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Reintroducing extirpated herbivores could partially reverse the late Quaternary decline of large and grazing species

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Title

- Reintroducing extirpated herbivores could partially reverse the late Quaternary decline of large and grazing species
- Global herbivore restoration potential

Abstract

Aim

Reinstating large, native herbivores is an essential component of ecological restoration efforts, as these taxa can be important drivers of ecological processes. However, many herbivore species have gone globally or regionally extinct during the last 50,000 years, leaving simplified herbivore assemblages and trophically downgraded ecosystems. Here, we discuss to what extent trophic rewilding can undo these changes by reinstating native herbivores.

Location

Global

Time period

We report functional trait changes from the Late Pleistocene to the present, and estimated trait changes under future scenarios.

Major taxa studied

Wild, large (≥ 10 kg), terrestrial, mammalian herbivores

Methods

We use a functional trait dataset containing all late Quaternary large herbivores ≥ 10 kg to look at changes in the body mass and diet composition of herbivore assemblages, a proxy for species' ecological effects. First, we assess how these traits have changed from the Late Pleistocene to the present. Next, we quantify how the current body mass and diet composition would change if all extant, wild herbivores were restored to their native ranges (and if no functional replacements were used), exploring scenarios with different baselines.

Results

Defaunation has primarily removed large and grazing herbivores. Reinstating extant herbivores across their native ranges would reverse these changes, especially when reinstating them to their prehistoric distributions. It would partially restore herbivore body mass and diet composition to pre-anthropogenic conditions.

However, in the absence of complementary interventions (e.g. introducing functional replacements), many herbivore assemblages would remain down-sized and browser dominated, relative to pre-anthropogenic conditions.

Main conclusions

Many terrestrial herbivore assemblages - and hence ecosystems - would remain trophically downgraded, even after bringing back all extant, native herbivores. Therefore, complementary interventions would be required to achieve complete functional restoration. Nevertheless, our findings suggest that reintroducing the remaining native herbivores would diversify the herbivory and disturbances of herbivore assemblages.

Keywords

extinction, functional ecology, large herbivores, late Quaternary, macroecology, restoration, rewilding, trophic downgrading,

MAIN TEXT

Introduction

Scientists and policymakers increasingly recognise that preserving the world's biodiversity will require the large-scale restoration of ecosystems (Suding, 2011). In recognition of this fact, the United Nations has named 2021-2030 as the UN Decade of Ecosystem Restoration. However, ecosystem restoration has traditionally focused on vegetation and soils (Catterall, 2018). In comparison, restoring the faunal component of ecosystems has received little attention (Catterall, 2018). Wild megafauna (i.e., large mammals), and especially large herbivores (here, herbivorous mammals ≥ 10 kg), play crucial roles in the restoration of ecosystems (Catterall, 2018; Svenning et al., 2016). They can be important drivers of ecological processes by influencing vegetation dynamics (Cromsigt & te Beest, 2014), fire regimes (Smit & Archibald, 2019), nutrient fluxes (le Roux, Kerley, & Cromsigt, 2018), and even climate (Smith et al., 2016). Furthermore, large herbivores have experienced widespread range losses as *Homo sapiens* has spread across the globe during the late Quaternary (Koch & Barnosky, 2006; Martin, 1966). Many have gone globally extinct. Others have disappeared from parts of their natural distribution (Ripple et al., 2015), making them great candidates for reintroduction efforts.

Consequently, various authors have advocated for trophic rewilding with large herbivores. Trophic rewilding is an ecological restoration strategy that aims to restore top-down trophic interactions and their associated trophic cascades by (re)introducing species with large impacts (Corlett, 2016; Svenning et al., 2016). Rewilding proponents argue that reinstating large herbivores can restore ecological processes that

disappeared following defaunation during the Late Pleistocene and Holocene. However, many herbivore taxa have become globally extinct since the global spread of *Homo sapiens* (Koch & Barnosky, 2006; Martin, 1966). Thus, it is uncertain to what extent trophic rewilding can restore the ecology of pre-anthropogenic herbivore assemblages if it reinstates only wild, native species that are still extant (Svenning et al., 2016). Some authors propose to solve this problem by substituting globally extinct species with functional replacements (Donlan et al., 2006; Martin, 1970) and functional replacements have even been introduced in some places (Svenning et al., 2016). However, functional replacements remain controversial due to risks associated with introducing non-native species (Corlett, 2016).

