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million (ppm) and then decreased to ~1.0 in the 1970s when atmospheric P_{CO_2} was 330 ppm. Models indicate that retreat of the ice edge past the continental shelf break will greatly enhance upwelling (*22*). In the Canada Basin, the summer ice edge has been located northward of the shelf break almost yearly since 1997 (fig. S4), and thus upwelling will bring water with Ω aragonite of <1 onto the continental shelves.

Although the possible impact of decreased Ω and undersaturation with respect to aragonite on the ecosystem is not fully understood, laboratory experiments on marine biota in an elevated CO_2 environment show that changes in Ω cause substantial changes in overall calcification rates for many species of marine organisms, including coccolithophore, foraminifera, pteropods, mussels, and clams (*4*). In the Arctic Ocean, the larvae of aragonite shell–forming pteropods *Limacina helicina* are concentrated in the top 50 m (*23*), and this is where the decrease in Ω and increase in sea ice meltwater is the most profound. Upwelling of low Ω subsurface water onto the continental shelves will also affect benthic communities, such as bivalve molluscs (*4*). Therefore, we expect that populations of both planktonic and benthic calcifying organisms in the Canada Basin are now being affected because of the rapid decrease in Ω, which is due to the melting of sea ice and upwelling. Because they are important elements of the food web, the Arctic ecosystem may be at risk and requires observation in order to predict future possible impacts on marine organisms, fisheries, and biogeochemical cycles on both regional and global scales.

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Pleistocene Megafaunal Collapse, Novel Plant Communities, and Enhanced Fire Regimes in North America

Jacquelyn L. Gill,[1,2] John W. Williams,[1,2] Stephen T. Jackson,[3] Katherine B. Lininger,[1] Guy S. Robinson[4]

Although the North American megafaunal extinctions and the formation of novel plant communities are well-known features of the last deglaciation, the causal relationships between these phenomena are unclear. Using the dung fungus *Sporormiella* and other paleoecological proxies from Appleman Lake, Indiana, and several New York sites, we established that the megafaunal decline closely preceded enhanced fire regimes and the development of plant communities that have no modern analogs. The loss of keystone megaherbivores may thus have altered ecosystem structure and function by the release of palatable hardwoods from herbivory pressure and by fuel accumulation. Megafaunal populations collapsed from 14,800 to 13,700 years ago, well before the final extinctions and during the Bølling-Allerød warm period. Human impacts remain plausible, but the decline predates Younger Dryas cooling and the extraterrestrial impact event proposed to have occurred 12,900 years ago.

In North America, Pleistocene-Holocene deglaciation [18 to 6 thousand years ago (ka); 1 ka = 1000 calendar years ago] was marked by massive biotic upheaval, including the extinction of 34 megafaunal genera (*1*), species migration and reorganization of terrestrial communities (*2*), the rise and decline of plant communities without modern analogs (*3*), and increased biomass burning (*4*). Individualistic plant species' responses to climate change transformed the composition and distribution of vegetation formations, with rates of change highest between 13 and 10 ka

(all ages are reported as calendar years before the present) (*2*). Many North American fossil pollen assemblages between 17 and 9 ka lack modern analogs, suggesting parent vegetation formations that were compositionally unlike any today (*5*). In the upper Midwest of the United States, "no-analog" pollen assemblages contained high percentages of temperate broadleaved trees, particularly *Fraxinus* (ash), *Ostrya*/*Carpinus* (hophornbeam/ironwood), and *Ulmus* (elm), coexisting with boreal conifers such as *Picea* (spruce) and *Larix* (larch) (*2*, *3*). These no-analog communities apparently formed in response to higher-than-present insolation and temperature seasonality, but it has been suggested that they may have been linked to the Pleistocene megafauna (*3*).

Deglaciation and vegetation turnover coincided with the end-Pleistocene megafaunal extinctions in North America, which was part of a global time-transgressive extinction wave that was taxonomically selective and more severe for species of large body size (*6*, *7*). In North America, >50% of all mammal species >32 kg and all species >1000 kg were extirpated (*1*). Hypothesized extinction drivers include climate change, human hunting, or a combination of the two; the relative importance of these mechanisms is debated (*1*, *8*). An extraterrestrial impact at 12.9 ka has also been proposed (*9*) but is disputed (*4*, *10*).

