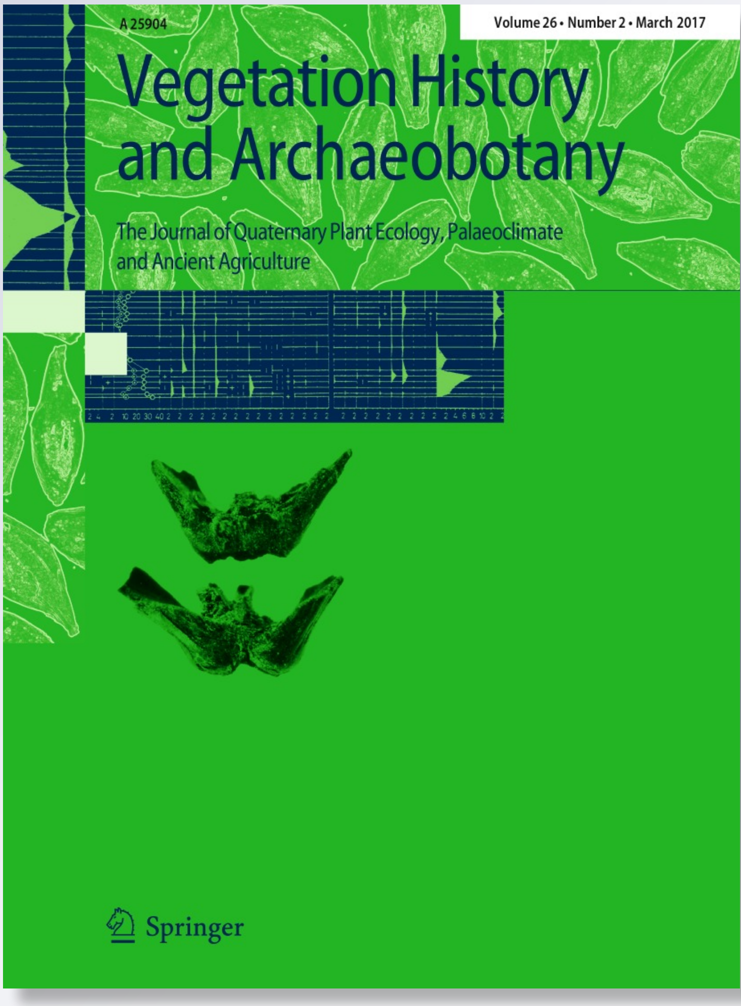
Historic grazing in southern New England, USA, recorded by fungal spores in lake sediments

Maria E. Orbay-Cerrato, W. Wyatt Oswald, Elaine D. Doughty, David R. Foster & Brian R. Hall

Vegetation History and Archaeobotany
The Journal of Quaternary Plant Ecology, Palaeoclimate and Ancient Agriculture - Official Organ of the International Work Group for Palaeoethnobotany

ISSN 0939-6314
Volume 26
Number 2

Veget Hist Archaeobot (2017)
26:159-165
DOI 10.1007/s00334-016-0577-8



Springer

Veget Hist Archaeobot (2017) 26:159–165
DOI 10.1007/s00334-016-0577-8

ORIGINAL ARTICLE

Historic grazing in southern New England, USA, recorded by fungal spores in lake sediments

Maria E. Orbay-Cerrato[1,2] · **W. Wyatt Oswald**[2,3] · **Elaine D. Doughty**[2] · **David R. Foster**[2] · **Brian R. Hall**[2]

Received: 11 December 2015 / Accepted: 29 April 2016 / Published online: 11 May 2016

Abstract Decadal-scale analyses of fungal spores in a lake-sediment core from Ware Pond, located in the town of Marblehead in northeastern Massachusetts, test the potential of this approach for reconstructing past sheep and cattle grazing in southern New England, USA. The influx of spores of *Sordaria* and other coprophilous taxa increases at AD 1650, which corresponds with the beginning of European settlement, and subsequent peaks in these taxa at AD 1840 coincide with maximum abundances of weedy and agricultural taxa in the pollen record. Historical data from Marblehead and neighbouring towns indicate that maximum numbers of cattle and sheep occurred at this time. These findings suggest that fungal spores in New England lake sediments can be used to reconstruct changes in grazing pressure over time at the landscape scale.

Keywords Charcoal · Coprophilous fungal spores · Fire · Land use · Massachusetts · Palaeoecology · Pollen analysis

Communicated by M. O'Connell.

