Quaternary Science Reviews 30 (2011) 269–272

Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Viewpoint

Fire and vegetation shifts in the Americas at the vanguard of Paleoindian migration

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ARTICLE INFO

Article history:
Received 26 July 2010
Received in revised form
7 December 2010
Accepted 8 December 2010
Available online 5 January 2011

Keywords:
Fire
Fire regime
Vegetation
Vegetation change
Climate
Climate change
Megafauna
Anthropogenic effects
Anthropocene

ABSTRACT

Across North and South America, the final millennia of the Pleistocene saw dramatic changes in climate, vegetation, fauna, fire regime, and other local and regional paleo-environmental characteristics. Rapid climate shifts following the Last Glacial Maximum (LGM) exerted a first-order influence, but abrupt post-glacial shifts in vegetation composition, vegetation structure, and fire regime also coincided with human arrival and transformative faunal extinctions in the Americas. We propose a model of post-glacial vegetation change in response to climatic drivers, punctuated by local fire regime shifts in response to megaherbivore-driven fuel changes and anthropogenic ignitions. The abrupt appearance of humans, disappearance of megaherbivores, and resulting changes in New World fire systems were transformative events that should not be dismissed in favor of climate-only interpretations of post-glacial paleo-environmental shifts in the Americas. Fire is a mechanism by which small human populations can have broad impacts, and growing evidence suggests that early anthropogenic influences on regional, even global, paleo-environments should be tested alongside other potential causal mechanisms.

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Many studies assume that early human populations and population densities were too small and pre-agricultural technologies too primitive to have contributed significantly to early paleo-environmental records. This may be true in some systems, particularly fire-insensitive ecosystems. But fire is a mechanism that can drive rapid and dramatic vegetation change, and anthropogenic fire has been a factor in shaping plant communities through human prehistory. In Australia, human colonization ca 50,000–45,000 BP (O'Connell and Allen, 2004) was accompanied by extinction of 90% of large fauna and the rapid decline of rainforest gymnosperms and other fire-intolerant plant taxa (Miller et al., 1999; Kershaw et al., 2003) and by sharp increases in charcoal (Kershaw, 1986; Kershaw et al., 2003; Miller et al., 2005; Black and Mooney, 2007). Although most workers see a human causal element in these paleo-environmental shifts in Australia, debate continues, including regarding the magnitude of coeval fire signals (Mooney et al., 2011). Tasmania was colonized ~5–10 kyrs later than mainland Australia, and megafaunal extinctions (Turney et al., 2008) and fire-driven devegetation and erosion (McIntosh et al., 2009) also occurred 5–10 kyrs later. New Zealand was colonized only in the late Holocene, ~1280 A.D. an event marked by fire and devegetation that largely eliminated the antecedent forest (McGlone and Wilmshurst, 1999; McWethy et al., 2009; McWethy et al., 2010), and marked by the extinction of New Zealand's 10 moa species and other native fauna of large ground birds (McGlone and Wilmshurst, 1999; Lee et al., 2010). Numerous other human colonization events worldwide, across a range of climatic conditions, climate-change vectors, and cultural contexts, have exhibited similar signatures (Barnosky et al., 2004; Burney and Flannery, 2005). In Africa, Europe, and western Asia, in contrast, pre-agricultural anthropogenic impacts on vegetation and fire systems tend to be more diffuse and more difficult to discern, probably in part because of the longer-term presence of humans in those areas.

