Minireview

Ecological impacts of the late Quaternary megaherbivore extinctions

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Summary

As a result of the late Quaternary megafaunal extinctions (50 000–10 000 before present (BP)), most continents today are depauperate of megaherbivores. These extinctions were time-transgressive, size- and taxonomically selective, and were caused by climate change, human hunting, or both. The surviving megaherbivores often act as ecological keystones, which was likely true in the past. In spite of this and extensive research on the causes of the Late Quaternary Extinctions, the long-term ecological consequences of the loss of the Pleistocene megafauna remained unknown until recently, due to difficulties in linking changes in flora and fauna in paleorecords. The quantification of *Sporormiella* and other dung fungi have recently allowed for explicit tests of the ecological consequences of megafaunal extirpations in the fossil pollen record. In this paper, I review the impacts of the loss of keystone megaherbivores on vegetation in several paleorecords. A growing number of studies support the hypothesis that the loss of the Pleistocene megafauna resulted in cascading effects on plant community composition, vegetation structure and ecosystem function, including increased fire activity, novel communities and shifts in biomes. Holocene biota thus exist outside the broader evolutionary context of the Cenozoic, and the Late Quaternary Extinctions represent a regime shift for surviving plant and animal species.

Introduction

Following the widespread loss of megafauna during the Late Quaternary Extinctions (LQEs; 50 000–10 000 before present (BP) on continents), modern biomes are depauperate of large herbivores relative to their evolutionary history (Koch & Barnosky, 2006). The surviving megaherbivores (see Box 1 for definitions), such as elephants, are often considered as ecological keystones for their well-documented impacts on plant community composition, structure and function (Owen-Smith, 1988); Pleistocene megafauna likely played similar roles in ice age ecosystems (Johnson, 2009). Herbivores have influenced the evolution of plant morphology and diversity, including the development of grasslands in the Miocene and the evolution of thorns, large fruits and chemical defenses (Crawley, 1983). While the role of megaherbivory has been recognized at both historic and geologic timescales, there have been comparatively few studies of the influence of large browsers and grazers on vegetation during the Quaternary (the last 2.5 million yr) in general, and the ecological consequences of the LQEs in particular. At Quaternary timescales (e.g. millennia), climate change has long been considered the predominant driver of vegetation change. Testing this assumption has been challenging, in large part because linking cause and effect in paleorecords has been hampered by the discontinuity of the vertebrate bone record in space and time, as well as the fact that animal remains are not typically found in the same depositional environments that preserve pollen, a proxy for paleovegetation change. Recently, several studies have used spores from *Sporormiella* and other coprophilous fungi to test the effects of the extinction of megaherbivores on vegetation dynamics during the late Quaternary (Burney *et al.*, 2003; Robinson *et al.*, 2005; Gill *et al.*, 2009, 2012; Rule *et al.*, 2012; Table 1). Unlike the vertebrate bone record, coprophilous fungi preserved in lake and mire sediments allow direct study of changes in local vegetation and megaherbivory

pressure in tandem. This growing body of research indicates not only that the local timing of megafaunal collapse is detectable in paleorecords, but also that the consequences of the LQEs include widespread ecological upheaval, biome reorganization (including novel communities) and changes in landscape fire regimes.

Box 1 A note about definitions

'**Megafauna**' (from the ancient Greek for *megas* 'large' and the New Latin *fauna* 'animal') has varied usage among scientists. The most common thresholds in the literature for modern herbivores are 44 or 100 kg; however, Owen-Smith (1987) uses 1000 kg specifically in the discussion of extinct Pleistocene megaherbivores, which is a size class that includes no extant taxa in North or South America, Eurasia or Australia. In this review, I use the 100 kg cutoff when referencing **megafauna** or **megaherbivores**, thus including important extant taxa such as the Cervidae and American bison (*Bison bison*) which have well-documented influences on vegetation. **Keystone species** are taxa that exert a disproportionately high influence on their habitats relative to their biomass; a **guild** is a group of species that exploit the same resources.

