High herbivore density associated with vegetation diversity in interglacial ecosystems

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The impact of large herbivores on ecosystems before modern human activities is an open question in ecology and conservation. For Europe, the controversial wood–pasture hypothesis posits that grazing by wild large herbivores supported a dynamic mosaic of vegetation structures at the landscape scale under temperate conditions before agriculture. The contrasting position suggests that European temperate vegetation was primarily closed forest with relatively small open areas, at most impacted locally by large herbivores. Given the role of modern humans in the world-wide decimations of megafauna during the late Quaternary, to resolve this debate it is necessary to understand herbivore–vegetation interactions before these losses. Here, a synthetic analysis of beetle fossils from Great Britain shows that beetles associated with herbivore dung were better represented during the Last Interglacial (132,000–110,000 y B.P., before modern human arrival) than in the early Holocene (10,000–5,000 y B.P.). Furthermore, beetle assemblages indicate closed and partially closed forest in the early Holocene but a greater mixture of semiopen vegetation and forest in the Last Interglacial. Hence, abundant and diverse large herbivores appear to have been associated with high structural diversity of vegetation before the megafauna extinctions at the end of the Pleistocene. After these losses and in the presence of modern humans, large herbivores generally were less abundant, and closed woodland was more prevalent in the early Holocene. Our findings point to the importance of the formerly rich fauna of large herbivores in sustaining structurally diverse vegetation in the temperate forest biome and provide support for recent moves toward rewilding-based conservation management.

paleoecology | forest structure | Vera hypothesis | dung beetles

Globally, megafauna species ($\geq$44 kg body weight) have been decimated during the last 50,000 y, a loss of biodiversity that is linked at least partially to the expansion of modern humans (1). The ecosystem consequences of these massive losses are still poorly understood (2–4), and the degree to which wild large herbivores may determine vegetation structure at the landscape scale is an important issue in ecology and conservation science (5–7). In Europe, this issue has been the subject of much controversy, with views on natural conditions ranging from a primarily open wood–pasture landscape maintained by large herbivores (8) to a primarily closed woodland landscape little affected by large herbivores (9). Intermediate scenarios with a heterogeneous forest-dominated landscape that includes open patches generated by grazing, fire, soils, and hydrology have also been proposed (10). This debate hinges on whether large herbivores formerly were sufficiently abundant to limit tree dominance within the temperate forest biome, as they do in contemporary African subtropical savannas (11, 12).

Paleoecological records are key resources for providing long-term perspectives to guide conservation management (13). Here, we use beetle macrofossils to compare herbivore density and woodland cover in Great Britain over four time periods: the Last Interglacial (132,000–110,000 y B.P.), the Last Glacial (here, 50,000–15,000 y B.P.), the early Holocene (10,000–5,000 y B.P.),

and the late Holocene (2,000–0 y B.P.) (see *Materials and Methods* for further details). The Last Interglacial and Holocene periods harbored temperate climates that allowed forest cover in the region but with highly divergent assemblages of large herbivores and under different human influences. The Last Interglacial had 11 species of large herbivores ($\geq$10 kg; Table S1) with a median body weight of 524 kg (range, 19–6,500 kg), the largest being *Elephas antiquus* (straight-tusked elephant) (Fig. 1), and no modern humans, because modern humans arrived in Europe only 40–50,000 y ago (14). Neanderthals were present in mainland Europe during this period but may have been absent or rare in the British Isles (15). By the early Holocene, modern humans had long been present, and only seven species of large herbivores (median weight, 167 kg; range 19–900 kg) remained in the region; the largest herbivore was *Bos primigenius* (aurochs). The loss by this time of all herbivores $\geq$1,000 kg body weight (megaherbivores) is noteworthy, given their particular ecological importance in modern ecosystems (16). Late Holocene Europe is characterized by agricultural landscapes with high domestic ungulate density but low median weight (117 kg; range, 19–900 kg) across the 11 species of domestic and wild large herbivores present. In contrast, the Last Glacial had 11 species of large herbivores and was a period in which cold climate restricted woodland cover.