✉ W. Wyatt Oswald
w_wyatt_oswald@emerson.edu

[1] Program in Biology, Division of Biology and Medicine, Brown University, Box G-A, Providence, RI 02912, USA

[2] Harvard Forest, Harvard University, 324 N Main St., Petersham, MA 01366, USA

[3] Institute for Liberal Arts and Interdisciplinary Studies, Emerson College, 120 Boylston Street, Boston, MA 02116, USA

Introduction

Over the last few centuries, New England landscapes have experienced profound ecological transformations. Beginning in the 1620s and continuing for two and a half centuries, European settlers cleared forests to make way for pastures and cultivated fields. By the mid-1800s, New England was largely an agricultural landscape, with forest cover reduced to <40 % across the region. Isolated woodlots were actively cut for fuel-wood and timber. However, during the second half of the 19th century various factors, including the expanding national transportation network, the shift of settlement to the Midwest and West Coast, and the industrialization of New England, led to the regional abandonment of farming. The decline of agriculture initiated broad-scale reforestation of New England. Today the region is >80 % forested (Foster 2002).

Economic and land-use changes within the agricultural era are of particular interest from an ecological standpoint. From the late 1700s to the first half of the 19th century, the New England economy shifted from small-scale farming and local consumption to market-oriented intensive agriculture. Pasture was the primary land use during the early 1800s, and wool, beef, cheese and butter were among the main agricultural products, such that further deforestation was motivated by the need for additional grazing lands. It is estimated that by the middle of the 19th century, >650,000 sheep and cattle grazed the pastures of Massachusetts (Hall et al. 2002). Studies of present-day New England forests suggest that ecological legacies of settlement-era deforestation and grazing remain important many decades after abandonment. For example, currently forested areas that were cleared for agriculture generally have plant assemblages distinct from those of permanently forested woodlots (Motzkin et al. 1996; Eberhardt et al.

2003; Verheyen et al. 2003). Similarly, some sites that were pastured or cultivated have higher soil nitrogen than adjoining woodlots, presumably because of the addition of manure during the agricultural period (Compton and Boone 2000).

While we have regional-scale estimates of the numbers of sheep and cattle and the acreage of pasture in New England during the agricultural era, we have little information to confirm that specific watersheds were grazed and no ability to characterize changes in grazing pressure over time at the landscape scale. The analysis of spores of coprophilous fungi in lake-sediment and peat records may present an opportunity to reconstruct the spatial and temporal patterns of past grazing. This approach has been used in various other settings (Baker et al. 2013), including analyses of Pleistocene and Holocene megafaunal extinctions (e.g. Burney et al. 2003; Davis and Shafer 2006; Gill et al. 2009, 2012; Rule et al. 2012), and multiple studies suggest that the abundance of coprophilous fungal spores in recent sediments reflects historic grazing (e.g. van Geel et al. 2003; Robinson et al. 2005; Davis and Shafer 2006; Cugny et al. 2010; Feeser and O'Connell 2010; Anderson et al. 2015; Farrell 2015). In the case of lakes, the spores are transported in streams and through sheet flow over open and frozen pastures, and hence represent the local presence of herbivores in the watershed (e.g. Raper and Bush 2009).

Here we present the first application of this method in New England, USA. We analysed fungal spores, including those from coprophilous taxa, in a lake-sediment core from eastern Massachusetts. The decadal-scale record covers the last six centuries, including the era of European settlement, and thus allows us to explore the potential of this approach for reconstructing historic sheep and cattle grazing in this region.

Study area

Ware Pond (42.482°N, 70.882°W, 4 m a.s.l.) is located in northeastern Massachusetts in the town of Marblehead (Fig. 1). Marblehead lies on the Atlantic coast, ~20 km northeast of Boston, and Ware Pond is 400 m inland from the ocean. Eastern Massachusetts is a region of lowlands and rolling hills, with cold winters (mean minimum January temperature for Marblehead is −6.5 °C) and warm summers (mean maximum July temperature is 26.7 °C). Mean annual rainfall for Marblehead is 123 cm and snowfall is 104 cm.

Pre-settlement forests in this area, as revealed by 18th century town proprietor surveys, featured various hardwoods, including *Quercus* (oak), *Carya* (hickory), *Betula* (birch), *Acer* (maple) and *Fagus grandifolia* (American beech). *Pinus strobus* (white pine) and *Tsuga canadensis* (eastern hemlock) were also common (Cogbill et al. 2002; Hall et al. 2002; Thompson et al. 2013). European settlement of eastern Massachusetts began in the 1620s (Hall et al. 2002) and Marblehead was settled in 1629. Like the rest of southern New England, eastern Massachusetts was largely deforested and converted to an agricultural landscape between the late 17th and late 19th centuries, with forest cover reduced to <30 % by 1850, the height of the agricultural era (Foster 2002).