Therefore, it is important to know whether reintroducing extirpated herbivores can restore the ecological effects of unimpacted herbivore assemblages. We address this question by analysing changes in the body mass and diet composition of wild herbivore assemblages. Body mass and diet are effect traits, (i.e. traits that affect ecosystem functioning (Violle et al., 2007)). They determine which plant biomass herbivores can access and digest and are key to understanding the impact of herbivores (Bakker et al., 2016; Gordon, 2003; Owen-Smith, 1988). Thus, quantifying changes in body mass and diet composition of herbivore assemblages can indicate how the impact of its herbivores has changed. We collected data on the body mass and diet of all large herbivores occurring during the last ~130,000 years. This period covers all late Quaternary extinctions across the globe. Using these data, we assess how anthropogenic extinctions have affected the body mass and diet composition of wild herbivore assemblages from the Late Pleistocene to the present. Next, we quantify how the composition of these traits would change in the future if all extant, wild herbivores were restored to their native ranges (and if no functional replacements were used).

Disagreement exists about what constitutes a species' native range (Crees & Turvey, 2015). Therefore, we explore three future scenarios (hereafter "rewilding scenarios"). Each scenario adopts a different temporal baseline for where species are considered "native" and where they would be reintroduced. We compare the outcomes of these three rewilding scenarios with both current and present-natural assemblages. Current assemblages are herbivore assemblages as they are today. Present-natural assemblages are predictions of what herbivore assemblages would be like today if humans had not changed herbivore ranges during the last ~130,000 years. Thus, our analysis quantifies the potential to restore the body mass and diet composition of herbivore assemblages, a proxy for herbivore impacts.

Materials and Methods

We collated graminoid consumption, browse (defined as non-graminoids) consumption, body mass and occurrence data for all herbivorous, terrestrial mammals weighing ≥ 10 kg in the PHYLACINE v1.2 dataset (Faurby et al., 2018). We generated the list of herbivorous mammals by creating a new, more detailed diet dataset for all species ≥ 10 kg in PHYLACINE v.1.2 and removing species that had a negligible plant consumption (graminoid consumption and browse consumption score ≤ 1 , "Functional trait data")

In total we compiled data for 518 species of herbivore: 315 extant wild species, two species that only survive as domestics (*Bos primigenius* and *Camelus dromedarius*) and 201 globally extinct species. Four herbivore species that fell within the appropriate body mass range (*Eudorcas rufina*, *Gazella marica*, *Ptilocolobus pennantii* and *Sus bucculentus*) were excluded from our analyses, either because their ranges had not been mapped in PHYLACINE v1.2 or because of their uncertain taxonomic status. Out of the 317 extant wild and surviving domestic species, 138 species had smaller current ranges than present-natural ranges. We considered them *reintroduction candidates*: species that could be reintroduced under the three rewilding scenarios.

Functional trait data

Body mass estimates were collected from the PHYLACINE v1.2 dataset (Faurby et al., 2018). Dietary data were collected from academic and grey literature. All diet references can be found in the supplementary information (Appendix S1). We divided diet into two categories: graminoid consumption and browse consumption, as they represent two major dietary strategies with different impacts on ecosystems (Gordon & Prins, 2008). We followed the MammalDIET system of Kissling et al. (2014) but we reranked the ordinal scale from 0-3, allocating high values to important dietary items and low values to less important items.

We inferred browsing and grazing habits of globally extinct taxa based on palaeoecological literature. We used direct data for species diets (e.g., coprolites, phytoliths in dental calculus) when available ($n = 9$), though we relied on proxy data (e.g., stable carbon isotopes of tooth enamel, craniodental ecomorphology) when needed ($n = 115$). For the cases where we found no direct or proxy data bearing on an extinct species' diet ($n = 56$) we relied on expert opinions published in literature. Finally, if no dietary data were available regarding the species' grazing or browsing preference ($n = 35$, both extant and extinct) we imputed their diets using the R package Rphylopars v. 0.2.9 (Goolsby, 2017) (Appendix S1). Phylopars was run with all default parameters including a Brownian motion evolutionary model. The result is based on phylogenetic relationship to all other mammal species ≥ 10 kg, using meat consumption, body mass, and life habits from PHYLACINE v1.1 as traits. Lastly, we used these graminoid and browse consumption scores to classify all species into functional types (herbivores with similar functional traits): grazers, mixed feeders and browsers (Fig. S2.1), and we mapped their distributions (Appendix 3).

Late Quaternary extinctions and functional change

We quantified body mass and dietary changes during the late Quaternary by developing a global extinction chronology consisting of four periods: The Late Pleistocene, the early Holocene, 1500 AD and 2019 AD (Fig. 1). The extant/extinct status of species was determined using the PHYLACINE v1.2 dataset, the list of Holocene mammal extinctions in Turvey (2009) and the IUCN red list. Note, that this analysis only considers wild herbivores. It does not incorporate the effects of livestock.

To test whether grazers have experienced relatively more severe extinctions than other herbivore functional types, we performed a chi-squared test of independence. Because the test indicated a significant association between variables, we performed a post-hoc comparison by looking at critical values of the residuals (Appendix 4). We calculated the critical value for a two-sided test and used a Bonferroni correction. To test whether grazers had experienced larger range restrictions than other herbivore functional types we performed a Kruskal-Wallis test on the differences in cells between present-natural and current ranges. Because the test showed a significant association between variables, we conducted a Dunn post-hoc pairwise comparison (Appendix 4). The comparison was done for a two-sided test and using a Bonferroni correction.