The dates of human arrival in the Americas remain controversial, although most credible estimates now fall between 15,000 and 13,000 cal BP (calendar/calibrated years before present). In Alaska, humans arrived by or before 14,000 cal BP (e.g., Kedrowski et al., 2008), followed by a rapid penetration into North and South

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doi:10.1016/j.quascirev.2010.12.010

America. Between 13,500 and 13,000 cal BP, the founder Paleoindian group gave rise to or was followed by the classic Clovis culture, which subsequently spread throughout North and South America (e.g., Goebel et al., 2008; Steele and Politis, 2009). This Paleoindian migration also coincided in time, and to a degree in space, with the extinction of North and South American mammalian megafauna (animals ≥44 kg): an estimated 33 genera in North America and 50 in South America (Barnosky et al., 2004). Several Caribbean megafauna survived until the mid-Holocene, outliving their mainland counterparts by up to 8000 years, until humans arrived on the islands (Higuera-Gundy et al., 1999; MacPhee, 1999; Steadman et al., 2005).

Post-glacial paleobotanical records from across North and South America document sharp changes in vegetation and vegetation structure, changes that vary in character and timing by region. Characteristics of the terminal Pleistocene paleobotanical transition often include its great magnitude and its abrupt timing – "consistently the most abrupt late-Quaternary pollen-stratigraphic boundary throughout the Middle West and eastward to New England" (Amundson and Wright, 1979), a change that was "abrupt, widespread, and of short duration" (Peros et al., 2008). In Alaska, a transition from herb tundra to shrub tundra and a sharp increase in burning ("as frequent as modern") occurred at 14,000–13,000 cal BP (Higuera et al., 2008). The events in Alaska are noteworthy because of the synchronicity of human arrival, vegetation change, evidence of increased burning, and faunal extinctions, and because the timing appears distinguishably earlier than comparable events elsewhere in the Americas (Buck and Bard, 2007; Kedrowski et al., 2008; Doughty et al., 2010). South of the ice sheets, the period of maximum vegetation change was ~14,000–11,000 cal BP (Jacobson et al., 1987; Peros et al., 2008). Prior to human arrival, a broad swath of the continent, from the northern Great Plains to New England, was an open spruce-dominated parkland consistent with vegetation control by mega-grazers and -browsers. In the Hudson Valley of New York, Robinson et al. (2005) identified a temporal sequence in which *Sporormiella* (a fungus that grows on the dung of large herbivores; Davis and Shafer, 2006; Van Geel et al., 2007) declined rapidly at the same time that *Picea* pollen increased (spruce indicating early successional expansion), followed after several centuries by a charcoal spike at all sites. Removal or large-scale reduction of herbivores in modern environments results in closure of such open patterns, gradual build-up of fuel loads, and sharp increases in fire intensity when ignition eventually occurs (e.g., Sankaran et al., 2005; Waldram et al., 2008). This pattern was corroborated in northern Indiana by Gill et al. (2009), where a similar *Sporormiella* decline and vegetation shift 14,800–13,700 cal BP was followed after a lag by a sharp charcoal spike. This pattern suggests a non-climatic mechanism – control by megaherbivory – previously known but still under-appreciated in the paleobotanical literature.

Coeval shifts in latest Pleistocene vegetation and fire have been reported at sites in Central and South America, and human influence has been inferred at several of these. At Pacific coastal and near-coastal sites, charcoal spikes dating to between about 13,500 and 11,500 cal BP coincide with paleobotanical shifts, generally from arboreal to more herbaceous and shade-intolerant vegetation (e.g., Heusser, 1994; Colinvaux et al., 1997; Moreno and León, 2003; Piperno and Jones, 2003; Massaferro et al., 2005; Maldonado et al., 2010). Along the Pacific coast of Panama, for example, pollen, microcharcoal, and phytoliths document a sharp decline in arboreal cover, a rise in weedy plants, and increased burning at about 12,900 cal BP, interpreted as "[e]arly human interference with the Panamanian forest involving the use of fire" (Piperno et al., 1990; Piperno and Jones, 2003). Sites in interior and eastern South America document similar changes although generally later than along the Pacific coast. Near the mouth of the Amazon River, a spike in burning is recorded at 12,900–12,000 cal BP (i.e., ~500–1000 years younger than the earliest Pacific coastal sites) and is interpreted as an anthropogenic signature (Behling, 2001). Continent-wide, Power et al. (2008) noted "an east-west gradient of charcoal anomalies across South America" at the end of the Pleistocene. Even tropical lowland rainforests, once believed to be largely immune to fire, have paleo-records documenting long-term histories of anthropogenic burning (e.g., Sanford et al., 1985; Power et al., 2010).