Census data can be used to determine the size of historic populations of cattle and sheep in Marblehead and/or Essex County, the county in which Marblehead is located (Fig. 2). For Marblehead, numbers of cattle are available between 1801 and 1895, peaking at 320 animals in 1845 and then declining to <250 in subsequent census years. At the county level, cattle numbers decline from >20,000 to <13,000 between 1837 and 1855, return to high values (>18,000 animals) between 1875 and 1895, and then drop below 15,000 for the remainder of the 20th century, falling to <3,000 animals by 1987. Sheep numbers are not available for Marblehead, but county-level data feature high values in 1837 (>5,800 animals) and 1845 (>4,400), followed by a steep decline to lower levels (~160–1,800 animals) between 1855 and 1992. The mid-19th century decline of sheep that occurred in Essex County is observed in state-wide data (Hall et al. 2002).

Ware Pond is a 1.54 ha kettle pond with a maximum depth of 150 cm. An area of wetlands extends 50 m north of the pond, and another pond, known as Oliver Pond, is located 200 m northwest of Ware Pond. A U.S. Coast Survey map from 1850 (Fig. 1b) indicates that both Ware and Oliver Ponds were surrounded by wetlands at that time, and also shows a wetland-filled channel running southeast from Ware Pond to the ocean. The 1850 map also depicts in great detail the land-use activities in the area around Ware Pond. The surrounding landscape is entirely deforested, with the nearest wooded area located ~2 km to the southwest (not shown). Orchards were located directly northeast of Ware Pond and to the northwest of Oliver Pond, but otherwise the ponds appear to have been surrounded by pastures. Maps of the Ware Pond area from 1902 to 1919 (Fig. 1c, d) show the pastures being invaded by trees and shrubs, indicating that the abandonment of agriculture was underway at that point. A railroad line built in the early 1870s can be seen just south of Ware Pond in the 1902 map (Fig. 1c). The area in the vicinity of Ware Pond was developed as a residential neighbourhood beginning in the 1920s (Fig. 1e), but the pond, wetlands, and shoreline vegetation remain undeveloped and today are managed as a conservation area (Fig. 1f).