Constructing herbivore assemblages

To evaluate how the reintroduction of native herbivores would influence the body mass and diet composition of herbivore assemblages world-wide, we estimated what future herbivore assemblages would look like if extant, native herbivores were brought back to their native ranges and if no functional replacements were used. As there is no agreed upon definition of nativity, we considered three different scenarios (“*rewilding scenarios*”). Each rewilding scenario used a different restoration baseline and looked at a different temporal interval when deciding where species are “native”. We selected three temporal intervals that are commonly considered in rewilding and restoration projects: The Late Pleistocene, the early Holocene and historical times around 1500 AD (Corlett, 2016). We refer to these scenarios by their baselines. We compared these “rewilded assemblages” with *current herbivore assemblages* and *present-natural herbivore assemblages*. Current assemblages are herbivore assemblages as they are today. Present-natural assemblages estimate what herbivore assemblages would be like today if the late Quaternary extinctions had not happened.

We first collected species’ current and present-natural ranges from the PHYLACINE v1.2 dataset (Faurby et al., 2018). The PHYLACINE v1.2 dataset provides these ranges as rasters, projected in the Behrmann equal area projection (96.5×96.5 km resolution at 30°N and 30°S). We kept this projection for all further spatial analyses. Using these ranges, we constructed herbivore community matrices and converted them into herbivore assemblages by overlaying all species ranges. We considered all species co-occurring within one raster cell to be part of the same herbivore assemblage. Note, again, that our analysis did not include livestock when constructing assemblages. While we do refer to *B. primigenius* and *C. dromedarius*, as “domestic species”, we consider them descendants of now-extinct wild types, and hence eligible for reintroduction as wild species. We do not consider their effects as farmed animals.

We constructed *current herbivore assemblages* by overlaying the current ranges of all extant herbivores. We constructed *present-natural herbivore assemblages* by overlaying the present-natural ranges of all extant and extinct herbivores. The three “rewilding scenarios” were constructed as follows:

Pleistocene baseline scenario: This scenario aims to restore herbivore assemblages by reintroducing extant herbivores that disappeared since the Late Pleistocene. The herbivore

assemblages in this scenario were constructed by overlaying the present-natural ranges of all extant wild and domestic herbivores (n = 317 species). Note that this scenario would introduce some species into areas where they might not be perceived as native today. Examples include *Equus ferus* in North and South America and *Hippopotamus amphibius* in Europe.

Holocene baseline scenario: This scenario aims to restore herbivore assemblages by reintroducing extant herbivores that disappeared since the early Holocene. Similar to the Pleistocene baseline scenario, the herbivore assemblages were constructed by taking the present-natural ranges of all extant wild and domestic herbivores (n = 317 species). However, we clipped their present-natural ranges to represent their distributions during the early Holocene. First, we removed species from continents if they had disappeared there by the early/mid Holocene (n = 6, e.g. *Equus ferus* in the Americas, *Hippopotamus amphibius* in Europe). Second, we removed species that have become restricted to islands during the late Quaternary from the mainland, if they had disappeared there by the early/mid Holocene (n = 1, i.e. *Pongo abelii*). All species range modifications can be found in Appendix S5.

1500s baseline scenario: This scenario aims to restore herbivore assemblages by reintroducing extant herbivores that disappeared since the European Age of Exploration, around 1500 AD. The herbivore assemblages were constructed by taking the present-natural ranges of all extant wild herbivores (n = 315 species), but clipping them to those countries where the IUCN Red List considers the species to be native (the IUCN Red List traditionally takes 1500 AD as the reference period for evaluating species' occurrences and threats). To account for any gaps in the list of native countries by the IUCN we also overlaid these ranges with the historic ranges according to the IUCN. Unlike the previous two scenarios, the two domesticated species *Bos primigenius* and *Camelus dromedarius* would not be reintroduced anywhere as the IUCN considers them extinct.

Quantifying trait composition and trait change

Using the aforementioned community matrices, we calculated the median (Fig. 2), maximum, standard deviation, skew and kurtosis (Appendix 3) of the body mass distribution of each herbivore assemblage (= a raster cell). We also calculated the diet score of each assemblage (Fig. 2) by calculating the median graminoid and median browse consumption score (both ranging from 0-3) of species occurring within a cell. To determine the most common form of herbivory, the browse consumption score was subtracted from the graminoid consumption score to generate a grazing–browsing anomaly. Higher values indicate assemblages where grazing is more prevalent, whereas low values represent assemblages where browsing is more prevalent. Values close to zero represent assemblages where neither form of herbivory dominates. Last, we calculated the function richness of each assemblage using the FD package in R (Appendix 3). We included

body mass, graminoid consumption and browse consumption as traits, and gave them respective weights of 0.5, 0.25 and 0.25 (so body mass and diet were weighed equally).