Table 1 Case studies of the effects of extinct Pleistocene megaherbivores

Case study	Region	Extinction consequences
Burney *et al.* (2003)	Madagascar	Increased fire activity
Robinson *et al.* (2005)	Upstate New York, USA	Increased fire activity, altered forest composition
Gill *et al.* (2009)	Indiana, USA	Novel plant associations, increased fire activity, altered forest composition
Gill *et al.* (2012)	Ohio, USA	Novel plant associations, increased fire activity, altered forest composition
Rule *et al.* (2012)	Australia	Increased fire activity, biome shift
Doughty *et al.* (2013)	Global	Disruptions to terrestrial biogeochemistry

Modern megaherbivore ecology

Modern megaherbivores have been shown to influence plant community composition, vegetation structure and openness, seed dispersal, rates and patterns of nutrient cycling, and fire regimes (see Supporting Information Table S1 for a select list of examples). Relative to smaller herbivores, megaherbivores exert disproportionate influences on vegetation relative to their biomass, because they (1) have long gut retention times, and are thus able to consume lower quality vegetation and woody material, (2) consume a greater relative fraction of landscape plant biomass, (3) are typically more general in their foraging habits, (4) exploit resources at broader spatial scales, and (5) are able to escape predation to the point where they may achieve sufficiently large populations to affect vegetation (Owen-Smith, 1988). As megaherbivores experience a wide range of seasonal, climatic and spatial heterogeneity of resource availability due to interannual variability in moisture, temperature or both (Illius, 2006), populations may migrate to track optimal

forage, micronutrients, water or reproductive habitats. Plants may therefore experience a wide spatiotemporal range in herbivory pressure, which can promote landscape heterogeneity (e.g. tree–grass coexistence in savannas; Sankaran *et al.*, 2005). The effects of herbivory depend in part on the material consumed (e.g. leaves, seeds or meristems), and may be positive (e.g. dispersal) or negative (e.g. mortality), as well as direct (e.g. inducible defenses) or indirect (e.g. altered competition for resources; Hester *et al.*, 2006). In the absence of empirical tests or direct observation, modern megaherbivores provide an important source of inference to link pattern and process in paleoecological records (Table S1).

The Late Quaternary Extinctions: patterns and causes

During the Pleistocene, megaherbivores were more diverse and widespread than today on all continents. By the early Holocene (*c.* 11 700 kyr BP), however, hundreds of species of large herbivores and their predators had disappeared from the continents as part of a global, time-transgressive extinction wave (Koch & Barnosky, 2006). The LQEs were more selective than any event in the preceding 65 million yr of mammalian evolutionary history, disproportionately targeting large mammals (> 10 kg). Causal debates have centered on natural vs anthropogenic mechanisms, including direct and indirect effects of climate change, rapid or protracted human overkill, or some combination of these (Koch & Barnosky, 2006). Determining a cause of the extinctions has been hampered by the fact that fossil faunal remains are discontinuous in space and time, and that the extinctions were contemporaneous with environmental change and human arrival, particularly in the Americas. Increasingly, interdisciplinary approaches and improved dating and analytical methods suggest that a combination of environmental stress and human hunting pressure contributed to the extinction of most species of megafauna (Lorenzen *et al.*, 2011).

Sporormiella: a dung fungus proxy of megaherbivory

While extensive efforts have been devoted to understanding the causes of the LQEs, the ecological *consequences* of those extinctions have received much less attention. This is due in part to the fact that the fossil faunal and vegetation records have different special and temporal coverage, depositional environments and dating uncertainties, and so establishing a precise order of events (e.g. population collapse followed by vegetation change) has been problematic. Recently, several studies have quantified spores of *Sporormiella* and other coprophilous fungi to establish the timing and environmental context of local megafaunal population collapse (Burney *et al.*, 2003; Robinson *et al.*, 2005; Gill *et al.*, 2009, 2012; Rule *et al.*, 2012).