The apparent coincidence between megafaunal extinction, peak rates of vegetation change, and the rise of the no-analog communities (*3*) in eastern North America suggests causal relationships, but the direction of causation remains unclear. Hypothesized extinction mechanisms linked to vegetation change include habitat loss and fragmentation, disruption of coevolved plant and animal communities, and loss of vegetation mosaics (*1*, *8*). Conversely, the removal of keystone megaherbivores might have triggered trophic

[1]Department of Geography, University of Wisconsin, Madison, WI 53706, USA. [2]Center for Climatic Research, University of Wisconsin, Madison, WI 53706, USA. [3]Department of Botany, University of Wyoming, Laramie, WY 82071, USA. [4]Department of Natural Science, Lincoln Center Campus, Fordham University, New York, NY 10023, USA.

effects (*11*). Contemporary exclusion experiments have highlighted megafaunal influences on plant community composition and structure though edaphic disturbance, selective herbivory, and seed dispersal and propagation (*12*). In African savannas, megaherbivores can suppress fire by reducing fuel loads and facilitating the growth of less-flammable species (*13*).

Testing causal hypotheses has been hampered by difficulties in establishing the precise temporal sequence of events, due to fossil scarcity and uncertainties in dating and cross-site correlations. Megafaunal remains are rare, particularly in the lakes and mires that archive late Quaternary pollen records, and changes in population densities cannot be inferred from most megafaunal fossil records.

Many bone radiocarbon dates are erroneously young because of contamination by humic acids, although dating of purified bone collagen can remove this effect (*14*). The last-dated fossil for a species is unlikely to be from the last surviving individual.

We precisely established local lead-lag relationships among the no-analog plant communities, changes in fire regimes, and megafaunal population declines through a multiproxy sedimentary study of *Sporormiella* dung fungal spores, fossil pollen, and charcoal from a lake in mid-continental North America. *Sporormiella* is a genus of coprophilous fungi in the family Sporormiaceae that requires herbivore digestion to complete its life cycle, producing spores on the dung of mammals and some birds (*15*). *Sporormiella* spores have been

found in mammoth (*Mammuthus* spp.) gut contents and coprolites (*16, 17*). *Sporormiella* spores track the end-Pleistocene megafaunal population decline: They are abundant in late-glacial sediments, scarce through the Holocene, and return to high abundances after the historic introduction of domestic grazers (*16, 18*). The spores are transported to lakes by slopewash, so *Sporormiella* abundances in lake sediments reflect both dung loadings in the watershed and distance to their source (*19*). Thus, *Sporormiella* abundances cannot be simply converted to dung volume and herbivore biomass, but *Sporormiella* abundances <2% of the arboreal pollen sum consistently indicate the extinction of megafauna at sites in Pleistocene North America (*16*) and in late Holocene Madagascar (*20*).

Appleman Lake (LaGrange County, Indiana; 41.6237°N, 85.2136°W), a 21-ha kettle pond situated on glacial till and outwash from the Lake Michigan Lobe, is centrally located within the no-analog vegetation formations (Fig. 1). An 11.5-m sediment core was extracted in 2005 (*21*). Thirteen wood, pollen, and charcoal samples were submitted for radiocarbon analysis (table S1), four anomalous dates were rejected, and a linear age model was constructed from the remaining dates (fig. S1). No-analog communities were identified by plotting the minimum squared chord dissimilarities (SCDs) between Appleman pollen assemblages and their closest matches from the North American Modern Pollen Database; fossil samples with minimum dissimilarities >0.3 were considered to have no modern analog.

