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Research

Down-sizing of dung beetle assemblages over the last 53 000 years is consistent with a dominant effect of megafauna losses

Andreas H. Schweiger and Jens-Christian Svenning

A. H. Schweiger (http://orcid.org/0000-0003-2656-5918) (andreas.schweiger@uni-bayreuth.de) and J.-C. Svenning (http://orcid.org/0000-0002-3415-0862), Section for Ecoinformatics and Biodiversity, Dept of Bioscience, Aarhus Univ., Ny Munkegade 114-116, DK-8000 Århus C, Denmark. AHS also at: Plant Ecology, Bayreuth Center of Ecology and Environmental Research (BayCEER), Univ. of Bayreuth, Bayreuth, Germany. JCS and AHS also at: Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Dept of Bioscience, Aarhus Univ., Aarhus, Denmark.

The ongoing down-sizing of the global mammal communities is assumed to have subsequent effects on mutualistic species communities. Dung beetles co-evolved with large-sized animals since millennia and depend on the megafauna feces of an appropriate size. Mammal community down-sizing as a result of past and ongoing megafauna losses is therefore likely to result in a down-sizing of dung beetle communities. However, empirical evidence for this co-down-sizing is lacking especially on larger spatial scales and over extended periods of time.

Here, we show a significant down-sizing of European dung beetle assemblages over the last ~53 000 years by relating Quaternary fossil records with trait information on body size of beetles. This significant down-sizing of dung beetle communities was thereby not linear, but characterized by a weak decrease until the early Holocene but a strong acceleration in the recent pre-history, from 6–7000 years BP onwards. This acceleration of down-sizing coincides with the completion of the Quaternary megafauna extinction and the start of major shifts in human agricultural land-use. In contrast, assemblage mean body size of non-coprophagous scarabids as well as ground beetles – two groups of beetles with no or weak relations to megafauna – was observed to increase towards the present with an acceleration of body size increase coinciding with the onset of late-glacial warming (14 200 years BP).

In summary, the observed late-Quaternary down-sizing of European dung beetle communities is consistent with an effect of pre-historic megafauna losses, and not with the coincident general warming. Ongoing down-sizing of mammal communities is therefore likely to result in further down-sizing of dung beetle assemblages, with potential effects on their important role for nutrient cycling and secondary seed dispersal in natural and extensive agro-ecosystems. Future nature management initiatives could halt or even reverse this functional diversity loss via effective protection or restoration of megafauna communities.

Keywords: body size – temperature relation, Coleoptera, defaunation, megaherbivores, Quaternary megafauna extinction, Scarabaeoidea, trophic rewilding

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Massive losses of large-sized animals during recent pre-history had pronounced effects on the species dependent on megafauna. However, empirical evidence for these concomitant, ecological effects of pre-historic megafauna losses has only recently begun accumulating. Dung beetles co-evolved with large-sized animals since millennia and depend on the feces of big animals ever since. Strong detrimental effects on dung beetles seem therefore to be quite likely. However, knowledge about effects of megafauna loss on dung beetles is mainly anecdotal and restricted to limited empirical evidence. Our study is the first to our knowledge showing that the human-induced downsizing of mammal communities can be coupled to a synchronous downsizing of dung beetle communities, on large spatial scale and over an extensive period of time.