In order to analyse the impacts of the respective rewilding scenarios on current assemblage patterns, we subtracted the values of the current assemblages from those of the rewilding scenarios (this was done for median body mass, median diet scores and species richness). This method provided us with a visual representation of what compositional changes would occur under each scenario (Fig. 3). It allowed us to identify the regions of the world that would experience the most widespread functional changes following the reintroduction of large herbivores, and the degree of change it would induce relative to current patterns of distribution. Next, we visualised the body mass and diet changes from the perspective of an assemblage (Fig. 4). Figure 4 shows the trait changes that took place in Western European herbivore assemblages and the predicted changes these assemblages would experience following the three rewilding scenarios (Fig. 4). The extinction chronology in Figure 4 is based on faunal finds in Belgium and its neighbouring countries. Supplementary materials S6 and S7 contain the sources for the extinction chronology and the animal silhouettes.

Last, we calculated the *relative body mass* of herbivore assemblages (median and maximum). For current herbivore assemblages and the assemblages resulting the three rewilding scenarios, we calculated the median and maximum body mass and divided it by the median and maximum value of the corresponding present-natural assemblages. The resulting ratios were then expressed as percentages and plotted as a boxplot and a density plot (Fig. 5).

Results

We find that extinctions have removed the largest herbivores since the Late Pleistocene (Fig. 1A), a trend also observed for megafauna in general (Smith, Elliott Smith, Lyons, & Payne, 2018). Consequently, current herbivore assemblages are down-sized compared to the present-natural assemblages that would have existed in the absence of human impacts (Fig 2A-B). Extinctions have also led to a decline in grazing herbivores. Even though they have lost fewer species in absolute terms, grazers have suffered relatively more extinctions than either mixed feeders or browsers (χ^2 -test of independence, $\chi^2 = 9.18$, $df = 2$, $p = 0.01$, supplementary Table S4.1). In total, grazers have lost 53% of their total species richness since the Late Pleistocene (48/90 species), whereas mixed feeders have lost 37% (65/177 species), and browsers have lost 36% (90/251 species) (Fig. 1A). Most of these extinctions happened during the Late Pleistocene (Fig. 1B). Grazers and mixed feeders, when compared to browsers, also possess a larger difference between their current and present-natural-ranges (Kruskal Wallis, $\chi^2 = 22.71$, $df = 2$, $p < 0.001$, supplementary Table S4.2). On average, the current range of a grazing herbivore was 991,767 km² smaller than their present-natural range (median difference between current and present-natural ranges). The range of a mixed feeder was 493,555 km² smaller and the range of a browser was 65,186 km² smaller. This suggests that grazers and, to a lesser extent, mixed feeders have experienced proportionally larger anthropogenic range restrictions than browsers

have. As a result of the late Quaternary extinctions and extirpations, current wild herbivore assemblages are mostly dominated by herbivores with browsing diets (Fig. 2C). In fact, wild grazers are absent from most of world's terrestrial ecosystems (supplementary Fig. S3.2)—contrasting strongly with the present-natural scenario. Most present-natural assemblages would have a more or less equal composition of grazing and browsing (Fig. 2D). Wild herbivore assemblages where grazing is common still exist, but are rare and restricted to eastern Africa, Patagonia, parts of Central Asia, and Australia (Fig. 2C). Australia appears to be an outlier, though. In contrast to most places, the continent has primarily lost browsing species (Fig. 2C-D). Historically it also possessed relatively few large grazers (Australian herbivores species ≥ 500 kg: Browsers: 6, Mixed feeders: 1, Grazers: 2).

Restoring body mass and diet

The late Quaternary extinctions and extirpations have lasting impacts on restoration efforts. Species that survived the extinctions, but underwent extirpation in portions of their ranges tend to have larger body masses than extant species that did not experience range restrictions (supplementary Fig. S3.3A). They also tend to consume more graze (supplementary Fig. S3.3B). In other words, the herbivores in need of reintroductions tend to be functionally different from the herbivores that have retained their distributions. As a result, all three rewilding scenarios would lead to herbivore assemblages with a greater median body mass and a higher prevalence of grazing compared to the current (Fig. 3).

The choice of restoration baseline influences the extent of these increases (Fig 4). All three rewilding scenarios in our study had access to the same pool of reintroduction candidates, but they would reintroduce them to different areas given divergent views on nativity. Scenarios with baselines located further back in time would introduce reintroduction candidates over larger areas (supplementary Fig. S3.4). Consequently, they would create more species-rich herbivore assemblages than scenarios using recent baselines (supplementary Fig. S3.5) They would also lead to larger increases in median body mass and the prevalence of grazing (Fig. 3). In turn, this would lead to larger increases in functional richness (supplementary Fig. S3.6).