At Appleman Lake, *Sporormiella* was initially abundant, began declining at ~14.8 ka, fell below 2% at 13.7 ka (Fig. 2G), and remained <2% thereafter. The youngest-dated bones of most North American megafauna cluster between 13 and 11.5 ka (*22*), so the *Sporormiella* decline apparently indicates local population collapse and func-
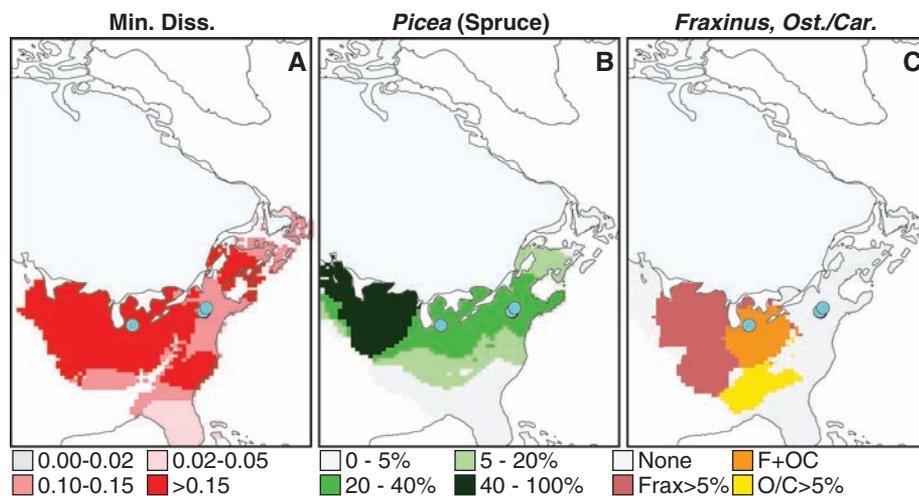

Fig. 1. Position of Appleman Lake, Indiana, and New York sites (blue circles) relative to (**A**) minimum squared chord dissimilarity for fossil pollen assemblages in eastern North America, (**B**) *Picea* pollen percentages, and (**C**) the distributions of *Fraxinus* and *Ostrya/Carpinus* pollen, all mapped for 14 ka. The mapped SCDs are based on a smaller list of taxa (25 pollen types) than used elsewhere in this paper; therefore, values >0.15 indicate fossil samples with no modern analog.

Fig. 2. Appleman Lake time series for (**A** to **F**) percent pollen abundances of selected taxa (NAP, nonarboreal pollen), (**G**) *Sporormiella*, (**H**) minimum squared chord dissimilarity, and (**I**) charcoal counts. Pollen abundances are expressed as a percentage of the upland pollen sum.
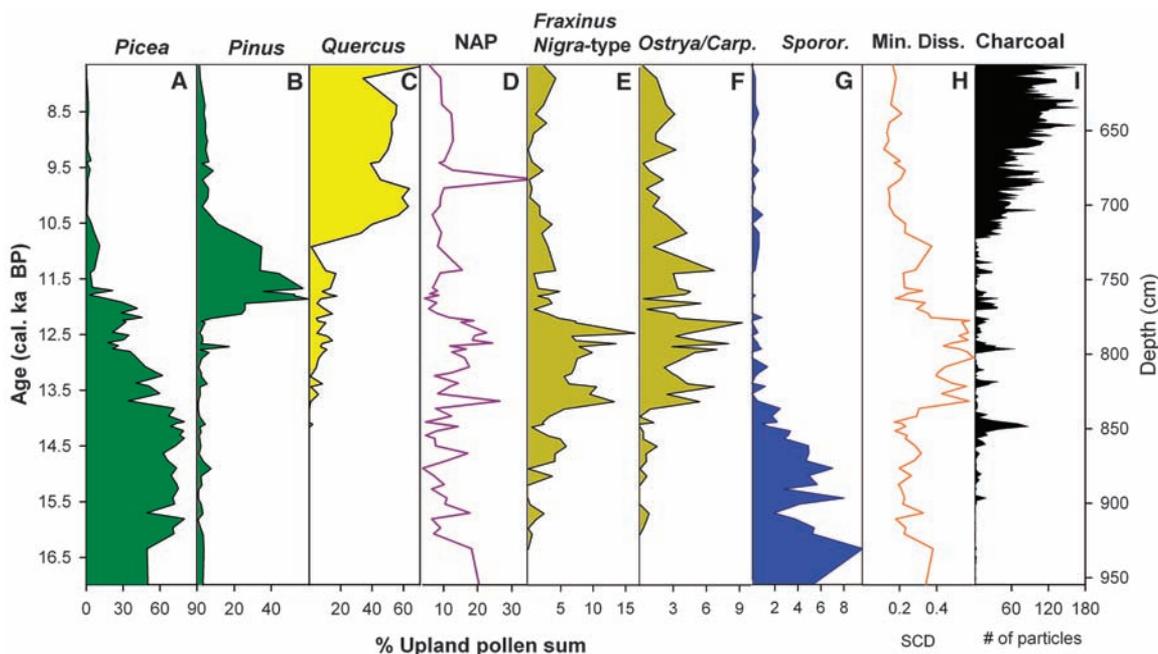
tional species extinction, not final extinction. The *Sporormiella* decline roughly coincided with the initiation of the Bølling-Allerød warm period, dated in Greenland at 14.69 ka (*23*). No-analog plant communities developed at 13.7 ka (Fig. 2H), after *Sporormiella* declined below 2%, and were marked by rises in *Fraxinus nigra*–type (black ash) and *Ostrya/Carpinus* (hophornbeam/ironwood) pollen abundances while *Picea* (spruce) abundances remained high (Fig. 2, A, E, and F). No-analog communities persisted until 11.9 ka (Fig. 2H) and were followed by a period of high *Pinus* (pine) abundances (Fig. 2B), then high abundances of *Quercus* (oak), marking the early Holocene establishment of deciduous forests in northern Indiana.