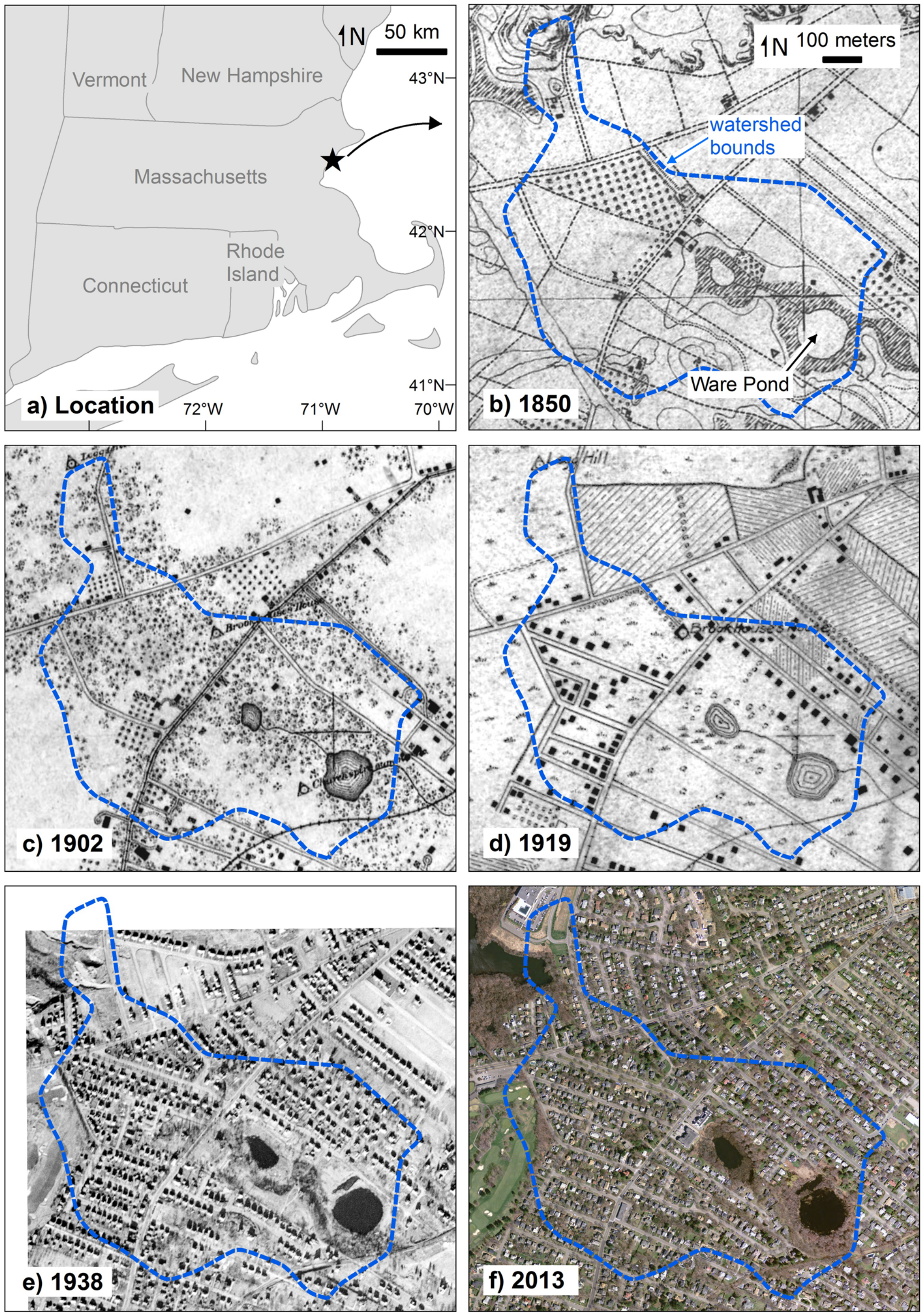


Fig. 1 **a** Location of Ware Pond, Marblehead, Massachusetts, USA, and **b-f** maps and aerial photographs of the Ware Pond area from 1850 (U.S. Coast Survey 1850), 1902 (U.S. Coast and Geodetic Survey 1902), 1919 (U.S. Coast and Geodetic Survey 1919), 1938 (Nationwide Environmental Title Research 2011) and 2013 (MassGIS 2013). *Blue broken line* indicates Ware Pond's watershed

Materials and methods

A 900 cm long sediment core was raised from Ware Pond in May 2014. The upper 150 cm of sediment, including an undisturbed mud-water interface, was collected with a 10 cm diameter plastic tube fitted with a piston. This surface core was transported to the laboratory and extruded vertically in 1 cm segments. Lower sediments were collected in 100 cm drive lengths using a 5 cm diameter modified Livingstone piston sediment sampler (Wright et al. 1984). Those core segments were extruded horizontally in the field, wrapped in plastic and aluminium foil,

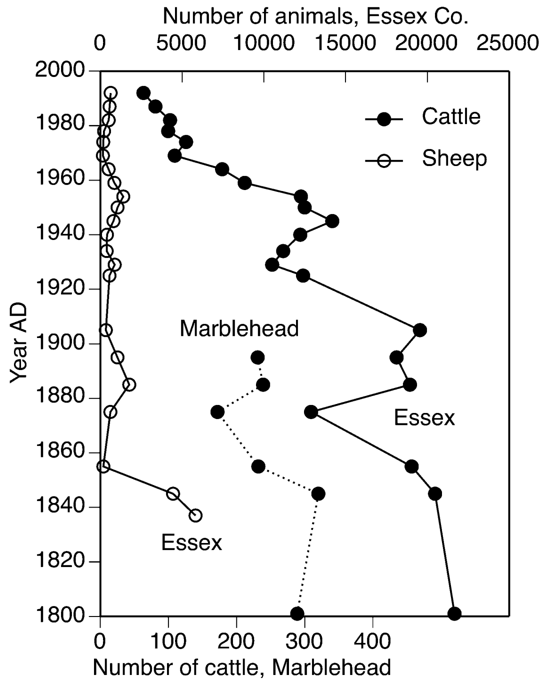


Fig. 2 Numbers of cattle and sheep in Essex County and the town of Marblehead, Massachusetts, USA, during 19th and 20th centuries (Foster et al. 2003)

and subsampled at 1 cm intervals in the laboratory. All samples were subsequently refrigerated.

For the present study we have analysed the upper 200 cm of the Ware Pond sediment core. The chronology for this interval of the core is based on accelerator mass spectrometry ^{14}C dating of bulk-sediment samples and an age assignment made on the basis of pollen evidence for European settlement. ^{14}C dates were converted to calendar years (AD) using CALIB 7.1 with the IntCal13 calibration curve (Reimer et al. 2013).

Sediment organic content was estimated for 1 cm^3 subsamples at selected depths by percent weight loss-on-ignition (LOI) at 550 °C. For charcoal analysis, 1 cm^3 subsamples were soaked in KOH and washed through a 200 µm sieve, and all charcoal fragments >200 µm were counted at 40× magnification. Sediment subsamples of 1–2 cm^3 were prepared for the analysis of pollen and spores following standard procedures (Fægri and Iversen 1989), and tablets containing *Lycopodium* spores were added to the samples for the estimation of pollen and spore accumulation rates (number cm^{-2} $year^{-1}$; Stockmarr 1971). Pollen and spore residues were mounted in silicone oil and analysed at 400× magnification. Fungal spores were identified following e.g. van Geel 1986; van Geel et al. 2007, 2011, and coded following Miola (2012). At least 300 pollen grains of terrestrial plant taxa were counted per sample. Pollen percentages were calculated relative to that sum, and fungal-spore abundances are presented in terms of accumulation rates and relative to the pollen sum (Wood and Wilmshurst 2013).