The standard deviation of herbivore body mass distributions would also increase when using older baselines (supplementary Fig. S3.7), indicating that herbivore body sizes would be spread further from the mean. Changes in the skew and kurtosis were more complex. The (positive) skew (supplementary Fig. S3.8) and kurtosis (supplementary Fig. S3.9) would increase under all three rewilding scenarios. So, compared to the current, rewilded assemblages would contain more large species, and more “outliers” (i.e. species with unique -i.e. very large- trait values compared to the mean of the assemblage). However, the body mass skew and kurtosis did not always increase with older baselines. Instead, the skew and kurtosis under the Late Pleistocene baseline would be lower than under the Holocene baseline.

Geographical changes following restoration

Geographically, the largest and most widespread body mass increases would happen in Europe, Asia, and North Africa (Fig 3A-C), as these areas have several large reintroduction candidates remaining (e.g. *Elephas maximus*, *Hippopotamus amphibius*, *Bison bonasus*). The Americas would experience small to moderate changes (Fig 3A-C), as most of their late Quaternary large species are extinct. Likewise, Australia would see few changes because it has few reintroduction candidates remaining (Fig 3A-C).

The most widespread and the largest increases in the prevalence of grazing would be seen in Eurasia, North Africa, and, to a lesser extent, in North America (Fig. 3D-F). This reflects the available number of reintroduction candidates with grazing diets (e.g. *Bison spp.*, *Bos primigenius*, *Equus ferus*) (Fig. 4). South America and Australia would experience few changes in dietary structure, regardless of the scenario, because few native reintroduction candidates remain (Fig. 3D-F). In Africa, trends would be mixed. Sub-Saharan Africa would experience relatively few dietary changes. In contrast, North Africa would experience some of the largest increases in the prevalence of grazing (Fig. 3D-F), as many of its extirpated grazing species (e.g. *Hippopotamus amphibius*, *Ceratotherium simum*, *Syncerus caffer*) persist in sub-Saharan Africa and could be reintroduced.

Restoring pre-anthropogenic body mass and diet composition

None of the three rewilding scenarios would completely restore the body mass distribution predicted by present-natural assemblages (Fig. 2E-G). The median assemblage body mass would increase substantially following all three scenarios. In many assemblages, it would even be possible to restore the median body mass to its present-natural value (Figure 5). However, the maximum assemblage body mass would change little. In most assemblages it would remain much lower than its present-natural value (Figure 5, supplementary Fig. S3.10). Similarly, the standard deviation, skew, and kurtosis (supplementary Fig. S3.7-9) would remain low compared to the present-natural. In other words, reinstating only native species would be reasonably effective at restoring the body size composition of medium-sized herbivores, but it would not bring back the largest species with their unique trait values.

Reinstating only native herbivores would also not fully restore the dietary composition of herbivore assemblages before widespread human impacts (Fig. 2H-J). While most assemblages would have a more even composition of browsing and grazing herbivores, the global bias towards browsing herbivores would persist. The largest dietary differences would remain in South America (which lost many of its grazing herbivores) and Australia (which lost many of its browsing herbivores). However, dietary differences were not restricted to these areas. Many Old World assemblages would remain dominated by browsing herbivores, though less so than without reintroductions.

Discussion

Our results show that the late Quaternary extinctions have left functional biases in contemporary wild herbivore assemblages, as large and grazing species have experienced more global extinctions and more

severe range restrictions. Consequently, most wild herbivore assemblages outside of sub-Saharan Africa are down-sized and browser-dominated relative to conditions before widespread human impact. The rewilding scenarios we considered partially restored the body mass and diet composition predicted by present-natural assemblages. In general, they would restore the trait composition of medium-sized herbivores to a large degree, but they would not restore the largest species and their unique traits. Thus, solely reinstating native herbivore species would not completely restore the herbivory and disturbance regimes that characterized terrestrial ecosystems before widespread human impact.

Discussions about the functional restoration of herbivore assemblages must consider the absence of prehistoric large and grazing herbivores and their ecological impacts. If the aim is to fully restore herbivory or disturbance regimes that existed before significant anthropogenic impact, bringing back only native species will not be sufficient and additional interventions will be required. This is particularly the case when restoring the impact of megaherbivores, most of which have gone globally extinct (Owen-Smith, 1988). One option would be to use functional replacements (Svenning et al., 2016) as substitutes for globally extinct herbivores, but this suggestion is controversial due to the risks of introducing non-native species (Corlett, 2016). Our study did not assess the potential for restoration with functional replacements, but we expect they would allow closer approximation to pre-anthropogenic trait compositions, provided that the functional replacements are good substitutes for extinct species. In fact evidence shows that in some instances, assemblages with introduced, non-native herbivores are functionally more similar to pre-anthropogenic herbivore assemblages, than assemblages including only extant, native herbivore species (Lundgren et al., 2020; Martin, 1970). Alternatively, one could use active anthropogenic management (Owen-Smith, 1989). Conservationists already apply various manual conservation interventions and these techniques (e.g., coppicing) may emulate some effects of extinct megafauna (Bocherens, 2018).