Fungal spores may be preserved in lakes and mires along with pollen; this makes *Sporormiella* particularly useful in paleoecology because, unlike the vertebrate bone record, it allows for the direct interpretation of pollen-based paleovegetation records in the context of herbivores. While there are many coprophilous fungi, *Sporormiella* spores have a distinct morphology (i.e. they may be identified to genus) and are obligately coprophilous, reproducing only in herbivore dung (though other coprophilous fungi can

augment the record; see Baker *et al.*, 2013). *Sporormiella* and other spores are found in association with the dung of a wide range of extant fauna, including megaherbivores (e.g. bison, cattle, horse, moose, elephants) and smaller mammals and birds (e.g. rabbits, geese, porcupines; Richardson, 2001). In North American records, *Sporormiella* spores are present (> 2% of the upland pollen sum) in Pleistocene-age sediments, rare in Holocene sediments, and increase in abundance following the historic introduction of domestic grazers (Davis, 1987). While some species of megafauna survived the LQEs (e.g. *Bison, Alces*), the low abundances of *Sporormiella* in Holocene sediments is assumed to be because megafaunal biomass was insufficient to produce the volumes of dung necessary to generate a signal in sediment records. Gill *et al.* (2013) linked *Sporormiella* abundance to grazing intensity of bison in a modern tallgrass prairie, establishing a local source area (< 100 m) for spores, and showed that *Sporormiella* was suitable to detect a megafaunal presence despite a background level produced by small mammals (e.g. hares). *Sporormiella* cannot be identified to species or linked to specific megafaunal hosts (Feranec *et al.*, 2011), and so should be considered a proxy for functional extinction or population collapse (Gill *et al.*, 2009).

Ecological consequences of the Late Quaternary Extinctions

Given the documented effects of modern megaherbivores on contemporary plant communities, it has been hypothesized that ancient landscapes were similarly influenced (Craine & McLauchlan, 2004; Johnson, 2009). To date, Quaternary vegetation dynamics were thought to have been primarily driven by climate change, although the wealth of modern data on megaherbivore influences on vegetation allow for the formulation of several predictions about the long-term ecological consequences of megafaunal extirpations in the paleorecord. Herbivores influence the physiology, form and growth of plants, and the paleorecord may not capture the full range of the effects of plant–herbivore interactions. Some effects, such as the influences of herbivory on species coexistence and competition, may only be inferred as a potential mechanism driving changes in community composition, although such inferences may be grounded with modern studies to identify mechanistic linkages between pattern and process. For this review, I have limited discussion to those effects that may be most readily observed in or inferred from paleorecords, using current and emerging methods. Additionally, while this review focuses on the ecological effects of the Pleistocene megafaunal extinctions, megaherbivore extirpations may also have influenced climate change, both directly (e.g. influencing atmospheric methane compositions; Smith *et al.*, 2010) or indirectly via changes to vegetation (e.g. albedo).

Community composition may have been altered by the release of plants from herbivory following the LQEs

Several pollen and *Sporormiella* records from eastern North America show an increase in hardwood deciduous taxa immediately following the decline in dung fungal spores, including an increase in *Fraxinus nigra*-type and *Ostrya*-type pollen at Appleman Lake,

Indiana (Gill *et al.*, 2009) and Silver Lake, Ohio (Gill *et al.*, 2012), and an increase in *Acer* in New York (Robinson *et al.*, 2005). At Appleman and Silver Lakes, pollen assemblages immediately following the local collapse of megaherbivores were highly dissimilar to present, indicating the widespread formation of plant associations without a modern analogue (Fig. 1). These novel communities were likely triggered by a combination of novel climates and herbivory release. Additionally, pollen and *Sporormiella* records from Australia (Rule *et al.*, 2012) during the penultimate glaciation and from late-Holocene Madagascar (Burney *et al.*, 2003) record major shifts in community composition immediately following the decline in megafauna in the absence of climate change, indicating that the loss of herbivores alone was sufficient to drive major shifts in vegetation. Indeed, in Australia, the changes from rainforest to sclerophyll vegetation following local megafaunal collapse were more dramatic than those driven by glacial–interglacial transitions (Rule *et al.*, 2012).

Holocene fire regimes may be enhanced relative to the Pleistocene, due to a build-up of landscape fuels

Fire is considered the primary form of (abiotic) consumer control of vegetation today (Bond *et al.*, 2005), but this may not have been the case during the Pleistocene, when megaherbivores were more widespread (Flannery, 1994). Joint analyses of fossil charcoal and *Sporormiella* records indicate that LQEs may have increased fire activity in Madagascar (Burney *et al.*, 2003), North America (Robinson *et al.*, 2005; Gill *et al.*, 2009, 2012; see Fig. 2), and Australia (Rule *et al.*, 2012). Megafaunal herbivory likely reduced litter and fuel loads during the Pleistocene, as has been observed in modern systems (Bond & Keeley, 2005); following the LQEs, increased fuel loads and a reduction in landscape heterogeneity would likely have facilitated the spread of fires. If fire frequency, severity and geographic extent were greater during the Holocene following the loss of herbivores, then Holocene fire regimes (as indicated by fossil charcoal analysis) should differ from previous interglacials. Global charcoal records do indicate that fire was less frequent during the last glacial period than in the Holocene (Daniau *et al.*, 2012), although interactions between climate, megaherbivory and fire will complicate future causal inferences.