Results

The chronology for the interval of the Ware Pond core analysed here (<200 cm) is based on linear interpolation between three data points: a calibrated ^{14}C age for the depth 250 cm (AD 844, i.e. the median calibrated age; all ages are quoted in calibrated/calendar years AD), the assignment of 1650 to the increase in *Ambrosia* (ragweed) pollen at 170 cm, and the sediment–water interface (Table 1; Fig. 3). The ^{14}C date returned for 170 cm (Table 1) appears to be too old and is thus not included in the age-depth model.

Sediment organic content increases gradually (from 65 to 75 %) between 1350 and 1660, declines (to 65 %) at 1690, then stabilizes (at 70 %) between 1700 and 1770 (Fig. 4). After 1770, organic content decreases to reach a minimum value (45 %) at 1860, then increases gradually (to ~65 %) between 1860 and the present. Charcoal influx values are low (<10 pieces cm^{-2} $year^{-1}$) prior to 1650, increase to 10–20 pieces cm^{-2} $year^{-1}$ between 1650 and 1750, and then return to <10 pieces cm^{-2} $year^{-1}$ in the interval ca. 1760–1810. Charcoal values are elevated (>15 pieces cm^{-2} $year^{-1}$) between 1810 and 1920, peaking at >40 pieces cm^{-2} $year^{-1}$ at ca. 1870–1880. Charcoal influx then declines, dropping to <10 pieces cm^{-2} $year^{-1}$ for most of the 20th century.

Pre-settlement pollen assemblages are dominated by *Quercus* (40–45 %), and also include moderate abundances (~10 % and lower) of *Pinus* (mainly *P. strobus*-type), *Tsuga*, *Carya*, *Fagus*, *Betula* and *Acer* (Fig. 4). European settlement is marked by a rise in total pollen influx and increases in several weedy and agricultural taxa, including Polypodiaceae (ferns), *Rumex* (dock), *Ambrosia* and Poaceae (grasses). Percentages of Polypodiaceae spores are high (10–15 %) between 1670 and 1840, *Rumex* percentages peak (8–10 %) at 1700–1740, and maximum abundances of *Ambrosia* (15 %) and Poaceae (>20 %) occur at 1840–1860. After European settlement, *Quercus* pollen percentages drop to ~20 %, *Tsuga*, *Carya* and *Fagus* decline slightly, while *Pinus*, *Betula* and *Acer* have minor increases.

Fungal-spore abundance is very low between 1350 and 1650, but increases soon after European settlement. Accumulation rates of *Sordaria*-type (HdV-55A) spores are elevated (>100 spores cm^{-2} $year^{-1}$) in the intervals 1650–1740 and 1820–1910, reaching a pronounced peak (>2,300 spores cm^{-2} $year^{-1}$) at 1840. Spores of other fungi, including *Delitschia* (TM-023), *Podospora*-type

Table 1 ^{14}C-dating results for Ware Pond, Marblehead

Depth (cm)	^{14}C lab. no. (OS-)	^{14}C date (BP) ± SD	δ^{13}C (‰)	Age ranges* (AD)	Median cal age (AD)
170	113786	520 ± 25	−28.94	1,329–1,340; 1,396–1,440	1,416
250	113787	1,170 ± 20	−30.53	774–897; 926–943	844

* 2σ probability ranges

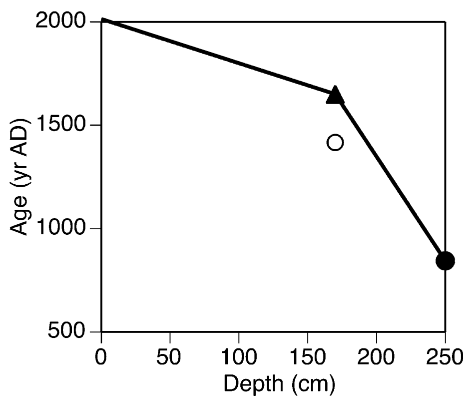


Fig. 3 Age-depth relationship for the Ware Pond sediment core. *Circles* indicate ^{14}C dates and *triangle* represents European settlement; the ^{14}C date at 170 cm (*open circle*) was not used in the age-depth model

(HdV-368) and *Coniochaeta* (type B; TM-211), are present at low abundances between 1800 and 1970. *Sporormiella* (HdV-113) spores, which are commonly encountered in lake-sediment cores, were not observed in the Ware Pond record. Total fungal-spore abundance reaches 5 % of the pollen sum at 1840.