Because of their high habitat specificity and good preservation, fossil and subfossil beetles are a valuable proxy for prehistoric ecosystems, allowing ecological calibration of relative

Significance

Megafaunas have been decimated worldwide during the last 50,000 y, with poorly understood ecosystem consequences. In Europe, the ability of the extinct megafauna to generate structurally diverse vegetation within the temperate forest biome is controversial and has important implications for conservation management. We used paleoecological beetle data to reconstruct the abundance of large herbivores and the vegetation structure in Great Britain before and after the megafaunal extinctions. We found indications of high abundances of large herbivores and a mosaic of closed forest and wood–pasture vegetation in the last interglacial period and primarily closed forests with lower herbivore abundance in the early Holocene. These findings support an important role for large herbivores in driving vegetation dynamics and in current efforts to promote landscape diversity through rewilding.

Fig. 1. Reconstruction of a Last Interglacial temperate landscape (Germany) with typical Late Pleistocene European large herbivores such as the now extinct straight-tusked elephant (*Elephas antiquus*), an extinct rhinoceros (*Stephanorhinus kirchbergensis;* in Britain only the closely related *S. hemitoechus* appears to have been present during the Last Interglacial), as well as the still common roe deer (*Capreolus capreolus*). Illustrator: Elke Gröning.

herbivore abundance and woodland cover (17). In a comparison of varying English landscapes, Smith et al. (18) estimated that subfossil terrestrial beetle faunas (thought to be one or two decades old at maximum) comprising >20–25% of individuals of woodland-associated species indicate a closed canopy, whereas values <5% indicate an open canopy or low vegetation; intermediate values (5–15%) characterize wood–pasture in modern landscapes. Smith et al. also suggested that where dung beetles make up >10% of the terrestrial beetle fauna, large herds of ungulates use the area (~2.5 or more animals per hectare) and that values <5% reflect lower densities (~0.5 or fewer animals per hectare).

Barnosky (1) suggests that the global megafauna biomass took ~9,700 y to recover from the Late Pleistocene megafauna extinctions and did so only via domestic animals. On this basis, we hypothesized that dung beetle representation should be significantly lower during the early Holocene than during the Last Interglacial. Correspondingly, assuming that wild large herbivores are important ecosystem engineers in temperate forest biomes, we predicted higher closed-woodland cover in the early Holocene than in the Last Interglacial. Beetles should indicate even higher herbivore densities and lower woodland cover during the late Holocene than during the Last Interglacial, reflecting the open and wood–pasture vegetation structure of historical agricultural landscapes. The Last Glacial offers another instructive reference, because during this period beetles should indicate low woodland cover as a result of the colder, less productive climatic conditions prevailing in Northwestern Europe during this period.

Results

The fossil and subfossil beetle assemblages recorded in each temporal period mostly support these predictions and indicate that, in terms of herbivore density and vegetation structure, Last Interglacial landscapes were intermediate between the semiopen agricultural landscapes of the late Holocene and the mostly closed or semiclosed woodlands of the early Holocene, or closer to the former (Fig. 2). Concerning dung availability and, by inference, the densities of large herbivores, pasture dung-associated beetles were significantly less abundant in the early Holocene than in the Last Interglacial [Generalized Linear Mixed Model (GLMM): $X^2 =$

5.370, *d.f.* $= (3, 2)$, $P = 0.020$] (Fig. 2*A*), as were dung indicator species [GLMM: $X^2 = 9.830$, *d.f.* $= (3, 2)$, $P = 0.002$]. Noticeably, 82% of sites from the late Holocene and 55% of sites from the Last Interglacial periods but only 29% of sites in the early Holocene and 11% of sites in the Last Glacial periods were in the "high dung" category (Fig. 2*B*). There also was a greater representation of dung-indicator beetle species [i.e., species especially reliant on dung as habitat or for reproduction (19)] in the Last Interglacial (16 species, with 82% of sites having at least one of these species) and in the late Holocene (20 species, with 55% of sites having at least one of these species) than in the early Holocene (13 species, with only 29% of sites having one or more of these species) (Fig. 2*A* and Dataset 1). The commonness of dung beetles such as *Copris lunaris*, *Onthophagus vacca*, and *Caccobius schreberi* (Fig. 3 and Dataset 1; also see ref. 20) in samples from the Last Interglacial indicates the frequent occurrence of open, sun-exposed habitats with high densities of large herbivores (21).