Introduction

Megafauna has been a fundamental component of life on Earth since more than 500 million years (Estes et al. 2016). However, large parts of the global megafauna vanished during the Late Pleistocene and early Holocene, and large-bodied animals have since then kept disappearing from many areas until the present day in an anthropogenically driven, size-selective defaunation process (Barnosky et al. 2004, Dirzo et al. 2014, Sandom et al. 2014a, Araujo et al. 2015). In Europe, 60% of the Pleistocene megafauna species went extinct during the last 100 000 years (Wroe et al. 2004). Herbivores of impressive size like the woolly mammoth *Mammuthus primigenius* with up to 3.5 m in height and 8000 kg in weight, the straight-tusked elephant *Palaeoloxodon antiquus* with a height of up to 3.8 m and a weight of 11 000–15 000 kg, the rhinoceros *Stephanorhinus kirchbergensis* with a weight of 1600 to 2900 kg and a height above 2 m or the giant deer (irish elk, *Megaloceros giganteus*, up to 2 m in height and 600 kg in weight) went extinct during the Last Glacial and Holocene, 30 000 to 4000 years ago (Stuart and Lister 2007). These massive losses of large-bodied animals would be expected to percolate through ecosystems with strong effects on the ecosystem integrity and functioning (Culot et al. 2013). However, only recently has evidence begun accumulating for the functional effects on ecosystems related to the megafauna losses (Doughty et al. 2016, Estes et al. 2016). Commensal species associated with big-sized animals are thereby assumed to be strongly affected by these megafauna losses (Galetti et al. 2018).

Dung beetles (coprophagous species in the superfamily Scarabaeoidea) have been suggested to have evolved in close association with feces of large-bodied animals for millions of years, potentially at least since dinosaurs started to forage on angiosperms in the mid-Cretaceous (Chin and Gill 1996, Gunter et al. 2016, Davis et al. 2017). The exact evolutionary age and generality of this close trophic associations with dinosaurs still remains somewhat controversial but the dung beetle–megafauna association at least goes back to the Palaeogene (Davis et al. 2017). Dung beetles adapted to mammal dung after the dinosaurs vanished during the Cretaceous–Paleogene mass extinction event (Gunter et al. 2016). As insects relying on the dung of large-bodied animals for food and nesting substrate ever since, dung beetles have been suggested to be sensitive to the loss of megafauna and respond with co-extinctions and strong changes in community composition (Andresen and Laurance 2007, Favila 2012, Culot et al. 2013). Losses of large-sized dung beetles closely associated with large-sized herbivores are reported from the Late Pleistocene as reviewed in Galetti et al. (2018).

By processing the feces of large animals, dung beetles facilitate ecosystem processes such as nutrient cycling and soil fertilization, bioturbation and aeration as well as secondary seed dispersal with advantageous effects on seed germination, plant growth and distribution (Nealis 1977, Mittal 1993, Andresen and Levey 2004, Coggan 2012). In addition, dung beetles reduce population sizes of important pest species like helminths and diptera larvae and, thus, provide additional, economically important services (Morelli et al. 2012). Dung beetles therefore represent indispensable components of most terrestrial natural and agro-ecosystems (Andresen and Laurance 2007). Globally ongoing mammal declines are therefore likely to have strong cascading effects on important ecosystem processes by altering dung beetle communities (Coggan 2012). Consequently, a better understanding about the effects of the large-scale losses of megafauna during the recent pre-history for dung beetle communities would be an important basis for forecasting the consequences of the ongoing defaunation. However, knowledge about effects of megafauna loss on dung beetles is mainly anecdotal and restricted to limited empirical evidence from short-term experimental studies (Culot et al. 2013). No quantitative study exists to our knowledge on the long-term changes of dung beetle assemblages during the recent pre-history.

In this study we use Quaternary fossil records of dung beetle occurrence from Europe spanning the last ~53 000 years to assess the long-term changes in beetle community composition associated to the pre-historical decline of megafauna, while also considering other factors like climate. We specifically focus on compositional shifts in beetle body size. We therefore quantified temporal changes in the body size distribution in beetle communities as a sensitive indicator for megafauna associated effects on beetle community composition. Such kind of compositional shifts can result