The degree to which additional interventions would be required depends on geographical location, as continents have experienced varying levels of extinction (Koch & Barnosky, 2006; Sandom, Faurby, Sandel, & Svenning, 2014). South America and Australia have suffered severe megafauna extinctions and have few remaining reintroduction candidates (Lundgren, Ramp, Ripple, & Wallach, 2018; Svenning & Faurby, 2017). So, these continents would likely benefit most from utilising additional interventions such as those mentioned above. Areas where many reintroduction candidates remain (i.e. North Africa, Europe, Asia) have greater potential to restore herbivore assemblages using only native species, though even in these places function restoration would require complementary methods when restoring the impact of the largest herbivores.

Causes of the late Quaternary extinction biases

The loss of large vertebrates during the late Quaternary extinctions is well-documented (Koch & Barnosky, 2006; Martin, 1966; Smith et al., 2018). Some authors have suggested that large species are inherently more at risk of extinction than small species, due to their life history characteristics (Cardillo et al., 2005).

However, a recent study showed that large mammals did not have a higher probability of extinction when viewed across the Cenozoic. Instead, the authors suggested that the extinction bias towards large body sizes is a signal of human impacts (Smith et al., 2018). Our observation – that there has been a net decline of large and grazing herbivores– falls in line with these earlier findings, and conforms with studies that have previously demonstrated grazer declines in Africa (Faith, 2014) and North America (Davis, 2017), and browser declines in Australia (Bowman, Murphy, & McMahon, 2010; Johnson & Prideaux, 2004). However, it is not clear why grazer extinctions and extirpations were relatively more common, nor why Australia deviates from the global pattern. Possibly, the pattern is caused by the extinction bias towards large species, as body mass and grazing habits are correlated (Clauss, Kaiser, & Hummel, 2008). This would explain the Australian anomaly, as Australia did not host many large grazers during the late Quaternary. However, we cannot exclude mechanisms that make grazing herbivores inherently at greater risk of extinction. Faith (2014) attributed the extinction bias towards African grazing ungulates to a decline in the prevalence of grassland habitats since the Last Glacial Maximum. It remains to be seen if this hypothesis can explain global extinctions as grasslands remained prevalent in Africa and many other parts of the world (Adams & Faure, 1997). Alternatively, grazers may have been more exposed to hunting or other direct interactions with people by living in open habitats (Johnson, 2002). The global spread of humans was also associated with an increase in grazing livestock (Sandom et al., 2020). So, grazers may have suffered more severely from resource competition (Madhusudan, 2004). However, this does not explain why most extinctions took place before the Holocene, i.e. before the spread of domestic grazers (Larson & Fuller, 2014).

Changes in trait composition and their ecological consequences

This study quantifies changes in trait composition and uses it to infer whether the ecological impacts of large herbivores can be restored. This assumes that functional traits, like body mass and diet, determine species' impacts (Violle et al., 2007), and that an intact trait composition is a necessary – although not sufficient – condition for the restoration of ecological impacts. It also assumes that our characterisation of herbivore trait composition is complete. We note, however, that this study does not consider non-mammalian herbivores. Yet, these can have important ecological impacts, particularly on islands (Hansen & Galetti, 2009). Second, this study does not incorporate animal abundances, as there are no empirical, global estimates available. Nonetheless, abundances strongly influence species' ecological effects (Violle et al., 2007), and they may be particularly important when considering the effect of introduced species, which often have small populations. Third, this study does not consider livestock. Yet, the spread of livestock may have been an important driver of ecological change. Many domestic species are grazing, ruminants (Sandom et al., 2020), and their introduction may have offset some impacts caused by the global decline of wild, grazing herbivores. We do not believe these reservations invalidate the study's findings, but we caution the results may apply best to continental, wild herbivore assemblages on macroecological scales.

Our method also assumes that extirpations and reintroductions have “symmetric counterbalancing effects” (Alston et al. 2019), the so-called assumption of reciprocity. Case-studies show that reintroducing herbivores can restore ecological processes, in certain cases. For example, Waldram et al. (2008) showed that removals of white rhino from Hluhluwe-iMfolozi National Park (South Africa) reduced the prevalence of short grass patches (grazing lawns). In contrast, Cromsigt and Te Beest (2014) showed that the reintroduction of white rhinos in Kruger National Park (South Africa) increased the prevalence of such patches. Alternatively, in Gorongosa National Park (Mozambique) the comeback of wildlife increased seed dispersal (Correia, Timóteo, Rodríguez-Echeverría, Mazars-Simon, & Heleno, 2017) and reduced the prevalence of an invasive shrub that had appeared following wildlife declines (Guyton et al., 2020). However, reciprocity effects are poorly studied. Evidence suggests they are variable, likely because ecosystems have changed since the time species disappeared (Alston et al., 2019): Novel species may have appeared, habitats may have changed and past predators may now be absent. As such, it remains to be seen how widely the results of the examples above can be extrapolated.