Discussion

The pre-settlement (ca. 1400–1650) pollen spectra from Ware Pond are similar to those from other pollen records from eastern Massachusetts (e.g. Oswald et al. 2007; Oswald and Foster 2011) and are also consistent with forest composition as reconstructed from town proprietor surveys (Cogbill et al. 2002; Hall et al. 2002; Thompson et al. 2013). Late-Holocene forests were dominated by *Quercus*, but also included *Carya*, *Betula*, *Acer*, *Fagus grandifolia*, *Pinus strobus* and *Tsuga canadensis*. Low abundances of herbaceous taxa (<3 %) suggest that the area around Ware Pond was largely forested prior to settlement.

The earliest deforestation by European settlers, beginning in the first half of the 17th century, progressed slowly, with limited areas of forest being cleared for small-scale, subsistence agriculture (e.g. Raup 1966; Foster 2002). The decline in organic content dating to 1690 in the Ware Pond core may reflect forest clearance and the erosion of upland soils in Ware Pond's watershed. The abundance of *Quercus* in the Ware Pond pollen record declined rapidly, with its percentages dropping from 35 to 20 % between 1650 and 1700. This decline likely represents the cutting of *Quercus* near Ware Pond and across the broader region.

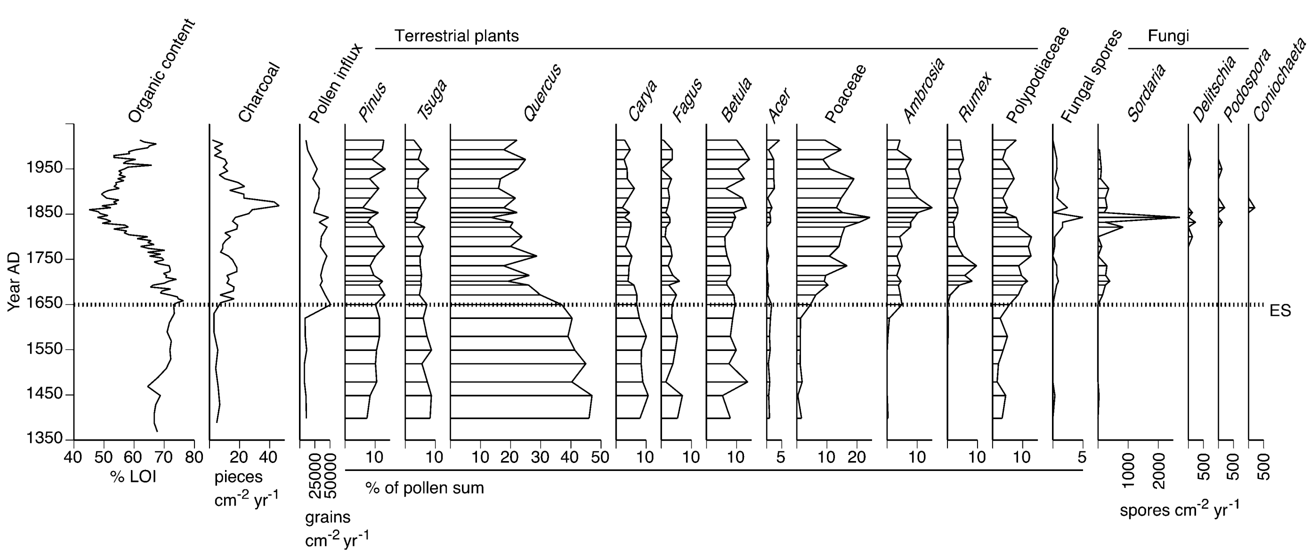


Fig. 4 Palaeoenvironmental proxies analysed in the Ware Pond sediment core: organic content (% LOI); charcoal influx; pollen influx; pollen percentages; and influx of fungal spores. *Horizontal line* indicates European settlement (ES)

The shift from relatively high abundances of *Rumex* and Polypodiaceae during the first part of the settlement era (1650–1840) to high abundances of Poaceae and *Ambrosia* during the latter part of the agricultural period (1840–1930) resembles the trends observed in this interval of other pollen records from across southern New England (e.g. Brugam 1978; Oswald and Foster 2011). The post-1820 decline of ferns and *Rumex*, which was viewed as a problematic weed, is most likely attributable to changing agricultural practices, including deep ploughing with steel ploughs, which would have destroyed the root systems of perennials like *Rumex* and ferns, and the application of lime to control *Rumex* by decreasing soil acidity.