Although paleo-environmental changes at sites across North and South America track as a group with post-glacial climate (Marlon et al., 2008), many individual sites record sharp vegetation changes coinciding with anomalous burning. The ages of these shifts hint at a diachronous pattern across the Americas, oldest in Alaska and then along the Pacific margin, with inferred gradients to the south and eastward, culminating with the Holocene shifts coeval with human arrival in the Caribbean. Parsing out the relative importance of humans from climate is complicated by the wide range of Pleistocene environments and wide diversity in natural ignition pattern and sources.

We suggest that regional patterns through the latest Pleistocene of the Americas support a model of long-term vegetation shifts in response to post-LGM climatic changes, punctuated by fire regime change in response to changes in fuel structure related to megaherbivore decline and to novel anthropogenic sources of ignition (Table 1). In ecosystems susceptible to burning but ignition-limited, the arrival of human ignitions would have resulted in an immediate change in fire regime and corresponding change in vegetation. A full transition to anthropogenic fire regimes – generally characterized by increased frequencies but reduced fire intensity (e.g., Bowman et al., 2004; Bird et al., 2008) – may have lagged by millennia, but even the sparse vanguard of the Paleoindian migration would have presented a novel and important ignition source in many fire-susceptible New World systems. In other areas, with abundant natural ignition sources but where fuel loads were strongly controlled by megaherbivory, extinction of those megaherbivores – whether human-induced or otherwise – would have led to an initial increase in vegetation biomass and landscape continuity of fuels as forest structure closed, followed by large-magnitude fires and the initiation of new fire regimes. This model does not advocate such early human impacts on fire regimes everywhere. Some areas with minimal human impact would have included settings with low fire susceptibility, for example due to high precipitation throughout the year, or landscapes fully saturated with natural fires. In both of these latter cases, sparse Paleoindian populations would have had little initial impact upon regional vegetation patterns or other paleoecological records. Only millennia later, following large increases in population, population density, technology, and land-use intensity, would some of these environments have responded to human fire use and other anthropogenic pressures.

Marlon et al. (2008) and Power et al. (2008) reviewed North American charcoal records and concluded that climate alone explains most fire regime changes since the LGM. Our model supplements that climate-driven model by recognizing multi-factorial mechanisms in which humans, herbivores, and climate affect fire and vegetation along landscape gradients. Our model is consistent with Marlon et al. (2008), in that their data focused on environments where natural ignitions were likely saturating and thus fire activity would have been largely influenced by climatic changes. However for landscapes where natural ignitions were limiting, large herbivores and humans both had the potential for greater transformative influence. For example, California was represented in Marlon et al. (2008) only from upper montane lake samples, where lightning is nearly saturating and human impacts minimal, whereas human influence was pervasive in lowland and foothill landscapes of

Table 1
Model of contrasting fire regime response to prehistoric human colonization and extinction of megaherbivores.