In line with the stronger representation of dung-associated beetles in the Last Interglacial, the relative abundance of woodland- and tree-associated beetles also was lower in the Last Interglacial than in the early Holocene [GLMM: $X^2 = 5.386$, *d.f.* $= (4, 3)$, $P = 0.020$] (Fig. 2*A*). Still, there were numerous beetle species in the samples from the Last Interglacial that indicate the presence of trees and woodland habitats, such as leaf miners and bark beetles on trees such as oak (*Rhynchaenus quercus*) and ash (*Hylesinus oleiperda* and others), dead wood-dependent woodborers (e.g., *Anobium punctatum*, *Xyloterus domesticus*), and species associated with old veteran trees (*Phloeophagus lignarius*) and otherwise weakened trees (*Platypus cylindrus*) (Dataset 1). Early Holocene sites predominantly reflect closed (57%) or semiclosed (21%) woodland landscapes with 14% wood–pasture and 7% open vegetation, whereas sites from the Last Interglacial reflect landscapes with a greater mix of open and closed vegetation communities and a greater representation of wood–pasture (55%), with 27% of sites indicating closed woodland and 18% indicating semiclosed woodland (Fig. 2*C*). In contrast to the early Holocene, the late Holocene was similar to the Last Interglacial in terms of woodland- and tree-associated beetles (Fig. 2*A*).

Climate and fire are two further factors of potential importance for vegetation structure. Climate reconstructions using the
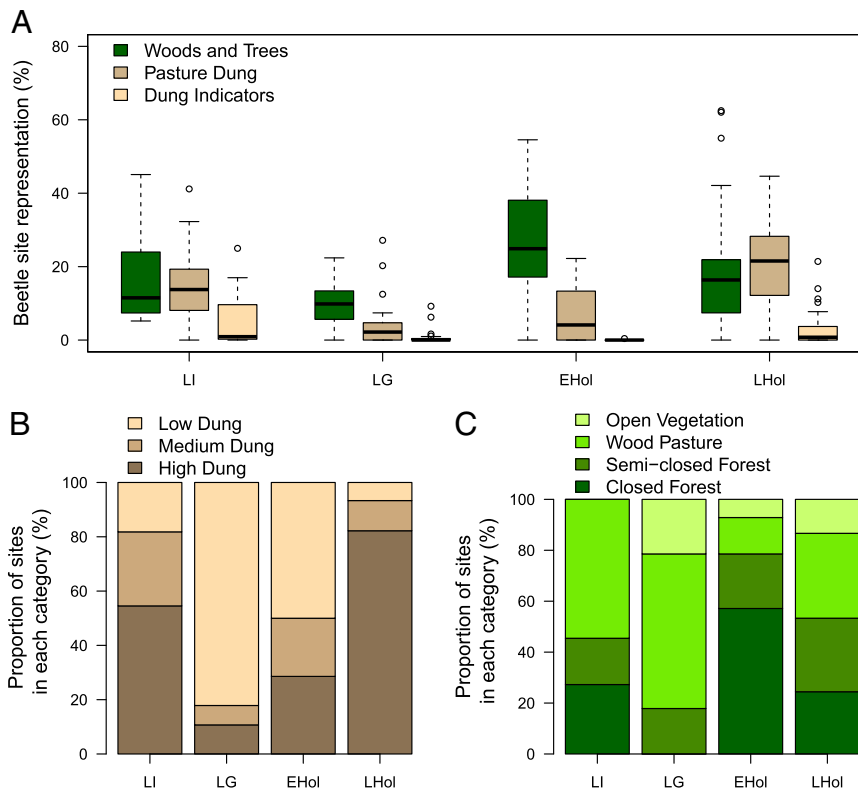
Fig. 2. Ecological characteristics of British beetle assemblages during the Last Interglacial ($n = 11$), Last Glacial ($n = 28$), early Holocene ($n = 14$), and late Holocene ($n = 45$). (*A*) Box and whiskers plot of site medians of beetle abundance per sample for species in a given ecological category relative to all individuals per sample for each given time period. The middle line and the box represent the median and the first through third quartiles, respectively, and whiskers extend to the most extreme data point, which is no more than 1.5 times the interquartile range. (*B*) Dung classifications are based on the proportion of beetle abundance associated with pasture dung; high dung is ≥10.0%; medium dung is <10.0% and ≥5.0%; and low dung is <5.0%. (*C*) Classifications of vegetation structure are based on the proportion of beetle abundance that represent woods and trees in each site; closed forest is ≥22.5%; semiclosed forest is <22.5% and ≥15.0%; wood–pasture is <15.0% and ≥5.0%; and open vegetation is <5.0%. For *B* and *C*, each bar segment represents the proportion of sites within each time period that meets the relevant classification criteria. LI, Last Interglacial; LG, Last Glacial, EHol, early Holocene; LHol, late Holocene.