Fire regimes at Appleman had three stages. Before 14.3 ka, charcoal was uncommon, indicating few or no local fires (Fig. 2I) or insufficient biomass to produce abundant charcoal. After 14.3 ka, charcoal peaks were intermittent against low background rates of charcoal deposition. Charcoal first peaked at 14.1 ka, during the *Sporormiella* decline and before the increase in hardwood pollen abundances. This stage persisted until 10.7 ka, when rates of charcoal deposition and *Quercus* pollen abundances increased rapidly.

The close linkage between *Sporormiella* and changes in vegetation and fire at Appleman Lake is consistent with evidence from several New York sites (Fig. 3) (*18*). There, the onset of the *Sporormiella* decline ranged from <13 ka to >14 ka; dating is less certain than at Appleman due to hard-water contamination of bulk sediment radiocarbon dates (*24*). The New York sites are on the periphery of the late-glacial no-analog communities (Fig. 1) (*3*), and minimum SCDs are lower than at Appleman Lake (Fig. 3). Nevertheless, as at Appleman, hardwood abundances increased immediately after the *Sporormiella* decline, contributing to an increase in vegetation dissimilarity, and charcoal abundances peaked during or after the *Sporormiella* decline (Fig. 3).

Our data thus rule out hypotheses that (i) climate-forced changes in vegetation drove the megafaunal decline, and (ii) no-analog plant communities were created by megaherbivory. The first hypothesis is rejected because the *Sporormiella* decline preceded the major palynological events (particularly the shift from *Picea* to *Pinus* and increased abundances of hardwood taxa). However, climate change might have directly forced the megafaunal population declines, given the similar timing between the *Sporormiella* decline and the onset of Bølling-Allerød warming in Greenland (*23*). If so, climatic forcing apparently did not operate through habitat change, which is the mechanism underlying most climate-based extinction hypotheses (*1*).

The second hypothesis is excluded because the no-analog communities arose after *Sporormiella* declined. Thus, the increase in hardwood taxa (*Fraxinus*- and *Ostrya/Carpinus* at Appleman and *Ulmus*, *Acer*, and others in New York) may represent both a response to warming and a release from herbivory pressure. Many extant megaherbivores prefer broadleaf forage because of its higher nutrient and water content (*12*, *25*). For example, moose (*Alces alces*) dietary preferences have reduced tree density and promoted shrubs and needle-leaved trees (*26*). Tradeoffs between fire and megafaunal consumption of biomass are documented in modern African ecosystems (*13*). A switch from herbivory- to fire-dominated disturbance regimes may explain why the first post-*Sporormiella* charcoal peak was consistently the largest across sites (Fig. 3), if this first fire burned both live biomass and litter untouched by herbivores.

The possibility that late-glacial vegetation and fire regimes were influenced by herbivory does not rule out climatic drivers of late Quaternary landscape change, which are well established (*27*, *28*). Rather, we suggest a hierarchy of controls on deglacial vegetation history, with climate driving changes in plant and megafaunal ranges and abundances, which engendered further herbivory- and fire-regulated biotic interactions. The rise in *Fraxinus nigra*–type and *Ostrya/Carpinus* pollen ~15.0 ka (Fig. 2, E and F) may indicate the establishment of small tree populations under newly favorable climates, whereas secondary increases at 13.7 ka may indicate the expansion of populations under decreased herbivory pressure and a new fire regime. Thus, the formation of no-analog plant communities may have been jointly controlled by novel climates (highly seasonal insolation and temperatures) (*5*) and release from herbivory.

