapidly changing over a broad 6000 year window between ~17000–11000 years ago [*Augustin et al.*, 2004] (Figure 2). *Betula* was present in 25 of 28 sites before the rapid increase in tree cover, indicating that the trees were physiologically able to survive the arid, cold, low CO_2 conditions of the Pleistocene. Temperature, precipitation, and atmospheric CO_2 concentrations all became more favorable to trees during the Holocene, but changes in environmental conditions may not completely explain the very rapid increase in *Betula* between ~14500–15500 YBP.

[15] We used a simple model that predicts megafauna impact on vegetation cover with a range of realistic, mature Siberian vegetation densities [*Usoltsev*, 2001] and a range of mammoth behavior scenarios (40–1200 trees/mammoth/year)

---

[1] Auxiliary materials are available in the HTML. doi:10.1029/2010GL043985.

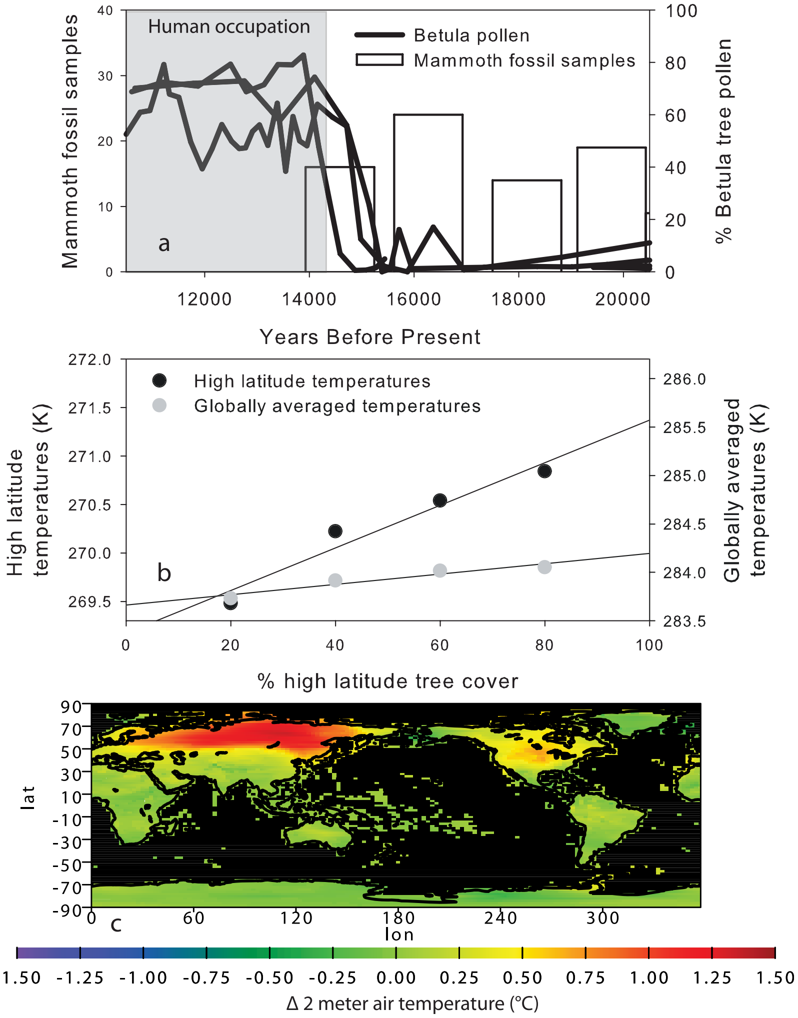

Figure 2. (a) Percent *Betula* tree pollen (Joe Lake, Screaming Yellowlegs Pond, and Rebel Lake, Alaska), Alaskan mammoth fossils and archeological evidence of human occupation in Alaska (grey box) from *Guthrie* [2006]. (b) Globally averaged surface temperatures (grey) and annually averaged high latitude (53–73°N) land surface temperatures (black) for scenarios where we varied high latitude vegetation cover from 20% to 80% deciduous dwarf tree cover. (c) A global map showing 2 meter air temperatures where we subtracted a run where dwarf trees cover 40% of high latitudes from a run where they cover 20% of high latitudes.

based on the wide range of behaviors present in elephant sub-populations (Figures 3 (top) and S2). Many mammoth behaviors mimic elephant behaviors, and mammoth steppes functioned in an ecologically similar way to African savannas [*Lister and Bahn*, 2007].