beetle fossils indicated warmer temperatures in the warmest month of the Last Interglacial than in the warmest month of the early Holocene but similar temperatures in the coldest month of the two periods (Fig. S1). Of the 64 species listed by Whitehouse (22) and Lundberg (23) as being fire-adapted, none were recorded from the Last Interglacial, whereas six species (9%) were recorded from the early Holocene.

A sensitivity analysis indicated that the results described above were robust to changes in threshold values used to reconstruct herbivore abundance and vegetation structure, with a couple of notable exceptions (Fig. S2). In the early and late Holocene periods the proportion of sites representing either closed or semiclosed forest was most sensitive to these changes, with closed forest ranging from 43–71% and from 16–44%, respectively. Smith et al. (18) recorded closed forest as having between 20–25% woodland-associated species, indicating some difficulty in determining the forest structure. Irrespective of this threshold value, the proportion of closed and/or semiclosed forest always is estimated as being high in the early Holocene. In the Last Interglacial 18% of sites are near the threshold for open or wood–pasture landscapes (Fig. S2). Still, the patterns in the vegetation structure and herbivore abundance in the different periods are maintained (Fig. S2). The removal of the two early Holocene Scottish sites, located at greater latitude and altitude than the other early Holocene and Last Interglacial sites, also gave qualitatively similar results (Fig. S3).

Discussion

Our results suggest that large herbivores played an important role in shaping vegetation structure in Great Britain during the Last Interglacial, in partial agreement with the controversial wood–pasture hypothesis (8), but were less effective in the early Holocene after and during the end-Pleistocene and early-Holocene megafaunal attrition. The latter result may reflect both the suppression of the remaining large herbivores by modern human hunters (1) and the absence of the extinct megaherbivores (Table S1) (24). In either case, the beetle assemblages suggest that by the early Holocene megafaunal attrition already had resulted in an insufficiently diverse and/or abundant herbivore guild to limit closed forest cover as effectively as earlier. The assemblages for the early Holocene thus are largely consistent with the closed or semiclosed woodland conditions inferred by Bradshaw et al. (6) and Whitehouse et al. (17). These observations also are in line with Barnosky's (1) estimation that the density of the megafauna was restricted in the early Holocene and did not recover until the spread of agriculture and domestic large herbivores such as cattle, sheep, and horses. Therefore the closed and semiclosed forest conditions estimated for the early Holocene, as well as the common reforestation that occurs in unmanaged nature reserves today, deviates from the vegetation structure and dynamics before modern human arrival. The moderately warmer temperatures recorded for the Last Interglacial cannot explain the differences in vegetation structure between the Last Interglacial and early Holocene, because the climate still was well within the temperate forest biome climate zone, and closed woodland also

Fig. 3. Dung beetles are associated with sun-exposed, dung-rich habitats that are well represented in interglacial beetle assemblages. Examples are *Copris lunaris* (*A*) and *Onthophagus vacca* (*B*), with (*C*) their modern habitat (Røsnæs, Denmark). (Photographs by M.D.D.H.)

develops as the dominant vegetation in Europe today under warm temperate and even in sub-Mediterranean climates in the absence of grazing or other disturbances (e.g., ref. 25). Fire regime is another consideration, but we found no indications of a higher abundance of pyrophilous species in the Last Interglacial than in the early Holocene.

Although Great Britain is an island during interglacial periods, the general similarity of its large-mammal assemblages to those in the rest of Northwest Europe in all periods (26) and the pollen record during the early Holocene (9) and the Last Interglacial (27) suggest that the processes in Great Britain should have been similar to those in continental settings and support the wider applicability of our results. Our findings also should apply to the temperate forest biomes in North America and Eastern Asia, which have suffered similar megafaunal losses (1, 28), and add to the increasing evidence for the ecosystem effects of the Late Pleistocene and early Holocene megafaunal losses around the world (2, 3, 29).