Pleistocene ecosystems may have been more open and/or patchy than present

Given the role that megaherbivores play in maintaining tree–grass coexistence today (Sankaran *et al.*, 2005), the end-Pleistocene extinctions may have reduced vegetation openness and decreased landscape heterogeneity in some biomes. Vera (2000) suggested that the early Holocene mosaics of grassland, thicket and forest in prehistoric central Europe were maintained by large herbivores, and that the closing of those forests in the mid- to late Holocene were the result of the extinction or extirpation of those species of megafauna that had survived the LQEs, including *Bos primigenius*, *Alces alces* and *Bison bonasus*. In the absence of herbivores, light-demanding woody taxa, including *Quercus* and *Corylus*, were out-
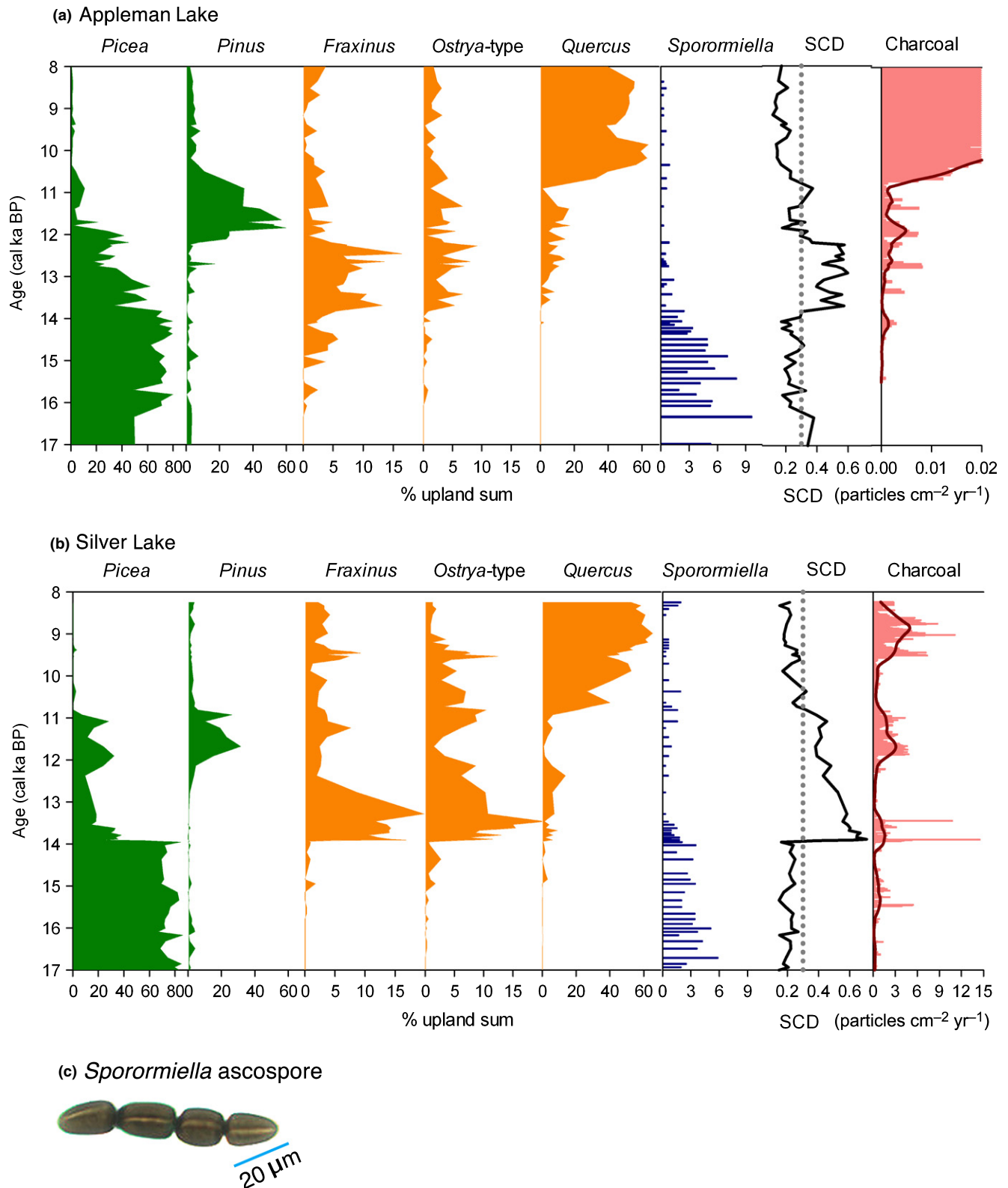
(a) Appleman Lake