[16] In regions with dense vegetation and active mammoth sub-populations, our model attributes >50% of the increase in *Betula* to the extinction of the mammoths, while in regions of sparse vegetation and non-active mammoth sub-populations our model attributes <10% of the increase in *Betula* to the extinction of the mammoths, with the remaining increase by default due to climate. Using 5000 Monte Carlo scenarios, we estimate that mammoths would have decreased *Betula* from carrying capacity, which was determined using actual changes in deciduous tree cover (Table S1) following the extinction of the mammoths, by an average of ~23% (Figure 3). Such a result is supported by a study that found a large increase in shrub cover (which has similar snow masking effects as trees [*Sturm et al.*, 2005]) relative to grasses during the Holocene versus the previous interglacial period [*Willerslev et al.*, 2003].

[17] Climate simulations indicate that globally averaged surface temperatures increased at a rate of 0.005°C for each percent increase of high latitude deciduous dwarf tree cover, or by 0.13° C with a 20% increase in dwarf tree cover (Figure 2). These temperature increases were concentrated in the high latitude regions (53–73° N) (Figure 2) with average surface temperatures increasing by 0.44° C when dwarf tree cover increased 20%, a rate of 0.022° C per % increase in dwarf tree cover. Our simulations indicate that for each percentage increase of forest cover at high latitude, atmospheric CO_2 decreases by ~0.05 ppmv [*Bala et al.*, 2007], causing a global cooling of ~0.0007°C. Combining albedo and carbon cycle feedbacks, globally averaged 2-meter air temperatures increase by ~0.0043°C (0.005°C − 0.00070° C) and regionally by ~0.021°C for each percent increase in dwarf tree cover at high latitudes. Similar feedbacks have been

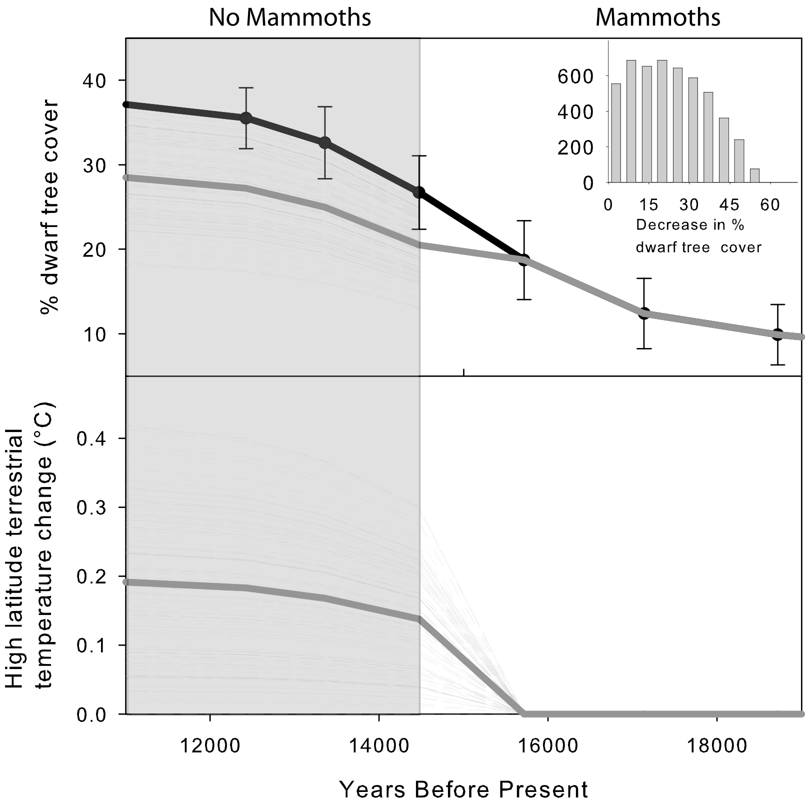

Figure 3. (top) Mean ± sd percentage *Betula* and other deciduous trees and shrubs of total land surface cover (black solid line) from 28 Siberian and N. American pollen datasets. The grey box indicates the period when mammoths were thought to have become extinct in Siberia and Beringia. Thin grey lines (n = 100, reduced from 5000 for clarity) are Monte Carlo simulations (average value is thick dark grey line) with modified tree densities [*Usoltsev*, 2001] and mammoth behavior to predict dwarf tree cover if mammoths were still present. The inset is a histogram of 5000 Monte Carlo simulations showing predicted percentage decrease in dwarf tree cover due to mammoths. (bottom) The predicted increase in high latitude (53–73°N) surface air temperatures (C) based on climate simulations for each of the Monte Carlo simulations (average is thick dark grey line).

demonstrated in several other studies [*Bala et al.*, 2007; *Bonan et al.*, 1992].

[18] We can combine the results of our climate simulations and vegetation model to estimate the climate impact of the rapid increase in Betula. Pollen datasets show that *Betula* increased to cover ~26 ± 11% of the total land surface through much of Siberia and Beringia, which our climate simulations indicate would warm high latitude terrestrial land surfaces by 0.54°C. If we estimate that, on average, 23% of this increase were due to mammoths, we could further estimate that due to the extinctions, Betula would cover 6% more of the total land surface (of the 26% total increase) than without extinctions, which would have a 0.13°C additional regional climate warming effect. By 10,000 YBP this effect would have increase to 0.2°C as total deciduous tree cover increased (Figure 3, bottom), with some regional effects of >1°C (Figure 2).