Humans may have affected late Quaternary vegetation history by intensifying fire regimes and contributing to the megafaunal extinctions. Increased sedimentary charcoal is associated with human arrival and megafaunal extinctions on islands (*20*), and
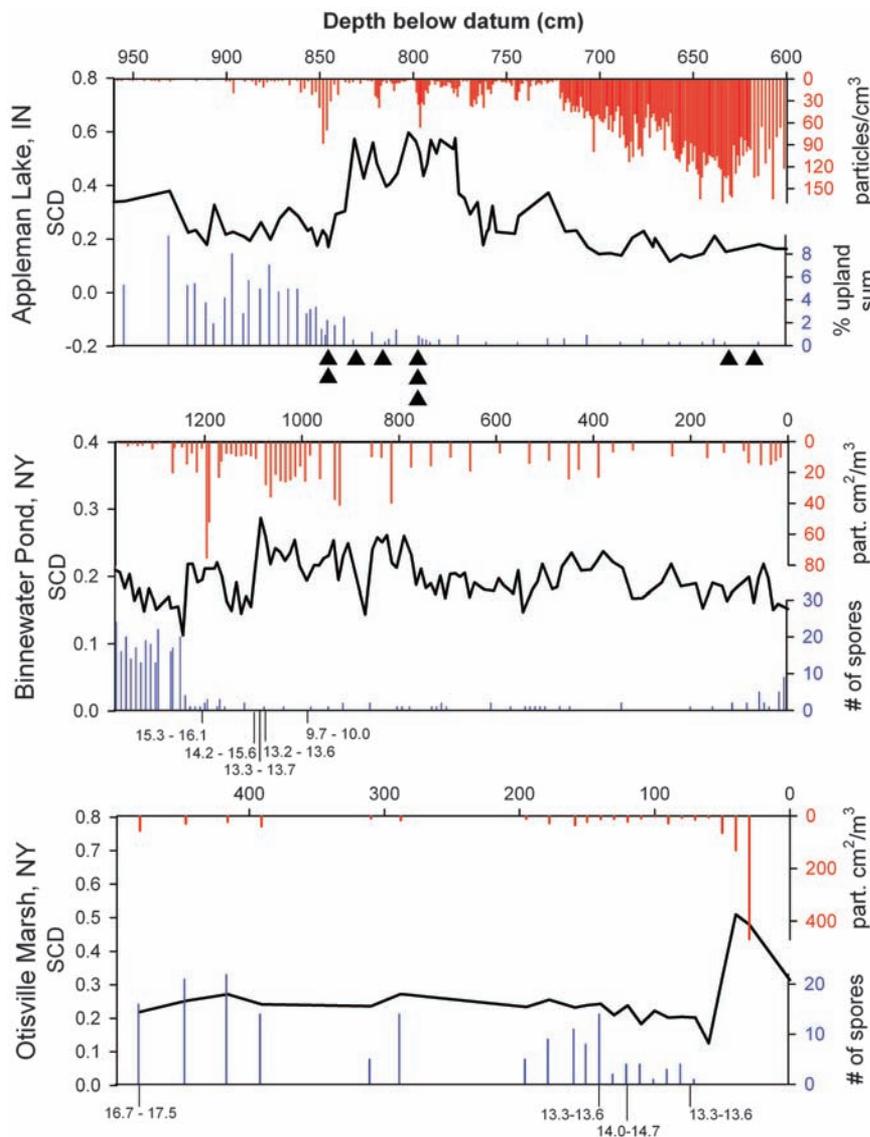

Fig. 3. Comparison of the Appleman record with two New York sites reinforces the close connection among the *Sporormiella* decline (blue histogram), the first large pulse of sedimentary charcoal (red histogram, inverted axis), and increased vegetation dissimilarity from that of the present (black line). Black triangles indicate locations of radiocarbon dates from Appleman.

the globally time-transgressive wave of late Pleistocene extinctions closely tracks human colonization history. Butchered mammoth bones excavated in southeastern Wisconsin date regional human presence to between 14.8 and 14.1 ka (29), coeval with the *Sporormiella* decline at Appleman Lake.