Beetle assemblages from the Last Interglacial indicate that an abundant and diverse large-herbivore guild was associated with high vegetation structural diversity within the temperate forest biome before the end-Pleistocene megafaunal attrition (Fig. 1). In contrast, assemblages from the early Holocene indicated lower herbivore density and correspondingly greater dominance by closed woodland. An important open question concerns the extent to which past herbivore influence on vegetation was modulated by abiotic landscape factors such as topography, hydrology, and soil conditions (10). Furthermore, the relative importance of large herbivore diversity and abundance remains unclear; however, a key message from our results is that a diverse and abundant wild large-herbivore guild is likely instrumental in maintaining a mosaic of vegetation structures under a temperate climate in the absence of human management and thus would help support landscapes with high biodiversity (30–33), as increasingly proposed for abandoned rural areas (34). Understanding ecological processes before modern human interventions thus provides insights that are important for restoring ecosystem function via low-intervention conservation management strategies such as rewilding (34–36).

Materials and Methods

The BugsCEP database (bugsdata v 8.01; 19) was downloaded on September 18, 2013 from www.bugscep.com. Beetle, sample, site, date, ecological category, and climate data were extracted from the database in Microsoft Access 2010 and imported to the R statistical environment, version 2.15 (37). A screening process was undertaken to identify the sites and samples relevant for our analysis. First, because continental European sites are scarce, only sites from the mainland of Great Britain were used. Samples recording beetle abundances were used, excluding samples recording partial abundances and presence/absence. Abundances are the minimum number of individuals represented by the fossil exoskeleton parts found (19).

Using the sample Period Name, Calendar Date, and Radiometric Date data provided by BugsCEP, we assigned each sample to one of four temporal periods: Last Interglacial, Last Glacial, early Holocene, or late Holocene. Samples falling outside these periods were excluded. The Last Interglacial lasted from *ca.* 132,000–110,000 y B.P. (38), corresponding to BugsCEP Period Names Ipswichian, Oxygen Isotope Stage 5e, and Eemian, which fall entirely within the dates for this period. Ten samples from three sites (Austerfield, Deeping St. James, and Elsing 1) had the BugsCEP Period Name "OIS-05e" but had not been assigned start and end dates in the database. A description field for these samples indicated they were from the Ipswichian, and this designation was supported by the literature (e.g., ref. 39, although recent work suggests uncertainty as to whether Austerfield belongs to the Ipswichian or OIS-9), so we included these sites in our analysis of Last Interglacial samples. Samples from the sites Stoke Goldington and Latton contained conflicting data regarding the date within the database [Green et al. (40) indicate that the Stoke Goldington samples come from MIS 7; likewise, Lewis et al. (41) indicate that the Pleistocene succession at Latton dates from MIS 7]. Therefore we excluded these sites from the analysis.

To focus on the full glacial as a clear climatic and vegetation contrast to the interglacials, the Last Glacial control period was defined as between 50,000 and 13,000 radiometric years B.P. (50,000–15,000 calendar years B.P.), corresponding to the BugsCEP Period Names Dimlington Stadial and Middle Devensian in the database. Samples with both maximum and minimum dates within these calendar/radiometric time spans were assigned to this period.

For the early Holocene period we selected the BugsCEP Period Names Atlantic, Mid Holocene, Pollen Zone VIIa, and Pollen Zone VI and calendar dates spanning 10,000–5,000 y B.P. [8,950–4,450 radiometric years B.P., calibrated using the IntCal09 dataset (42)] as a period representing climatic conditions suitable for the formation of closed forest and before high human agricultural impacts that began in the Neolithic. Samples with these period names and samples with maximum and minimum dates within these dates were assigned to this period. To avoid including sites directly affected by human settlements, samples recorded as being from an archaeological

context in the BugsCEP database were excluded from the final selection for this period. Whitehouse and Smith (17) analyzed vegetation structure and the change in herbivore abundance over the early Holocene and identified a series of suitable sites. Two sites with dates appropriate for inclusion within the early Holocene, Bole Ings and Westward Ho, were included in their analysis but were not captured by our initial search. A search of the BugsCEP database indicated samples from these sites recorded the BugsCEP Period Name Holocene. The notes provided with these samples indicated they were from the early to mid Holocene, and therefore they were included within our analysis.