Another consideration is the data quality of this analysis. This study compiles traits of extant and extinct herbivores, even though their traits are estimated using different methods. The body masses of extant species come from weighed specimens. In contrast, the masses of extinct species derive from indirect methods, such as allometric equations from skeletal measurements. Likewise, diets of extant herbivores derive from direct observations, such as foraging time or dung content. The diet of extinct herbivore comes from indirect methods, such as functional morphology or stable isotopes (Davis & Pineda Munoz, 2016). In the case of “expert opinions” or “imputed values”, the estimate may be a “guesstimate” of a researcher or a probabilistic estimate informed by the traits of relatives. Thus, parts of the analysis that involve traits of globally extinct species (i.e. past trait changes and present-natural maps) may be more uncertain.

With these reservations in mind, what changes could one expect if herbivores were reintroduced? Large herbivores can physically and nutritionally access vegetation that small herbivores cannot (Owen-Smith, 1988). Therefore, we hypothesise rewilding with large herbivores would particularly affect vegetation of low nutritional quality and vegetation that is difficult to access for small herbivores. The presence of herbivores with larger body sizes, particularly megaherbivores, would increase the ability of herbivores to modify vegetation structure and create open habitats (Bakker et al., 2016; Owen-Smith, 1988). Unfortunately, most assemblages have lost their megaherbivores. So, restoration involving only extant native species would not fully restore the ability of herbivore assemblages to limit woody cover. How the dietary changes would affect vegetation composition is less clear. Due to the increased prevalence of grazing herbivores, herbivore assemblages would likely utilise open, grassy habitats more intensely, which might limit the regeneration of woody vegetation. There are known cases where high densities of grazing herbivores have prevented vegetation transitions to forest (Cornelissen, Bokdam, Sykora, & Berendse, 2014), but, other studies find that the presence of grazing herbivores can facilitate woody vegetation, through indirect effects on other herbivores, selective feeding or via the reduction of the fire frequency (Goheen,

Palmer, Keesing, Riginos, & Young, 2010; Madany & West, 1983). Overall, though, diverse traits beget diverse impacts, and the resulting heterogeneity often benefits biodiversity (Fuhlendorf et al., 2006; Loucougaray, Bonis, & Bouzillé, 2004).

Restoration baselines in rewilding

Our data show normative views on nativity influence the outcome of ecological restoration attempts. Reinstating native herbivores would increase the body mass and the prevalence of grazing in herbivore assemblages, regardless of the restoration baseline used. However, the choice of restoration baseline would affect the extent of the increase. When restoration projects use recent baselines to determine which species are candidates for reintroduction, they exclude many of the large and grazing species that assemblages contained in the past, and they lead to smaller functional changes. The same applies to the global extinction of herbivore species and their potential replacement by functional analogues or anthropogenic management.

Our study only considered body mass and diet, but we expect similar patterns exist for other traits that were selectively lost during the late Quaternary, such as slow reproductive rates, and terrestrial or diurnal habits (Johnson, 2002). Whenever extinctions have been non-random and have led to the loss of specific traits, temporal differences between restoration baselines will be associated with functional differences. As an example, Figure 4 illustrates how rewilding in western Europe using a 1500s baseline would maintain a mostly browser-dominated herbivore assemblage. In contrast, rewilding using an early Holocene or Pleistocene baseline would lead to a more even composition of grazing and browsing herbivores, as they would reinstate more species, including larger grazers (e.g. *Bos primigenius*, *Hippopotamus amphibius*, *Equus ferus*). If such functional differences lead to different ecological states (e.g. semi-open vs closed forest ecosystems) (Bakker et al., 2016; Sandom, Ejrnæs, Hansen, & Svenning, 2014) the choice of baseline can affect the biodiversity of ecosystems and our ability to conserve threatened species.

Conclusion

Our study highlights how long-term anthropogenic extinctions have functionally biased herbivore assemblages by selectively removing the large and grazing species. These changes have undoubtedly influenced the ecology of terrestrial ecosystems, and affect contemporary restoration efforts. Bringing back extant, native herbivores would almost universally lead to a shift towards heavier herbivore assemblages with more grazing diets. These changes would go a long way in bringing back the body mass and diet composition of past assemblages, and they would diversify herbivory and disturbance regimes. However, they would still leave many assemblages down-sized and browser-dominated, relative to conditions before widespread human impact. Thus, many terrestrial ecosystems would remain trophically downgraded, even after bringing back all extant native herbivores, and complementary conservation interventions would be required to restore pristine herbivory and disturbance regimes. We conclude that large herbivores need better integration into ecological restoration efforts. Furthermore, we argue that restoration efforts need to recognise the long history of anthropogenic extinctions, the functional legacies of these extinctions, and the

normative views that underlie restoration decisions. Otherwise, we risk inadvertently restoring past conditions already downgraded by the anthropogenic extinctions that preceded them (Pauly, 1995; Vera, 2010).