At all sites, the *Sporormiella* decline substantially predated initiation of the Younger Dryas, ruling out abrupt climatic cooling and the hypothesized extraterrestrial impact at 12.9 ka as a cause (9). More generally, the megafaunal declines apparently progressed over several thousand years, given the 1000-year duration of the *Sporormiella* decline at Appleman and the difference in timing between the onset of the *Sporormiella* decline (14.8 ka) and the final extinctions (~11.5 ka) (1). This evidence excludes rapid-extinction hypotheses such as an extraterrestrial impact or a Paleo-Indian blitzkrieg (30).

Our work thus shows close connections among the late-glacial histories of fire, vegetation, and mammalian herbivores and suggests that the loss of a broad guild of consumers contributed to substantial restructuring of plant communities and an enhanced fire regime. The sequence of events at Appleman rules out several hypothesized causes and effects of the megafaunal extinction but does not conclusively resolve the debate over climatic versus human causation (or both) of the North American megafaunal extinctions. However, several promising avenues exist. One is to search for spatial and temporal patterns in the late Pleistocene *Sporormiella* decline (time-transgressive versus synchronous) and to further check its association with vegetation and fire history. Another is to analyze the *Sporormiella* record at sites spanning the penultimate deglaciation (when humans were absent from North America) and in sites near well-dated records of Paleo-Indian activity. Such analyses should be extended to other continents, to study the ecological effects of the end-Pleistocene extinctions under different contexts of human, climate, and vegetation history (31). By resolving the causes and consequences of the late Pleistocene megafaunal extinctions, such work would address concerns about trophic effects arising from the contemporary widespread declines, extinctions, and restorations of megaherbivores.

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High Symbiont Relatedness Stabilizes Mutualistic Cooperation in Fungus-Growing Termites

Duur K. Aanen,[1]* Henrik H. de Fine Licht,[2] Alfons J. M. Debets,[1] Niels A. G. Kerstes,[1] Rolf F. Hoekstra,[1] Jacobus J. Boomsma[2]

It is unclear how mutualistic relationships can be stable when partners disperse freely and have the possibility of forming associations with many alternative genotypes. Theory predicts that high symbiont relatedness should resolve this problem, but the mechanisms to enforce this have rarely been studied. We show that African fungus-growing termites propagate single variants of their *Termitomyces* symbiont, despite initiating cultures from genetically variable spores from the habitat. High inoculation density in the substrate followed by fusion among clonally related mycelia enhances the efficiency of spore production in proportion to strain frequency. This positive reinforcement results in an exclusive lifetime association of each host colony with a single fungal symbiont and hinders the evolution of cheating. Our findings explain why vertical symbiont transmission in fungus-growing termites is rare and evolutionarily derived.

Horizontal symbiont transmission is the rule in ancient and ecologically important mutualisms, such as those between plants and mycorrhizas or nitrogen-fixing bacteria. The stability of such interactions is puzzling, because multiple symbiont lineages compete for host resources, and hosts have frequent opportunities to exchange resident symbionts with new and potentially superior lineages (1–3). Here we address the evolutionary stability of an analogous animal-microbial mutualism in the fungus-growing termites (subfamily Macrotermitinae), which coevolved with a single genus of basidiomycete fungi, *Termitomyces*, while retaining horizontal symbiont transmission in most genera (4).

The termite-fungus mutualism is of major ecological importance in Old World tropical regions for decomposition and mineral cycling (5). The termites cultivate their fungal symbiont in well-protected gardens inside the nests on a substrate (comb) of predigested plant material (Fig. 1A). The mutualistic fungus provides most of the termite food, both directly, when termites eat nodules of fungal material containing asexual spores (Fig. 1B), and indirectly, when they ingest the partially degraded comb biomass later on (6, 7). The symbiosis has a single African rain forest origin, more than 30 million years ago (8–11) and has radiated into 10 extant genera with about 330 described species (12).

No reversals to a solitary life-style are known (4). This is remarkable, as partners in most genera have retained independent reproduction by means

[1]Laboratory of Genetics, Wageningen University, 6700 AH Wageningen, Netherlands. [2]Centre for Social Evolution, Department of Biology, University of Copenhagen, 2100 Copenhagen, Denmark.

*To whom correspondence should be addressed. E-mail: duur.aanen@wur.nl