Representing the historical cultural landscape, we defined the late Holocene as the last 2,000 y (2,050–0 radiometric years B.P.). This period included the BugsCEP Period Names Pre-Columbian, Roman Britannia, Late Roman UK, Post-Roman, Medieval, Early Saxon, Saxon, Byzantine, Arab, Viking, Anglo-Scandinavian, Late Medieval UK, Spanish adobe, Post Medieval, Modern, Recent, and Historical. Samples with calendar or radiometric dates were included if the maximum and minimum dates fell within the period. Samples collected using modern census techniques for contemporary ecological assemblages, such as pitfall trapping, were removed.

Each beetle species recorded in the database is associated with one or more ecological categories (Bugs EcoCodes) (19). Beetles associated with aquatic habitats (Ecolabels: Aquatics; Indicators: Standing water and Indicators: Running water) were removed from the analysis following Smith et al. (18). Only specimens identified to the species level were used, excluding all specimens recorded as "sp.," "spp.," or "indet" in the species column. Samples containing fewer than 10 individual beetles were excluded.

The proportions of beetles representing each ecological category were calculated by dividing the beetle abundance in a given ecological category by the total beetle abundance per sample. Macrofossils are better preserved in wet areas; beetle assemblages indicated that samples from the late Holocene were drier than earlier periods. To increase comparability between the late Holocene and the two main study periods, the Last Interglacial and early Holocene, 100 random selections of 75 samples (a quarter of the total available) were chosen from the late Holocene. Among these selections the combination that best matched the distribution of sample wetness from the Last Interglacial and early Holocene was chosen using the Kolmogorov–Smirnov test (lowest test statistic) and was used in all analyses and figures.

In total, we analyzed 32 samples from 11 sites from the Last Interglacial, 57 samples from 28 sites from the Last Glacial, 75 samples from 14 sites in the early Holocene, and 75 samples from 45 sites from the late Holocene (Fig. S4). The ecological category Woods and Trees was selected to represent woodland cover, and the categories Pasture Dung and Dung Indicator were selected to represent grazed habitats and herbivore abundance, respectively. All ecological categories are reported in Fig. S5. GLMM with a binomial error distribution were used to compare the proportional representation of beetles associated with each of our three selected ecological categories between the Last Interglacial and early Holocene, using the lmer function from the lme4 package (43). Site name was included as a random effect to control for multiple sampling from different sites. Models were checked for over-dispersion; to account for slight overdispersion in the model testing woods and trees, the sample identification number was included as an additional random effect. P values were generated by comparing each full model with a null model that included all random effects using likelihood ratio tests (χ^2).

To compare the herbivore abundance and the vegetation structure of each of the four focal temporal periods, the median sample percentage representation per ecological category was calculated for each site. Sites then were assigned to one of three dung categories (Low, Medium, and High) and to one of four vegetation categories (open, wood–pasture, semiclosed forest, and closed forest) in accordance with Smith et al. (18). Dung classifications are based on the proportion of beetle abundance associated with pasture dung; high dung is ≥10.0%, medium dung is <10.0% and ≥5.0%, and low dung is <5.0% (18). Classifications of vegetation structure are based on the proportion of beetle abundance that represent forest and trees; closed forest is ≥22.5%, semiclosed forest is <22.5% and ≥15.0%, wood–pasture is ≥5.0% and <15.0%, and open vegetation is <5.0% (18). It was noticeable that for the early Holocene 46% of dung indicator species were found at only a single site, Runnymede 1, where the influence of an early human agricultural settlement (44) cannot be excluded.

Climate and fire also are important factors in vegetation community dynamics. The BugsCEP database reports thermal summary data—the thermal tolerance extremes across six categories—for 436 species (19). To compare the relative thermal conditions in each of our four temporal periods, sample mean temperatures in degrees Celsius for each category were calculated from the species for which thermal data were available. Site median temperatures were calculated from the sample averages and are reported in Fig. S1. To explore the importance of fire, 64 pyrophilous beetle species were identified from Whitehouse (22) and Lundberg (23), and their prevalence in the Last Interglacial and in the early Holocene was compared.