from differences in performance (abundance) and occurrence for differently sized beetle species as a consequence of size-selective resource limitation (Ohlberger 2013). Dung beetle body size is well-known to be closely related to dung size, which again scales with body size of the dung-producing animal (Hanski and Cambefort 1991). Several paleoecological as well as present-day ecological studies suggest a down-sizing of dung beetle communities as consequence of the down-sizing of mammals during recent pre-history (Nichols et al. 2009, Nichols and Gardner 2011, Sanchez et al. 2013). Reduction in cattle stocking has been shown to reduce the representation of big species in dung beetle assemblages (Halffter and Arellano 2002). We therefore expect the medium body size of fossil dung beetle assemblages to have decreased during the recent pre-history as a consequence of the massive decline of large-bodied, wild animals and the concomitant decline in the availability of big-sized dung. Understanding these long-term dynamics in dung beetle communities and their coupling to mega-fauna abundance versus to other drivers like climate will help to forecast potential future dynamics and provide guidance for trophic rewilding initiatives (Svenning et al. 2016) to facilitate the maintenance of functional ecosystems in a human-dominated world.

Material and methods

Dung beetle occurrences trough time came from the BugsCEP (Bugs Coleopteran Ecology Package) database, a comprehensive database on European Quaternary fossil records for beetles (Buckland and Buckland 2006, <www.bugscep.com>). We used the latest update of the database from 1 October 2014 including information on species identity, location and age of beetle macrofossils available for 1124 fossil collection sites

in total complied from international entomological literature and analogue fossil insect datasets (Buckland 2014). Relevant information was extracted from the database using Microsoft Access 2010. We excluded specimens identified with insufficient taxonomic resolution (recorded as 'sp.,' 'spp.,' or 'indet' in the species column of the database). We furthermore excluded all samples with less than 10 individuals of beetles from our analysis and restricted our analysis to the last 53 400 years due to insufficient information on dung beetle occurrence and body size for earlier periods of time. We used calendar date as time variable in our analyses. For each sampling location / time (equals sample) we calculated the community mean of beetle body size. Information on dung beetle body size was taken form Bunalski (1999). Body size is thereby measured as the insect's body length (caput to abdomen). For species with sex-specific differences in body size we took the mean of male and female size. In total, we analyzed 66 samples from 27 sites spanning the last 53 400 years, covering parts of Great Britain and, to a lesser extent, France (Fig. 1a).

Temporal trends in mean body size of beetle assemblages through time were analyzed using simple linear and quantile regression analyses. All regression-based temporal trend analyses were tested and corrected for spatial autocorrelation following an approach suggested by Petty et al. (2012). This approach is based on the method of semiparametric filtering used in ordinary least-squares regression (Tiefelsdorf and Griffith 2007). We therefore selected the set of eigenvectors for each regression model, which reduced spatial autocorrelation most by using the SpatialFiltering() command of the 'spdep' R package (ver. 0.6-13, Bivand and Piras 2015). Spatial autocorrelation is thereby quantified by Moran's I. The respective set of eigenvectors was then incorporated as an additional predictor into the respective simple or quantile regression model (for more details see Petty et al. 2012).
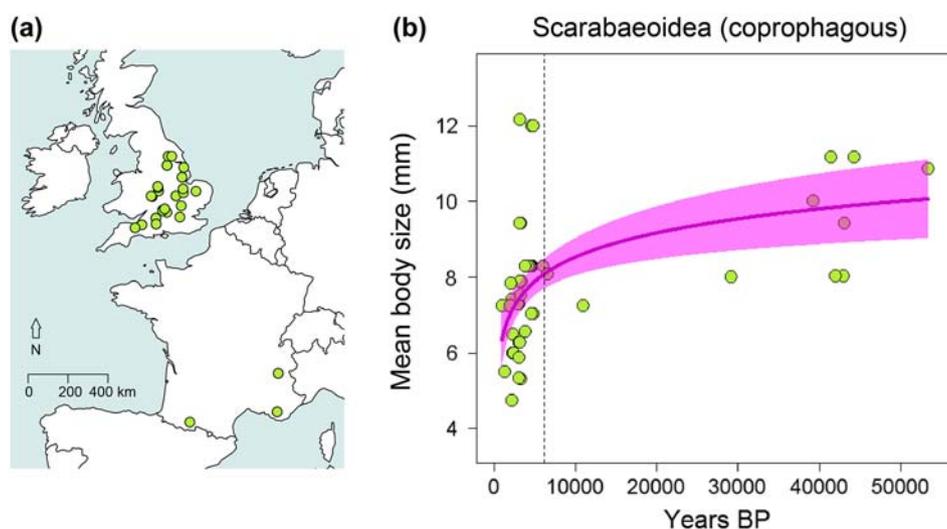