(b) Silver Lake

(c) *Sporormiella* ascospore

20 μm

Fig. 1 Simplified pollen diagrams from Appleman Lake, Indiana, USA (a) and Silver Lake, Ohio, USA (b), including conifers (green), deciduous taxa (orange), and the dung fungus *Sporormiella* (blue), a proxy for megaherbivore presence. Pollen data are represented as a portion of the upland pollen sum; *Sporormiella* (blue bars) abundances are represented as a portion of the upland pollen sum but are not included in that sum. Squared-chord distance (SCD; black line) is a measure of minimum dissimilarity between fossil pollen assemblages and all possible modern matches; values > 0.3 (indicated by the dotted grey line) are assemblages considered to have no modern analog. Charcoal data are represented as charcoal accumulation rates (CHAR; solid red); the background component of charcoal is indicated by the red line; individual fire events are peaks above background. The figure is modified from Gill *et al.* (2009, 2012). (c) An ascospore of four *Sporormiella* spore cells; spore cells are typically detached in the fossil record.
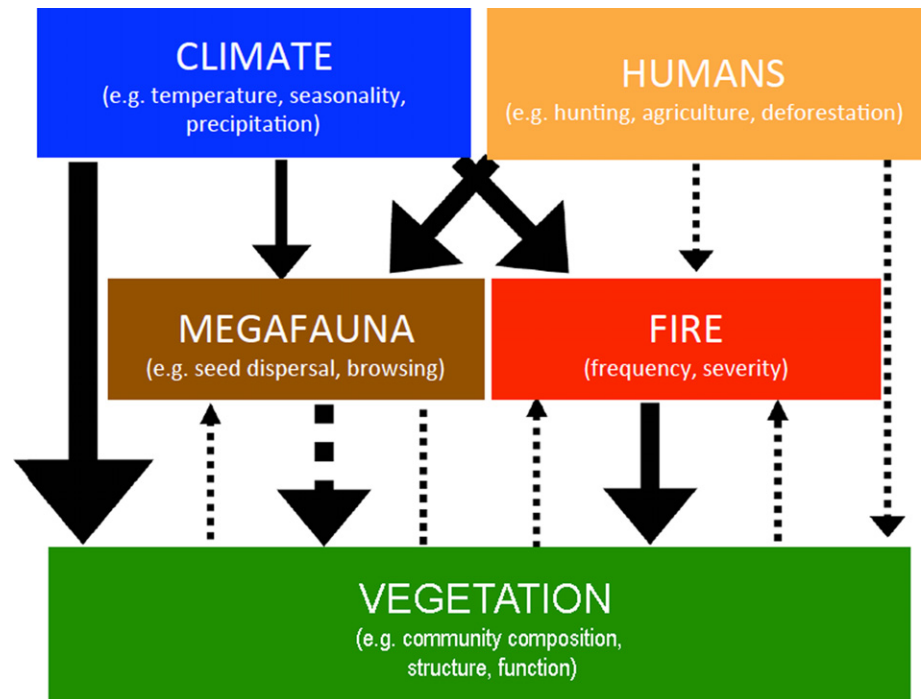
Fig. 2 An updated, integrative conceptual model of drivers of vegetation dynamics on Quaternary timescales. Line thickness indicates the hypothesized relative strength of each coupling; dashed lines indicate interactions that are poorly understood in the paleorecord. Adapted from Gill *et al.* (2012).