A series of sensitivity analyses were performed to test our approach. First, to test the sensitivity of our approach to selecting late Holocene samples that were more representative of the wetness of the Last Interglacial and early Holocene, nine further random selections were analyzed. The approach was found to be robust with a maximum SE of ±1.8% recorded, which came from the category closed forest. To test the sensitivity of the site environmental characterizations based on threshold values reported by Smith et al. (18), the analysis was repeated first by decreasing and then by increasing the original thresholds by 20% (Fig. S2). To test the importance of site localities, the two Scottish sites from the early Holocene, which were located at a higher altitude and latitude than the Last Interglacial and other early Holocene sites, were removed, and the analyses were repeated (Fig. S3).

1. Barnosky AD (2008) Colloquium paper: Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *Proc Natl Acad Sci USA* 105(Suppl 1):11543–11548.
2. Rule S, et al. (2012) The aftermath of megafaunal extinction: Ecosystem transformation in Pleistocene Australia. *Science* 335(6075):1483–1486.
3. 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(5956):1100–1103.
4. Owen-Smith N (1987) Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13(3):351–362.
5. Birks HJB (2005) Mind the gap: How open were European primeval forests? *Trends Ecol Evol* 20(4):154–156.
6. Bradshaw RHW, Hannon GE, Lister AM (2003) A long-term perspective on ungulate–vegetation interactions. *For Ecol Manage* 181(1-2):267–280.
7. Sutherland WJ (2002) Conservation biology: Openness in management. *Nature* 418(6900):834–835.
8. Vera FWM (2000) *Grazing Ecology and Forest History* (CABI Pub., New York).
9. Mitchell FJG (2005) How open were European primeval forests? Hypothesis testing using palaeoecological data. *J Ecol* 93(1):168–177.
10. Svenning J-C (2002) A review of natural vegetation openness in north-western Europe. *Biol Conserv* 104(2):133–148.
11. Moe SR, Rutina LP, Hytteborn H, Du Toit JT (2009) What controls woodland regeneration after elephants have killed the big trees? *J Appl Ecol* 46(1):223–230.
12. O'Kane CA, Duffy KJ, Page BR, Macdonald DW (2011) Are the long-term effects of mesobrowsers on woodland dynamics substitutive or additive to those of elephants? *Acta Oecol* 37(5):393–398.
13. Willis KJ, Birks HJB (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science* 314(5803):1261–1265.
14. Higham T, et al. (2011) The earliest evidence for anatomically modern humans in northwestern Europe. *Nature* 479(7374):521–524.
15. Lewis SG, Ashton N, Jacobi R (2011) Testing human presence during the last interglacial (MIS 5e): A review of the British evidence. *The Ancient Human Occupation of Britain, Developments* in Quaternary Science, eds Ashton N, Lewis SG, Stringer CB (Elsevier, Amsterdam), Vol 14, pp 125–164.
16. Owen-Smith RN (1988) *Megaherbivores: The Influence of Very Large Body Size on Ecology* (Cambridge Univ Press, Cambridge, UK).
17. Whitehouse NJ, Smith D (2010) How fragmented was the British Holocene wildwood? Perspectives on the "Vera" grazing debate from the fossil beetle record. *Quat Sci Rev* 29(3-4):539–553.
18. Smith D, Whitehouse N, Bunting MJ, Chapman H (2010) Can we characterise 'openness' in the Holocene palaeoenvironmental record? Modern analogue studies of insect faunas and pollen spectra from Dunham Massey deer park and Epping Forest, England. *Holocene* 20(2):215–229.
19. Buckland PI, Buckland PC (2006) BugsCEP Coleopteran Ecology Package. *IGBP PAGES/World Data Center for Paleoclimatology Data Contribution Series 2006-116* (NOAA/NCDC Paleoclimatology Program, Boulder, CO). Bugsdata version 8.01. Available at www.bugscep.com. Accessed September 18, 2013.
20. Coope GR (2000) The climatic significance of coleopteran assemblages from the Eemian deposits in southern England. *Neth J Geo* 79(2-3):257–267.
21. Wassmer T (1995) Selection of the spatial habitat of Coprophagous beetles in the Kaiserstuhl area near Freiburg (SW-Germany). *Acta Ecol* 16(4):461–478.
22. Whitehouse N (2000) Forest fires and insects: Palaeoentomological research from a subfossil burnt forest. *Palaeogeogr Palaeocl* 164(1):231–246.
23. Ludberg S (1984) Den brända skogens skalbaggsfauna i Sverige. *Entomol Tidskr* 105(4):129–141, Swedish.
24. Owen-Smith N (1989) Megafaunal extinctions: The conservation message from 11,000 years B.p. *Conserv Biol* 3(4):405–412.
25. Keen D, et al. (1999) Sedimentology, palaeoecology and geochronology of last interglacial deposits from Deeping St James, Lincolnshire, England. *J Quaternary Sci* 14(5):411–436.