Figure 1. Temporal trend in community mean body size of dung beetles (coprophagous scarabids) over the last 53 400 years inferred from European Quaternary fossil records. (a) Location of the fossil collection sites. (b) Temporal trend in community mean body size. Solid line indicates the model prediction and the shaded area the 0.95 confidence intervals form a simple linear regression model with log-transformation of time. The vertical dashed line indicates the threshold between weak and strong temporal change detected by log-likelihood optimization.

To detect thresholds related to changes in the temporal trends of dung beetle body size we estimated the optimal breakpoint for each relationship by assuming different linear relationships between mean body size and time before and after a potential breakpoint in time. We therefore ran a log-likelihood optimization algorithm which automatically tested 1000 evenly distributed potential breakpoints along the examined period of time of 53 400 years (cf. Schweiger et al. 2015, Schweiger and Beierkuhnlein 2016).

Quantile regression analyses were performed using the rg() command of the 'quantreg' R package (ver. 5.29, Koenker 2016). To comprehensively test for temporal trends throughout the whole body size distribution of the examined beetle communities (from the small sized species to the big sized species), we reran the quantile regression analyses by varying quantiles between 0.1 and 1. The predictive success of the quantile regression models was quantified by calculating pseudo-R^2 as a goodness-of-fit measure suggested by Koenker and Machado (1999). In this approach the sum of weighted deviations for the model of interest is compared with the same sum from a model which assumes no relation between response and predictor variable (by just fitting an intercept but setting the slope constant in the model).

Besides testing temporal trends for coprophagous beetle species of the superfamily Scarabaeoidea, i.e. species feeding on dung, we repeated the analysis for all non-coprophagous species of the superfamily, which includes phytophagous, saprophagous and nidicolous species. Diet and body size information was obtained from Bunalski (1999). To increase the robustness of our analysis and minimize biases in temporal beetle body size trends due to e.g. sampling biases we furthermore tested body mass temporal trends in ground beetles (Carabidae) as a group of beetles. Ground beetles should not be directly sensitive to changes in megafauna abundance, but should be generally responsive to climate to a similar degree as dung beetles and non-coprophagous scarabids. We tested this group of beetles in the same manner as we did for scarabids. While information on carabid community composition through time was extracted from the BugsCEP database, species-specific information on carabid body size (body length) was retrieved from an extensive trait database for Palearctic carabids (Homburg et al. 2013, <www.carabids.org>). All analyses were conducted with all 27 sites included as the results obtained from the regression analyses were robust when excluding the sites in France.

To increase the robustness of our analyses regarding climatic drivers of temporal body mass changes, we furthermore tested the effect of current climatic conditions (mean annual temperature) on the spatial body size patterns based on distribution information for all three considered groups of beetles. We therefore combined information on the current distribution of the beetle species considered for our temporal analyses in Europe with body size information of the respective species and climatic information (mean annual temperature) for the occurrence locations. Information on present-day species occurrence was retrieved form GBIF (2016) using the rgbif R package (ver. 0.9.8, Chamberlain 2017) and was restricted to Europe (Individual references for used occurence data see Supplementary material Appendix 2). Climatic information for mean annual temperatures (bioclim 1) was retrieved from the worldclim 2 dataset with a spatial resolution of 10 minutes (Fick and Hijmans 2017) which was aggregated by factor 10. To generate gridded information on community mean body size we calculated mean body size for each aggregated grid cell based on species occurrences falling into the respective grid cell. Sweden turned out to be over presented in the GBIF dataset in terms of sampling effort compared to the other European countries. To prevent any bias caused by this over representation of reported occurrences we subsampled the Swedish dataset by randomly drawing 1% of the reported data points which then were combined with the occurrences reported form the other European countries for further analyses. Relationships between mean body size and mean annual temperature derived from the aggregated grid cells were afterwards tested for all three groups of beetles (coprophagous and non-coprophagous scarabids as well as carabids) with simple linear regression analysis by accounting for spatial autocorrelation (detailed procedure see above).