The Ware Pond charcoal record suggests that the prevalence of fire increased at the time of European settlement, as has been found in other fire-history studies carried out in New England (Parshall and Foster 2002; Parshall et al. 2003). The peak in charcoal influx at ca. 1870–1880 postdates the highest percentages of grass and *Ambrosia* pollen and the peak in *Sordaria* spores at 1840–1860. This sequence may reflect an abrupt increase in fire as agricultural fields were abandoned and invaded by shrubs and trees, rapidly creating the biomass needed to support substantial fires. Trains running on the railroad line just south of Ware Pond may have served as an ignition source. Subsequently, burning was greatly reduced after residential development began around Ware Pond in the 1920s.

The temporal pattern and types of fungal spores encountered in the Ware Pond record are consistent with our understanding of the agricultural history of the region. Spores of *Sordaria* occur regularly between 1650 and 1910, paralleling the relative abundance of pollen of weedy plant taxa, and reaching a pronounced peak at 1840. This fungus, as well as the less-frequently encountered *Delitschia*, *Podospora* and *Coniochaeta*, is known to be coprophilous (Krug et al. 2004; Ejarque et al. 2011). Given that the *Sordaria* peak at 1840 coincides with the timing of maximum numbers of cattle and sheep in Marblehead and surrounding towns, it appears that the stratigraphy of such fungal spores in lake sediments records not only the local presence of grazers, but also reflects changes in their abundance through time.

Conclusions

The relationship between the numbers of sheep and cattle in the town of Marblehead, Massachusetts and the lake-sediment abundance of spores of fungi associated with herbivore dung illustrates the potential of this approach for studying the history of grazing in this region. By carrying out this type of analysis at other sites in eastern Massachusetts and elsewhere in New England, we will be able to reconstruct changes in grazing through time and across space, yielding new insights into the history of European agriculture in this region. Moreover, by comparing fungal-spore and pollen data in additional sediment records, the timing and magnitude of grazing can be related to changes in other agricultural practices, such as the advent of steel ploughs, as evidenced by the decline of *Rumex* pollen. Finally, the history of sheep and cattle grazing in particular watersheds can be compared with modern-day vegetation composition and soil characteristics, helping us to further understand the consequences of past land-use activities for contemporary forest ecosystems.

Acknowledgments We thank Jon Honea for field assistance. Bas van Geel, Michael O'Connell, and an anonymous referee provided constructive feedback that improved the manuscript. This research was funded by National Science Foundation grants DEB-1146207, DEB-1237491, and DBI-1459519.

References

Anderson RS, Ejarque A, Rice J, Smith SJ, Lebow CG (2015) Historic and Holocene environmental change in the San Antonio Creek Basin, mid-coastal California. Quat Res 83:273–286

Baker AG, Bhagwat SA, Willis KJ (2013) Do dung fungal spores make a good proxy for past distribution of large herbivores? Quat Sci Rev 62:21–31

Brugam RB (1978) Human disturbance and the historical development of Linsley Pond. Ecology 59:19–36

Burney DA, Robinson GS, Burney LP (2003) *Sporormiella* and the late Holocene extinctions in Madagascar. Proc Natl Acad Sci USA 100:10,800–10,805

U.S. Coast and Geodetic Survey (1902) Beverly to Marblehead including Salem Massachusetts. Sheet No. T 2603. http://nosimagery.noaa.gov. Accessed 1 Dec 2015

U.S. Coast and Geodetic Survey (1919) Register No. 3766. http://nosimagery.noaa.gov. Accessed 1 Dec. 2015

U.S. Coast Survey (1850) Map of the N.W. shore of Mass. Bay from Saugus River to Marblehead. Sheet No. T 305-1. http://nosimagery.noaa.gov. Accessed 1 Dec 2015

Cogbill CV, Burk J, Motzkin G (2002) The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. J Biogeogr 29:1,279–1,304

Compton JE, Boone RD (2000) Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81:2,314–2,330

Cugny C, Mazier F, Galop D (2010) Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. Veget Hist Archaeobot 19:391–408

Davis OK, Shafer DS (2006) *Sporormiella* fungal spores, a palynological means of detecting herbivore density. Palaeogeogr Palaeoclimatol Palaeoecol 237:40–50

Eberhardt R, Foster DR, Motzkin G, Hall B (2003) Conservation of changing landscapes: vegetation, land-use history, and fire on Cape Cod National Seashore. Ecol Appl 13:68–84

Ejarque A, Miras Y, Riera S (2011) Pollen and non-pollen palynomorph indicators of vegetation and highland grazing activities obtained from modern surface and dung datasets in the eastern Pyrenees. Rev Palaeobot Palynol 167:123–139

Fægri K, Iversen J (1989) In: Fægri K, Kaland PE, Krzywinski K (eds) Textbook of pollen analysis, 4th edn. Wiley, Chichester

Farrell M (2015) Later prehistoric vegetation dynamics and Bronze Age agriculture at Hobbister, Orkney, Scotland. Veget Hist Archaeobot 24:467–486

