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commentary

Ecological complexity at the forest–grassland transition revealed by lake sediment records

Understanding how ecological processes play out over time scales relevant to long-lived species such as trees, and through periods of significant climate change, remains a major hurdle in translating climate-change projections into biological impacts. Over the past few decades, paleoecologists have embraced the prospect of using separate lines of evidence of climate, vegetation, and disturbance from sediment records to assess biogeographic responses to climate change. Well-known complexities in responses to climate change include positive feedbacks within ecosystems, lag times, and the possibility of multiple potential states. This requires paleoecologists to have a robust understanding of past climate, and thus they have been thrust into the field of paleoclimatology. As there are multiple approaches to reconstructing past climate, researchers are often faced with the task of reconciling their climatic reconstructions with a myriad of existing paleoclimate studies.

In a new paper (Shuman et al. 2009), a climate reconstruction based on fluctuating lake levels found evidence of a severe drought concurrent with a non-intuitive vegetation response. Shuman's group studied the paleoclimatic context for the development of the Big Woods, Minessota, a large patch of mesic-adapted forest trees that occurred at the forest–grassland transition at the time of pre-European settlement but is now largely converted to agriculture and suburbia. Earlier paleoecological studies had determined that open woodland and grassland began being replaced by Big Woods vegetation at ca. 1300 AD, concurrent with a decrease in fire and, assumed but never addressed explicitly, increased moisture that favored tree establishment. The new study, however, claims that lake levels, and thus regional moisture, were lower during the Big Woods development than at any other time during the past 1800 years. The authors also show, using age distributions of trees, that a comparable drought during the 1930's was not severe enough to preclude establishment of mesic tree species such as sugar maple. The "ecological surprise" from these findings is that the local-scale controls of the forest–grassland transition may operate, at times, in the opposite direction from the regional moisture gradient that explains the broad-scale pattern of the forest-to-grassland transition.

The mechanisms underlying the Big Woods establishment, if indeed it happened during drought, require rethinking. Shuman et al. (2009) invoke a previously published hypothesis (Umbanhowar 2004) that fire may have declined because of drought-caused fuel discontinuity, and thus increasing fire-free intervals permitting recruitment of Big Woods tree species. This hypothesis fits broadly with the assertion that over large expanses of the planet where productivity is marginally sufficient for forest, the observed vegetation is largely determined by fire and herbivores (Bond & Keeley 2005). The primary role of disturbance over climate in these areas leaves wiggle-room for complexities including processes that reverse the climate–vegetation relationship at small spatial scales. One of these complexities not discussed with respect to the Big Woods is the effect of fluctuating populations of grazers, such as bison. The influence of grazer populations on the forest–grassland transition may be as great or greater than other factors, and because paleoecologists rarely discuss grazing impacts, they represent an "elephant in the room" in the interpretation of these records (Craine & McLauchlan 2004). For example, increased grazing pressure during drought may have been required to reduce fuel continuity and fire extent. Of course, developing sediment proxies of grazer populations, such as from spores of the dung-fungus *Sporormiella*, would further the discussion of these dynamics (e.g., Gill et al. 2009; see also the update by Koch in this issue).

The search for concordance among paleoclimate records is a difficult task because of uncertainties in sediment chronologies, in the climate proxies themselves, and in the multiple dimensions of climate that are integrated into any one proxy. Shuman et al. (2009) conducted a large literature review of proximal records to support the existence of drought at the time of Big Woods expansion. However, a more recent reconstruction (Tweiten et al. 2009) of vegetation, climate, and fire at sites 160 km northeast of the Big Woods is not in total agreement and shows that more work is needed. The climate record of Tweiten et al. (2009) is based on moisture-sensitive testate amoebae in peat bogs, and shows great decadal-scale variability during the past 2000 years but less longer-term variability, as found in their vegetation history or in the Big Woods lake-level study. Rather, the bog record indicates the onset of drought at ca. 1100 AD but then shows increased moisture at 1300-1500 AD during the Big Woods expansion period. Inconsistencies among these records suggest the climate story remains incomplete.

Tweiten et al. (2009) make the important point that each proxy measured in sediment cores, whether it is lake levels, vegetation, fire, or surface moisture in peat bogs, has its own form of persistence over time based on its functional relationship with climate. They note that change in forest vegetation may be slow and integrative of century-scale patterns in climate, while groundwater hydrology is more sensitive to climate. Thus, long-term patterns in vegetation could be explained by "white noise"-like climatic variability that sets vegetation on long-term trajectories. Given the positive feedbacks operating in the fire–vegetation relationship at the forest–grassland transition, the dynamics of the Big Woods provides an excellent setting for revealing the transient effects of short-term or long-term climate change. Together, the studies by Shuman et al. (2009) and Tweiten et al. (2009) show that insights from multiple sediment proxies, although challenging to obtain, will continue to provide fruitful insights into vegetation dynamics.

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Daniel G. Gavin
Dept. of Geography, University of Oregon, USA
e-mail: dgavin@uoregon.edu
http://geography.uoregon.edu/gavin/gavin.html

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commentary

Effects of community invasion across multiple spatial scales

Species do not exist in isolation, and to understand their distribution in space we must understand the biotic environment in which they live. Community phylogeneticists examine whether an area's biota is phylogenetically clumped or overdispersed, where the former's close phylogenetic relatedness between species is assumed to reflect habitat filtering according to shared traits, and in the latter these same shared traits bring close relatives into 'excluding competition'. Such