Data processing as well as data analyses was performed in R (ver. 3.3.3, <www.r-project.org>) with a level of significance of alpha = 0.05. Spatial visualizations and analyses were realized with the 'maps' (ver. 3.1.1, Becker et al. 2016), 'maptools' (ver. 0.9-2, Bivand and Lewin-Koh 2017) and 'raster' (ver. 2.5-8, Hijmans 2016) R packages.

Results

We observed a significant decrease in the community mean body size of dung beetles (coprophagous scarabids) through the last 53 400 years (adj. $R^2 = 0.26$, F = 11.48, p = 6.487 × 10^{-5}). The rate of decrease in body mass was less pronounced in the Late Pleistocene, but strongly accelerated in the Holocene with a temporal threshold between weak and strong temporal change detected at 6300 years before present (Fig. 1b). The strongest non-linearity in the temporal change in body size was detected for dung beetle communities dominated by bigger species indicated by a maximum predictive power and maximum slope of the quantile regression analyses for the 80% quantile (pseudo-$R^2 = 0.25$, F = 14.2, p = 3.96 × 10^{-4}, slope = 1.21, Supplementary material Appendix 1 Fig A1a, Table A1). The was no relation between species numbers and mean body size of the tested dung beetle communities (adj. $R^2 = 0.02$, p = 0.16).

In contrast to the coprophagous species we observed a strong, non-linear increase of mean community body size through time for the non-coprophagous scarabids with a temporal threshold between weak and strong temporal body size increase detected at 14 200 years before present (adj. $R^2 = 0.39$, p = 3.59 × 10^{-5}, Fig. 2a). We detected the strongest acceleration in body size increase for communities characterized by a prevalence of large-bodied species with a maximum non-linearity (maximum slope of linear regression with log-transformed predictor) for tau = 0.89 (pseudo-$R^2 = 0.19$,
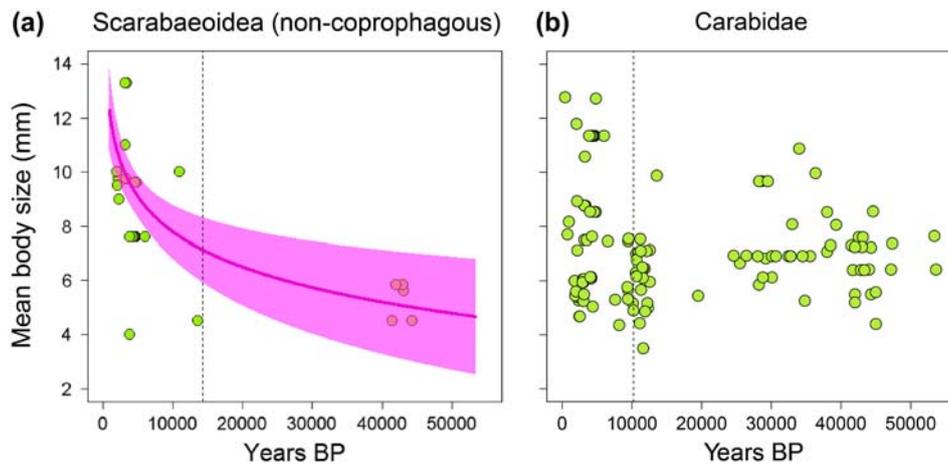
Figure 2. Temporal trends in community mean body size of non-coprophagous scarabids (a) and ground beetles (Carabidae, b) over the last 53 400 years inferred from European Quaternary fossil records. The purple, solid line indicates the model prediction and the shaded area the 0.95 confidence intervals form a simple linear regression model with log-transformation of time. The vertical dashed lines indicate the thresholds between weak and strong temporal changes detected by log-likelihood optimization.