Feeser I, O'Connell M (2010) Late Holocene land-use and vegetation dynamics in an upland karst region based on pollen and coprophilous fungal spore analyses: an example from the Burren, western Ireland. Veget Hist Archaeobot 19:409–426

Foster DR (2002) Thoreau's country: a historical-ecological perspective to conservation in the New England landscape. J Biogeogr 29:1,537–1,555

Foster D, Hall B, Burk J (2003) Massachusetts historical landcover and census data 1640–1999. Harv For Data Arch 40:3,557–3,569

Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. Science 326:1,100–1,103

Gill JL, Williams JW, Jackson ST, Donnelly JP, Schellinger GC (2012) Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution multi-proxy record from Silver Lake, Ohio. Quat Sci Rev 34:66–80

Hall B, Motzkin G, Foster DR, Syfert M, Burk J (2002) Three hundred years of forest and land-use change in Massachusetts, USA. J Biogeogr 29:1,319–1,335

Krug JC, Benny GL, Keller HW (2004) Coprophilous fungi. In: Mueller GM, Bills GF, Foster MS (eds) Biodiversity of fungi: inventory and monitoring methods. Elsevier Academic Press, Burlington, pp 467–499

MassGIS (2013) USGS color ortho imagery. Office of Geographic Information, MassIT, Commonwealth of Massachusetts

Miola A (2012) Tools for Non-Pollen Palynomorphs (NPPs) analysis: a list of Quaternary NPP types and reference literature in English language (1972–2011). Rev Palaeobot Palynol 186:142–161

Motzkin G, Foster DR, Allen AE, Harrod JC, Boone RD (1996) Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecol Monogr 66:345–365

Nationwide Environmental Title Research (2011) 1938 USGS aerial photo (1 November to 22 December 1938). http://www.historicaerials.com. Accessed 1 Dec 2015

Oswald WW, Foster DR (2011) A record of late-Holocene environmental change from southern New England, USA. Quat Res 76:314–318

Oswald WW, Faison EK, Foster DR, Doughty ED, Hall BR, Hansen BCS (2007) Post-glacial changes in spatial patterns of vegetation across southern New England. J Biogeogr 34:900–913

Parshall T, Foster DR (2002) Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. J Biogeogr 29:1,305–1,317

Parshall T, Foster DR, Faison EK, MacDonald D, Hansen BCS (2003) Long-term history of vegetation and fire in pitch pine-oak forests on Cape Cod, Massachusetts. Ecology 84:736–738

Raper D, Bush M (2009) A test of *Sporormiella* representation as a predictor of megaherbivore presence and abundance. Quat Res 71:490–496

Raup HM (1966) The view from John Sanderson's farm: a perspective for the use of the land. For Hist 10:2–11

Reimer PJ, Bard E, Bayliss A et al (2013) IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1,869–1,887

Robinson GS, Burney LP, Burney DA (2005) Landscape paleoecology and megafaunal extinction in southeastern New York State. Ecol Monogr 75:295–315

Rule S, Brook BW, Haberle SG, Turney CSM, Kershaw AP, Johnson CN (2012) The aftermath of megafauna extinction: ecosystem transformation in Pleistocene Australia. Science 335:1,483–1,486

Stockmarr J (1971) Tablets with spores used in absolute pollen analysis. Pollen Spores 13:615–621

Thompson JR, Carpenter DN, Cogbill C, Foster DR (2013) Four centuries of change in northeastern United States forests. PLoS One 8:e72540. doi:10.1371/journal.pone.0072540

Van Geel B (1986) Application of fungal and algal remains and other microfossils in palynological analyses. In: Beglund BE (ed) Handbook of Holocene palaeoecology and palaeohydrology. Wiley, Chichester, pp 497–505

Van Geel B, Buurman J, Brinkkemper O, Schelvis J, Aptroot A, van Reenen G, Hakbijl T (2003) Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), w1ith special reference to coprophilous fungi. J Archaeol Sci 30:873–883

Van Geel B, Zazula GD, Schweger CE (2007) Spores of coprophilous fungi from under the Dawson tephra (25,300 C-14 years BP), Yukon Territory, northwestern Canada. Palaeogeogr Palaeoclimatol Palaeoecol 252:481–485

Van Geel B, Gelorini V, Lyaruu A et al (2011) Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya. Rev Palaeobot Palynol 164:174–190

Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR (2003) Response of forest plant species to land-use change: a life-history trait-based approach. J Ecol 91:563–577

Wood JR, Wilmshurst JM (2013) Accumulation rates or percentages? How to quantify *Sporormiella* and other coprophilous fungal spores to detect late Quaternary megafaunal extinction events. Quat Sci Rev 77:1–3

Wright HE Jr, Mann DH, Glaser PH (1984) Piston corers for peat and lake sediments. Ecology 65:657–659