	Fire Regimes	
	Natural ignitions limiting	Natural ignitions saturating
(1) Fire-prone vegetation and contiguous fuel structure	Fire frequency low, pattern of coarse-grained high-intensity fires	Fire frequency high, coarse-grained pattern of low-intensity fires
	Little or no lag	
After human arrival and addition of ignitions	Fire frequency increases and exceeds threshold for some vegetation elements	Regional fire frequency and pattern minimally affected by humans; climate remains the primary determinant of vegetation distribution
(2) Fire-prone vegetation with structure altered by megaherbivores, creating a patchwork of available fuels	Fire frequency very low, fine-grained pattern of high-intensity fires	Fire frequency moderately high, fine-grained pattern of variable-intensity fires
	Lagged response	*Lagged response*
After human arrival and extinction of megaherbivores, which alters vegetation and fuel structure; and addition of ignitions	Fire frequency increases and pattern is more coarse-grained, tolerance thresholds for fire frequency exceeded for some vegetation elements	Fire frequency doesn't change, but pattern becomes coarse-grained; climate remains the primary determinant of vegetation distribution
(3) Relatively non-fire-prone mesic forest vegetation	Fire frequency very low	Fires localized to ignition-prone microsites, e.g., ridgelines
After human arrival and addition of ignitions	Potential increases in localized fire frequency where brief dry season exists; changes in vegetation composition	Regional fire frequency and pattern remain unchanged

California (Keeley, 2002). Another issue with studies like Marlon et al. (2008) and Mooney et al. (2010) is that by smoothing and averaging age control regionally, and by mixing older and newer radiocarbon dates as well as different calibration curves, more detailed and punctuated local events are inherently blurred and obscured.

In contrast, several other studies have explored the limits of climatic causation. Miller et al. (2005) used a Global Circulation Model to show that burning and vegetation change following human arrival in Australia may have blocked the monsoonal climate that governed Australia during previous interglacials. Doughty et al. (2010) suggested a link between megafaunal extinctions in Beringia and Bølling warming, whereas Smith et al. (2010) linked continental-scale extinctions to Younger Dryas cooling. Nevle and Bird (2008) tested the hypothesis (Ruddiman, 2003) that atmospheric CO_2 reductions due to reduced burning and revegetation following post-Conquest depopulation of the Americas (population reductions of up to ~90%) could have been sufficient to cause the Little Ice Age.

We suggest that the questions above are worth asking, although the web of complex causal interactions needs to be fully fleshed out and rigorously tested. There is a paradigm in many paleo-environmental studies that climate is the "universal independent variable." This paradigm assumes that hunter-gatherer populations were too small and pre-agricultural technologies too primitive for their effects to be significant. Many authors have despaired of disentangling human versus climatic contributions to fire, vegetation, and other landscape-scale changes in paleo-records: e.g., "it is difficult, indeed probably futile, to try to partition burning regimes between natural and cultural drivers" (Turner et al., 2009). Given this inherent ambiguity, however, many climate-focused studies have assumed early anthropogenic influences to be negligible, even at times when significant hunter-gatherer populations are known to have been present. While acknowledging that climate change has exerted first-order controls on latest Pleistocene paleo-environments of the New World and worldwide, we emphasize here that climate need not be the *only* control.

The suggestion of early anthropogenic influence on landscapes and ecosystems invites additional testing. Linkages between humans, fire, fauna, vegetation, and geomorphology suggest a number of testable hypotheses. Use of *Sporormiella* as a proxy for megafaunal populations invites more multi-proxy studies such as Robinson et al. (2005) and Gill et al. (2009). Studies should focus on tightly defining local and regional timing of human arrival, faunal extinctions, vegetation change, and fire incidence. New studies should also include geomorphic, sedimentary, and paleo-hydrologic proxies in order to identify contemporaneous changes in surficial processes tied to vegetation change. We predict that periods of extreme paleobotanical change may also record rapid changes in landscape dynamics at many locations – perhaps even periods of corresponding "no-analogs" geomorphology and paleo-hydrology. Finally, the model outlined here invites examination of multi-proxy records in areas colonized by humans at other times in the climatic cycle. If controls on paleo-environmental response are primarily climatic, then ecological and geological responses to anthropogenic influence should differ significantly and in keeping with the climatic conditions and directions of change at the time of human arrival.

Fire is a mechanism by which small numbers of people can have large impacts over broad areas. The main difference between the colonization of the Americas and other migrations may have been that humans arrived in the New World at a time of rapid climatic change that masks the same anthropogenic effects expressed at the vanguard of human migrations in other areas.

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