$F = 14.0$, $p = 6.24 \times 10^{-4}$, slope $= -2.85$, Supplementary material Appendix 1 Fig. A1b, Table A2). Similar to the coprophagous species, there was no relationship between species numbers and mean body size for the non-coprophagous scarabid communities (adj. $R^2 = -0.018$, $p = 0.58$).

No significant temporal trend in mean body size was detected for the tested ground beetle communities based on a simple linear regression model (adj. $R^2 = 0.01$, $F = 1.97$, $p = 0.14$) although mean body size tends to increase towards the more recent pre-history and a threshold for change in the temporal trend was detected at 10 200 years – similar to the detected threshold for non-coprophagous scarabids (Fig. 2b). Quantile regression with varying quantiles showed changing temporal trends in mean body size for differently size-structured carabid communities. Significant increases in mean body size (negative slopes) were detected for communities predominated by bigger species while significant decreasing trends (positive slopes) were detected for communities with a higher prevalence of smaller species (Supplementary material Appendix Fig. A1c, Table A3). There was no relation between species numbers and mean body size for the tested carabid communities (adj. $R^2 = -5.6 \times 10^{-3}$, $p = 0.64$).

Discussion

The widespread megafauna extinctions during the Late Pleistocene and early Holocene resulted in detrimental effects on ecosystem integrity by affecting numerous mutualistic species (Galetti et al. 2018). Dung beetles have a long phylogenetic history of interaction with large-bodied animals, proposed to even date back far beyond the mammalian megafauna (Chin and Gill 1996). Due to this close mutualistic relationship between dung beetles and megafauna one would expect co-extinction and marked shifts in beetle community composition to happen – a scenario already suggested by Janzen (1983) for the pre-historical loss of South American megafauna and

shown by later studies (summarized in Galetti et al. 2018). Paleoecological as well as recent ecological studies suggest the negative effect of megafauna loss is size-selective, resulting in a down-sizing of dung beetle communities as consequence of the down-sizing of mammals (Nichols et al. 2009, Nichols and Gardner 2011, Sanchez et al. 2013).

By relating Quaternary fossil records of beetles with trait information on species specific body size we observed that dung beetle communities strongly decreased in size during the last ~53 000 years. This significant down-sizing of dung beetle communities was not linear, but characterized by a rather weak decrease in the Late Pleistocene and early Holocene and a strong acceleration of the size decreasing in the recent pre-history, from 6–7000 years BP onwards. We assume this down-sizing in dung beetle communities to be a consequence of reduced availability of large-sized dung as a result of the extirpation of wild megafauna and changes in human land-use practice during this period of time in Europe. Although the Quaternary Megafauna Extinction started much earlier around 50 000 years BP it extended into the Holocene and was largely completed by 7000 years ago (Barnosky 2008), in Europe notably in terms of loss of mega-herbivores (Sandom et al. 2014b). Empirical evidence for the assumed link between mammal and beetle down-sizing is provided by other studies on recent forest fragmentation and overhunted sites where decreases in dung beetle species numbers and abundances are generally attributed to impoverished mammal communities, with a lower availability of large feces leading to increased competition for dung and favoring more generalist beetle species (Andresen and Laurance 2007, Barragán et al. 2011, Culot et al. 2013). Previous analysis on a subset of the BugsCEP database has revealed that beetles associated with large-herbivore dung were generally more dominant during the Last Interglacial (132 000–110 000 years BP), before human arrival, than in the early Holocene (10 000–5000 years BP) where humans were already dominating the landscape and had reduced the