26. Stuart AJ (1995) Insularity and Quaternary vertebrate faunas in Britain and Ireland. *Geol Soc Lond Spec Publ* 96(1):111–125.

27. Phillips L (1974) Vegetational history of the Ipswichian/Eemian interglacial in Britain and continental Europe. *New Phytol* 73(3):589–604.

28. Louys J, Curnoe D, Tong H (2007) Characteristics of Pleistocene megafauna extinctions in Southeast Asia. *Palaeogeogr Palaeocl* 243(1-2):152–173.

29. Kienast F, et al. (2011) Paleontological records indicate the occurrence of open woodlands in a dry inland climate at the present-day Arctic coast in western Beringia during the Last Interglacial. *Quat Sci Rev* 30(17):2134–2159.

30. Macagno A, Palestrini C (2009) The maintenance of extensively exploited pastures within the Alpine mountain belt: Implications for dung beetle conservation (Coleoptera: Scarabaeoidea). *Biodivers Conserv* 18(12):3309–3323.

31. Barbero E, Palestrini C, Rolando A (1999) Dung beetle conservation: Effects of habitat and resource selection (Coleoptera: Scarabaeoidea). *J Insect Conserv* 3(2):75–84.

32. Verdú J, Crespo M, Galante E (2000) Conservation strategy of a nature reserve in Mediterranean ecosystems: The effects of protection from grazing on biodiversity. *Biodivers Conserv* 9(12):1707–1721.

33. Tocco C, Negro M, Rolando A, Palestrini C (2013) Does natural reforestation represent a potential threat to dung beetle diversity in the Alps? *J Insect Conserv* 17(1):207–217.

34. Navarro L, Pereira H (2012) Rewilding abandoned landscapes in Europe. *Ecosystems (N Y)* 15(6):900–912.

35. Hodder K, Bullock J, Buckland P, Kirby K (2005) Large herbivores in the wildwood and modern naturalistic grazing systems. *Natl Eng* ENRR648:30–54.

36. Donlan J (2005) Re-wilding North America. *Nature* 436(7053):913–914.

37. R Development Core Team (2012). R: A language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna). Available at: www.R-project.org/. Accessed June 22, 2012.

38. Shackleton NJ, Chapman M, Pailler D, Lancelot Y (2002) The Classic Marine Isotope Substage 5e. *Quat Res* 58:14–16.

39. Coope GR (2001) Biostratigraphical distinction of interglacial coleopteran assemblages from southern Britain attributed to Oxygen Isotope Stages 5e and 7. *Quat Sci Rev* 20(16-17):1717–1722.

40. Green C, et al. (1996) Pleistocene deposits at Stoke Goldington, in the valley of the Great Ouse, UK. *J Quaternary Sci* 11(1):59–87.

41. Lewis SG, et al. (2006) Pleistocene fluvial sediments, palaeontology and archaeology of the upper River Thames at Latton, Wiltshire, England. *J Quaternary Sci* 21(2):181–205.

42. Reimer PJ, et al. (2009) INTCAL09 and MARINE09 radiocarbon age calibration curves, 0-50,000 years cal BP. *Radiocarbon* 51(4):1111–1150.

43. Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. Available at: http://CRAN.R-project.org/package=lme4. Accessed June 22, 2012.

44. Whitehouse NJ (2006) The Holocene British and Irish ancient forest fossil beetle fauna: Implications for forest history, biodiversity and faunal colonisation. *Quat Sci Rev* 25(15):1755–1789.