competed by shade-tolerant *Fagus*, *Ulmus*, *Carpinus*, *Tilia* and *Ostrya*. The Vera Hypothesis has been highly contested: Mitchell (2005) compared pollen records from Europe with Ireland, which lacked mid-Holocene megafauna, and found that *Corylus* and *Quercus* were abundant even in the absence of browsers. However, fossil beetle evidence indicate that some regions of early Holocene Europe were more open than present, particularly in the lowlands, which is presumably due to both herbivory and (possibly anthropogenic) fire (Svenning, 2002). Thus, the Vera Hypothesis may in fact be more applicable to pre-Holocene landscapes (when the very largest megaherbivores were more widespread) than the current interglacial epoch.

Graham & Lundelius (1984) hypothesized that a shift from mosaic to zonal vegetation gradients was a primary cause of the megafaunal extinctions in North America, but in modern studies, megaherbivores have been found to maintain landscape heterogeneity (Table 1). Therefore, closing landscapes and the development of more continuous vegetation may have been a consequence, rather than a cause, of the end-Pleistocene extinctions. Bakker *et al.* (2004) tested whether modern European thorny and light-demanding taxa, including *Quercus robur* and *Prunus spinosa* were ecological anachronisms, adapted to now-extinct megaherbivores. They tested the response of vegetation to modern cattle and horse grazing, and found that extensive grazing in floodplains established a shifting mosaic of grasses, shrubs and trees similar to conditions during the Pleistocene (and to modern savannas). Ultimately, the role that extinct megafauna played in maintaining openness or landscape heterogeneity remains uncertain in Europe, and has yet to be tested in other parts of the world, although there is supporting experimental evidence from modern African savannas (Asner & Levick, 2012) and Siberia (Zimov *et al.*, 2012).

Megafaunal influences on vegetation may have varied with landscape position

Modern megafaunal populations often exhibit spatial patterning resulting from ties to resources or landscape barriers (Danell *et al.*, 2006). The effects of the LQEs should thus be more readily detectable in areas of suitable habitat, such as lowlands with ample water sources and soil nutrients (Bakker *et al.*, 2004). Svenning (2002) found evidence for open vegetation in the lowlands, while uplands remained closed high forests during the last glacial period. In the early Holocene, however, nonarboreal pollen abundances were reduced in both upland and lowland sites, suggesting that Holocene Europe was dominated by a more closed canopy than during previous interglacials.

The end-Pleistocene extinctions may have affected both the rate and spatial dynamics of biogeochemical cycling

Very little is known about the role of Pleistocene megafauna on nutrient cycles, though a recent modeling effort suggests that there may have been long-term disruptions in nutrient transport and depositions following the LQEs that persist today in many parts of the world (Doughty *et al.*, 2013). Recent advances in lake sediment proxies of ecosystem function may shed light on the role that extinct megaherbivores played on nitrogen and other nutrient dynamics (McLauchlan *et al.*, 2013). One major challenge will be to differentiate allochthonous from autochthonous processes governing lake sediment records of biogeochemistry. Additionally, any sedimentary proxy will integrate processes at the watershed level, and so differentiating spatial heterogeneity at the sub-watershed scale will likely not be possible. This may be an opportunity for modern experimentation to test a paleoecological

hypothesis; in a recent test simulating the impacts of the New Zealand moa extinction on nitrogen cycles, Tanentzap *et al.* (2013) found that avian-derived nitrogen inputs increased native forest regeneration.