presence of megafauna in Europe (Sandom et al. 2014b). Concomitant with the observed acceleration of dung beetle down-sizing, human land-use practice changed dramatically in Europe. The expansion of advanced agricultural societies into central and northern Europe 6–7000 years ago increased human agricultural land-use and, thus, habitat fragmentation (Shennan et al. 2013). Furthermore, this major shift in land-use practice probably also changed the availability of megafauna, thus, dung availability in the landscape. Although domesticated livestock could have replaced in principle wild megafauna species in their role of dung provisioning, livestock was probably more concentrated and perhaps not functionally equivalent.

Further evidence for a link between mammal and dung beetle community down-sizing is provided by our analyses for beetles with no or only weak relations to megafauna, namely non-coprophagous scarabids and carabids. For the non-coprophagous scarabids (phytophagous, saprophagous and nidicolous species) we observed a significant increase in community mean body size with rather a weak increase in the Late Pleistocene and a strong acceleration of body size increase in the Holocene. The threshold we detected between the weak and strong temporal change at 14 200 years BP falls together with the onset of late-glacial warming which strongly hints at a climatic driver for the body size increase in non-coprophagous scarabid beetle communities. This increase of body size for non-coprophagous scarabids, and the temporal threshold for dung beetles thousands of years later than the onset of Holocene warming support the critical role of megafauna loss rather than climate changes as a driver of community down-sizing in dung beetles. We did not observe a significant temporal trend in the mean community body size of ground beetles based on all sampled communities. However, we observed a significant, non-linear size increase for carabid communities predominated by big species using quantile regression analysis. This missing / positive temporal trend in body size for carabids – another group of beetles not directly dependent on megafauna – further strengthens our proposal for a mechanistic link between the down-sizing of mammal and dung beetle communities during the last ~53 000 years.

For the two groups of beetles with no or at most weak relations to megafauna, climate forcing is a plausible driver of the temporal changes in mean community body size. The effect of climate warming on ecotherm body size is still unresolved, with empirical studies reporting both increasing as well as decreasing body size for single species as well as communities as a direct consequence of past and current climate warming (Ohlberger 2013). Whether ecotherm body sizes increases or decreases is understood to be related to resource availability and population density with warming being observed to facilitate growth under sufficient food supply and low population density but diminishing growth and thus body size under limited resources and high population density (Crozier et al. 2010, Brodersen et al. 2011). Although adult body size is a phylogenetically very conserved, fixed species-specific trait for beetles, similar effects could be assumed to