[19] In this paper, we challenge the idea that climate alone drove the rapid increase in *Betula* across Siberia and Beringia between 14,000 to 15,000 YBP and the extinction of the mammoths had a minimal impact on land surface cover. *Betula* is considered a pioneer species that can rapidly colonize open ground following disturbance. Even with no assumptions about mammoth behavior, we would, however, still predict a rapid expansion of existing *Betula* populations due to the extinction of the Pleistocene megafauna. Many of the extinct Pleistocene mega fauna were keystone herbivores that consumed much Net Primary Production. In the absence of this herbivory, both grasses and trees would tend to increase in size, but the trees would eventually overtop the grasses and establish their dominance. Many complex factors affect the transition between grasses and trees including fire, temperature, aridity, growing season length, and winter temperatures, which all were changing in the transition from the Pleistocene to the Holocene. However, increased tree growth from all these factors would be further accelerated in the absence of the herbivory of the mega herbivores [*Scholes and Archer*, 1997].

[20] It is a highly controversial issue, but there is evidence indicating that humans hunted mammoths and may have been partially responsible for their extinction [*Barnosky et al.*, 2004; *Guthrie*, 2006]. The timing of the palynologic evidence suggests that the extinction of the mammoths contributed to a rapid increase in dwarf tree cover, which according to our climate simulations, has a high-latitude warming effect. Together, these results suggest that the human influence on climate began even earlier than previously believed [*Ruddiman*, 2003] and that the onset of the Anthropocene should be extended back many thousand years.

[21] **Acknowledgments.** This work is funded by a Carnegie fellowship (CED) and a NASA ESS fellowship (AW). We thank Julia Pongratz for comments on the manuscript and Joe Berry for advice.

References

Alley, R. B. (2000), The Younger Dryas cold interval as viewed from central Greenland, *Quat. Sci. Rev.*, *19*(1–5), 213–226, doi:10.1016/S0277-3791(99)00062-1.

Alroy, J. (2001), A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction, *Science*, *292*(5523), 1893–1896, doi:10.1126/science.1059342.

Asner, G. P., S. R. Levick, T. Kennedy-Bowdoin, D. E. Knapp, R. Emerson, J. Jacobson, M. S. Colgan, and R. E. Martin (2009), Large-scale impacts of herbivores on the structural diversity of African savannas, *Proc. Natl. Acad. Sci. U. S. A.*, *106*(12), 4947–4952, doi:10.1073/pnas.0810637106.

Augustin, L., et al. (2004), Eight glacial cycles from an Antarctic ice core, *Nature*, *429*(6992), 623–628, doi:10.1038/nature02599.

Bala, G., K. Caldeira, M. Wickett, T. J. Phillips, D. B. Lobell, C. Delire, and A. Mirin (2007), Combined climate and carbon-cycle effects of large-scale deforestation, *Proc. Natl. Acad. Sci. U. S. A.*, *104*(23), 9911, doi:10.1073/pnas.0704096104.

Bar-Yosef, O. (2002), The Upper Paleolithic revolution, *Annu. Rev. Anthropol.*, *31*, 363–393, doi:10.1146/annurev.anthro.31.040402.085416.

Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel (2004), Assessing the causes of Late Pleistocene extinctions on the continents, *Science*, *306*(5693), 70–75, doi:10.1126/science.1101476.

Binney, H. A., et al. (2009), The distribution of late-Quaternary woody taxa in northern Eurasia: Evidence from a new macrofossil database, *Quat. Sci. Rev.*, *28*(23–24), 2445–2464, doi:10.1016/j.quascirev.2009.04.016.

Bonan, G. B., D. Pollard, and S. L. Thompson (1992), Effects of boreal forest vegetation on global climate, *Nature*, *359*(6397), 716–718, doi:10.1038/359716a0.

Caughley, G. (1976), The elephant problem-an alternative hypothesis, *J. East Afr. Wildlife*, *14*, 265–283.

Collins, W. D., et al. (2006), The Community Climate System Model version 3 (CCSM3), *J. Clim.*, *19*(11), 2122–2143, doi:10.1175/JCLI3761.1.

Davis, O. K., and D. S. Shafer (2006), Sporormiella fungal spores, a palynological means of detecting herbivore density, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *237*(1), 40–50, doi:10.1016/j.palaeo.2005.11.028.