Many Holocene plants may be dispersal-limited relative to the Pleistocene

Janzen & Martin (1982) hypothesized that the large, fleshy fruits of some neotropical plants were an adaptation to dispersal by megaherbivores, and that such 'ecological anachronisms' now exist out of their coevolutionary context in the absence of extinct Pleistocene dispersers. In addition to bearing large, nutritious fruits, New World trees such as the papaya (*Cerica papaya*), avocado (*Persea americana*), honey locust (*Gleditsia triancanthos*), Kentucky coffee tree (*Gymnocladus dioicus*), pawpaw (*Asimina triloba*) and Osage orange (*Maculra pomifera*) all show adaptations to megafaunal herbivory and dispersal, including clonal growth, root suckers and large thorns (Barlow, 2002). While such taxa are often cited as iconic examples of the ecological implications of the LQEs, there are few empirical tests of whether such plants are dispersal-limited in modern landscapes (but see Campos-Arceiza & Blake 2011 for a review of the importance of extant Probosci-deans as seed dispersers). Guimarães *et al.* (2008) calculated that 103 species of South American plants show the evolutionary traits of megafaunal dispersal. I predict that these plants would exhibit reduced gene flow and increased population structuring due to clustering, reduced geographic ranges and reduced migration rates in the absence of megafaunal dispersers. Janzen (1984) also hypothesized that smaller-seeded plants may be dispersed by large herbivores when consumed with surrounding foliage. Indeed, Vellend *et al.* (2003) found that deer likely played an important role in the postglacial migration of *Trillium*; known levels of dispersal by ants would not be sufficient to explain *Trillium*'s postglacial range expansions.

The Late Quaternary Extinctions may have had cascading effects on small mammal communities

Megafaunal-induced changes to vegetation composition and structure may have cascaded to smaller mammals, which are more tied to high-nutrient forage and are often less selective than megaherbivores (Crawley, 1983). Small mammals would also have been affected by changes in landscape openness, as well as the availability of herbaceous taxa and seeds for foraging. Thus far, effects of the megafaunal influences on small-mammal habitats have been largely untested in the paleorecord, although Blois *et al.* (2010) suggested that megafaunal extinctions may have contributed to reductions in small mammal richness and evenness at a site in California during the Pleistocene/Holocene transition. It will be especially difficult to discriminate megafa-unal effects from climate change, but multi-proxy paleorecords (e.g. packrat middens, cave deposits) that record small mammal communities, changes in animal diets (such as those measured in stable isotopes in tooth enamel), and independent records of climate may prove useful.

Conclusions and future directions

Previously, climate change was thought to be the primary driver of vegetation dynamics at Quaternary timescales, but the studies cited here are part of a growing body of literature that indicate that megaherbivores – and their extinction – left detectable influences in paleorecords. These effects have been shown to include biome reorganization, novel communities and changes in fire regimes; altered dispersal patterns, nutrient cycles, and other cascading effects are likely. I suggest an updated, integrative model of vegetation dynamics at Quaternary timescales (Fig. 2), including the effects of megaherbivores and interactions between climate change, humans, vegetation, herbivores and fire. In this model, vegetation dynamics are driven by multiple, interacting top-down mechanisms, as well as the feedbacks amongst them. Fundamentally, this model is underlain by the growing evidence that the biotic interactions observed on ecological timescales were also important drivers of vegetation change throughout the Quaternary.

Modern and paleoecological analyses have much to offer one another, particularly with regard to linking the patterns observed by paleoecologists with the processes observed by neo-ecologists. key needs include a better understanding of: (1) direct and indirect effects of herbivores on nutrient cycling (including feedbacks); (2) post-extinction trophic cascades to other species, including insects, birds and small mammals; (3) the role of megafauna in influencing fire regimes, particularly in forested landscapes; (4) factors influencing palatability and preference through time; (5) density-dependent plant–herbivore interactions; (6) synergies between the effects of herbivores and climate change on other biota; (7) the evolutionary consequences of changing defense needs following the release of herbivory pressure; and (8) the effects of megaherbivores on plant dispersal and migration. Potential ways forward will benefit from an integrative approach that includes megaherbivore effects in dynamic global vegetation models (Allen *et al.*, 2010), multi-proxy paleoecological reconstructions, and modern experiments using the closest modern analogs of extinct species.

Growing evidence supports the hypothesis that the loss of megaherbivores – particularly in tandem with changes in climate and anthropogenic activity – resulted in a global ecological regime shift by the early Holocene. Modern megaherbivores are among some of the most threatened species today (Maisels *et al.*, 2013); like their Pleistocene counterparts, extant megafauna face the combined threats of anthropogenic land use and climate change. The ecological consequences of the end-Pleistocene extinctions may thus have relevance not only to understanding the dramatic vegetation changes of the early Holocene, but also in understanding and managing ecosystems in the Anthropocene.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Selected effects of megaherbivores on vegetation in modern landscapes

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