act for non-coprophagous scarabids and carabids by differently affecting growth and competitive ability of larvae of small versus big beetle species. Furthermore, being bigger can also be disadvantageous for the energy budget and, thus, fitness of ecotherms like beetles. Although bigger body size increases heat conservation and, thus, cooling rates, larger ectotherms experience also lower heating rates and, thus, a reduced capability to gain heat in cold environments reducing the locomotal and, thus, competitive ability (Pereboom and Biesmeijer 2003, Olalla-Tárraga and Rodríguez 2007, Azócar et al. 2015). This thermal inflexibility of big-sized thermoconformers like beetles strongly hampers species survival and reproduction in cold environments (Peterson et al. 1993, Olalla-Tárraga and Rodríguez 2007) and might be especially relevant for scarabids, well-known for their adaptation to warm climates (Hortal et al. 2011). Overall, we therefore assume climate rather than other factors to be the driver of the temporal body size trends for non-coprophagous scarabids and carabids during the last ~53 000 years. Evidence for this assumption is provided by our analysis on the spatial body size patterns of all three groups of beetles and their relation to mean annual temperature. Based on recent occurrence records from Europe for the beetle species considered in our temporal analyses we observed a positive but weak relation between mean body size and annual temperature for coprophagous scarabids (adj. $R^2 = 0.06$, p = 1.3 × 10^{-4}, Supplementary material Appendix 1 Fig. A2a), i.e. in contrast to their temporal down-sizing, which has occurred in the face of a generally warming climate. The relationship between mean body size and annual temperature was stronger and positive for carabids (adj. $R^2 = 0.10$, p = 2.2 × 10^{-4}, Supplementary material Appendix 1 Fig. A2b) but very weak and negative for non-coprophagous scarabids (adj. $R^2 = 0.04$, p = 0.05, Supplementary material Appendix 1 Fig. A2c). Although evidence from our analyses is weak, climate could still be assumed as an additional driver of the temporal body size changes we observed for dung beetles as Hortal et al. (2011) showed that current day distribution and spatial diversity patterns of European dung beetles, well-known for their adaptation to warm climates, is strongly shaped by the climatic conditions during the Last Glacial Maximum. However, for our study, we exclude climate as a major driver for the temporal changes in dung beetle body size 1) because of the contrasts between the spatially derived positive relation between dung beetle body size and temperature and the temporal body mass decline of this group of beetles despite increasing temperatures through time, 2) because of the contrasting temporal patterns observed for non-coprophaous and coprophagous scarabids, and 3) because of the temporal threshold between weak and strong body size change being detected for dung beetles significantly later than the thresholds for non-coprophagous scarabids and carabids, which are in congruence with the onset of the current interglacial period.

Ongoing impoverishment of the global megafauna due to human activity is expected to have drastic effects on mutualistic species like dung beetles with strong

consequences for ecosystem integrity, functioning and service provisioning (Galetti et al. 2018). Even in regions with fairly intact megafaunas like parts of Africa, large-sized dung beetles dependent on dung from megaherbivores such as elephants are highly endangered (Hanski and Cambefort 1991, Chown et al. 1995, Kryger et al. 2006). However, temporal lags in the response of dung beetle communities to changes in megafauna abundance can be pronounced (Favila 2012). Furthermore, dung beetles can sometimes adjust to missing megafauna by establishing new interactions with humans and/ or their domesticated animals (Hanski and Cambefort 1991, Andresen and Laurance 2007). However, this ability to adjust strongly depends on the degree of plasticity dung beetle species have in terms of foraging and breeding. The more specialized a species is on dung from large-bodied animals, the higher the detrimental effects on its performance a consequence of megafauna loss are. This is especially relevant for large-bodied dung beetle species which are limited in their flexibility due to the fact that they need a certain size of dung for breeding, and thus a certain size of dung-producing animal (Peck and Howden 1984, Goh et al. 2014).

Conclusions

Overall, we expect a marked, but perhaps delayed downsizing of global dung beetle communities as a consequence of the past and ongoing losses of megafauna. This effect on dung beetle community structure is expected to affect the integrity, functioning and service provisioning of natural and agro-ecosystems due to the important role dung beetles play in terms of nutrient cycling and soil fertilization, bioturbation and aeration as well as secondary seed dispersal with advantageous effects on seed germination, plant growth and distribution. We are confident about a mechanistic link between the down-sizing of mammal and dung beetle communities across the late-Quaternary documented here, given the multiple lines of evidence provided. We exclude a significant bias in the observed pattern due to phylogenetic effects as the tested species grouped in non-coprophagous and coprophagous scarabids consist of members of the same families and subfamilies, but show significant different temporal trends in body size. However, anthropogenic changes in vegetation structure, soil characteristics and climatic conditions like temperature and water availability will additionally affect the abundance and distribution of dung beetles (cf. Andresen and Laurance 2007, Hortal et al. 2011). Gaining an understanding of temporal lags and adaptive capacity of species, communities and whole ecosystems is thereby a prerequisite to forecast or mitigate detrimental ecological effects of recent and future human activities in the Anthropocene.

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