Duffy, K. J., B. R. Page, J. H. Swart, and V. B. Bajic (1999), Realistic parameter assessment for a well known elephant-tree ecosystem model reveals that limit cycles are unlikely, *Ecol. Modell.*, *121*(2–3), 115–125, doi:10.1016/S0304-3800(99)00091-5.

Edwards, M. E., et al. (2000), Pollen-based biomes for Beringia 18,000, 6000 and 0 C-14 yr BP, *J. Biogeogr.*, *27*(3), 521–554, doi:10.1046/j.1365-2699.2000.00426.x.

Fairbanks, R. G., R. A. Mortlock, T. C. Chiu, L. Cao, A. Kaplan, T. P. Guilderson, T. W. Fairbanks, A. L. Bloom, P. M. Grootes, and M. J. Nadeau (2005), Radiocarbon calibration curve spanning 0 to 50,000 years BP based on paired Th-230/U-234/U-238 and C-14 dates on pristine corals, *Quat. Sci. Rev.*, *24*(16–17), 1781–1796, doi:10.1016/j.quascirev.2005.04.007.

Foley, J. A., J. E. Kutzbach, M. T. Coe, and S. Levis (1994), Feedbacks between climate and Boreal forests during the Holocene epoch, *Nature*, *371*(6492), 52–54, doi:10.1038/371052a0.

Gill, J. L., J. W. Williams, S. T. Jackson, K. B. Lininger, and G. S. Robinson (2009), Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America, *Science*, *326*(5956), 1100–1103, doi:10.1126/science.1179504.

Guthrie, R. D. (2003), Rapid body size decline in Alaskan Pleistocene horses before extinction, *Nature*, *426*(6963), 169–171, doi:10.1038/nature02098.

Guthrie, R. D. (2006), New carbon dates link climatic change with human colonization and Pleistocene extinctions, *Nature*, *441*(7090), 207–209, doi:10.1038/nature04604.

Lister, A., and P. Bahn (2007), *Mammoths: Giants of the Ice Age*, Univ. of Calif. Press, Berkeley.

Owens-Smith, R. N. (1988), *Megaherbivores: The Influence of Very Large Body Size on Ecology*, Cambridge Univ. Press, London.

Pitulko, V. V., P. A. Nikolsky, E. Y. Girya, A. E. Basilyan, V. E. Tumskoy, S. A. Koulakov, S. N. Astakhov, E. Y. Pavlova, and M. A. Anisimov (2004), The Yana RHS site: Humans in the Arctic before the Last Glacial Maximum, *Science*, *303*(5654), 52–56, doi:10.1126/science.1085219.

Ruddiman, W. F. (2003), The anthropogenic greenhouse era began thousands of years ago, *Clim. Change*, *61*(3), 261–293, doi:10.1023/B:CLIM.0000004577.17928.fa.

Scholes, R. J., and S. R. Archer (1997), Tree-grass interactions in savannas, *Annu. Rev. Ecol. Syst.*, *28*, 517–544, doi:10.1146/annurev.ecolsys.28.1.517.

Sturm, M., T. Douglas, C. Racine, and G. E. Liston (2005), Changing snow and shrub conditions affect albedo with global implications, *J. Geophys. Res.*, *110*, G01004, doi:10.1029/2005JG000013.

Sugita, S. (2007), Theory of quantitative reconstruction of vegetation I: Pollen from large sites REVEALS regional vegetation composition, *Holocene*, *17*(2), 229–241, doi:10.1177/0959683607075837.

Usoltsev, V. A. (2001), *Biomass of Forests in Northern Eurasia: Database and Geography* (in Russian), 707 pp., Russ. Acad. of Sci., Ural Branch, Ekaterinburg, Russia.

Willerslev, E., A. J. Hansen, J. Binladen, T. B. Brand, M. T. P. Gilbert, B. Shapiro, M. Bunce, C. Wiuf, D. A. Gilichinsky, and A. Cooper (2003), Diverse plant and animal genetic records from Holocene and Pleistocene sediments, *Science*, *300*(5620), 791–795, doi:10.1126/science.1084114.

Williams, J. W., B. N. Shuman, T. Webb, P. J. Bartlein, and P. L. Leduc (2004), Late-quaternary vegetation dynamics in North America: Scaling from taxa to biomes, *Ecol. Monogr.*, *74*(2), 309–334, doi:10.1890/02-4045.

Zimov, S. A., V. I. Chuprynin, A. P. Oreshko, F. S. Chapin, J. F. Reynolds, and M. C. Chapin (1995), Steppe-tundra transition: A herbivore driven biome shift at the end of the Pleistocene, *Am. Nat.*, *146*(5), 765–794, doi:10.1086/285824.

C. E. Doughty, C. B. Field, and A. Wolf, Department of Global Ecology, Carnegie Institution for Science, 260 Panama St., Stanford, CA 94305, USA. (cdoughty@stanford.edu)