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Data accessibility statement

All data needed to evaluate the conclusions in the manuscript are presented in this manuscript and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Figures

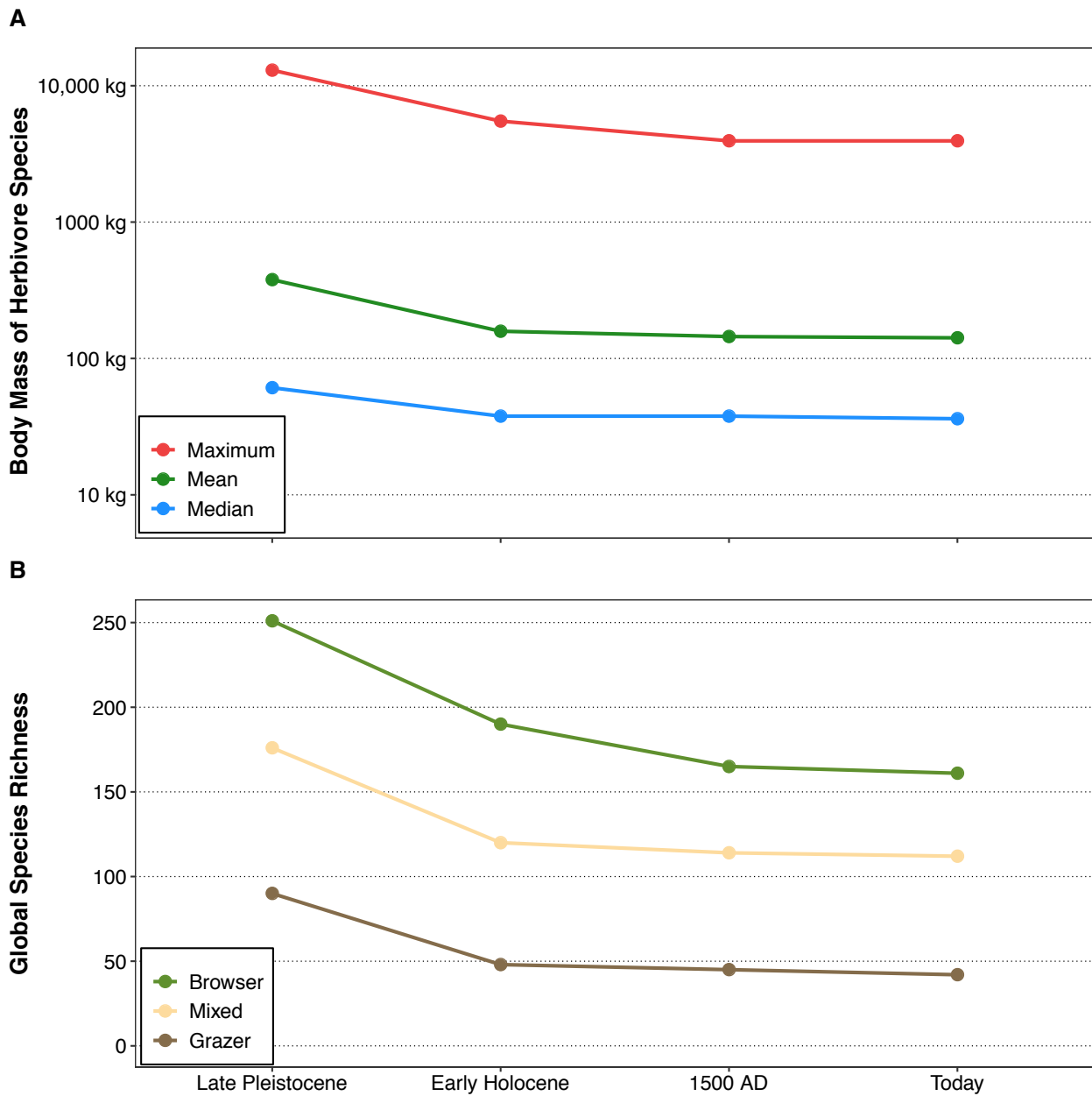


Fig. 1. Changes in the body mass and diet of herbivore species from the Late Pleistocene to the present-day. A) Change in body mass of herbivore species globally since the Late Pleistocene. B) Global species richness declines of grazers, mixed feeders, and browsers since the Late Pleistocene.

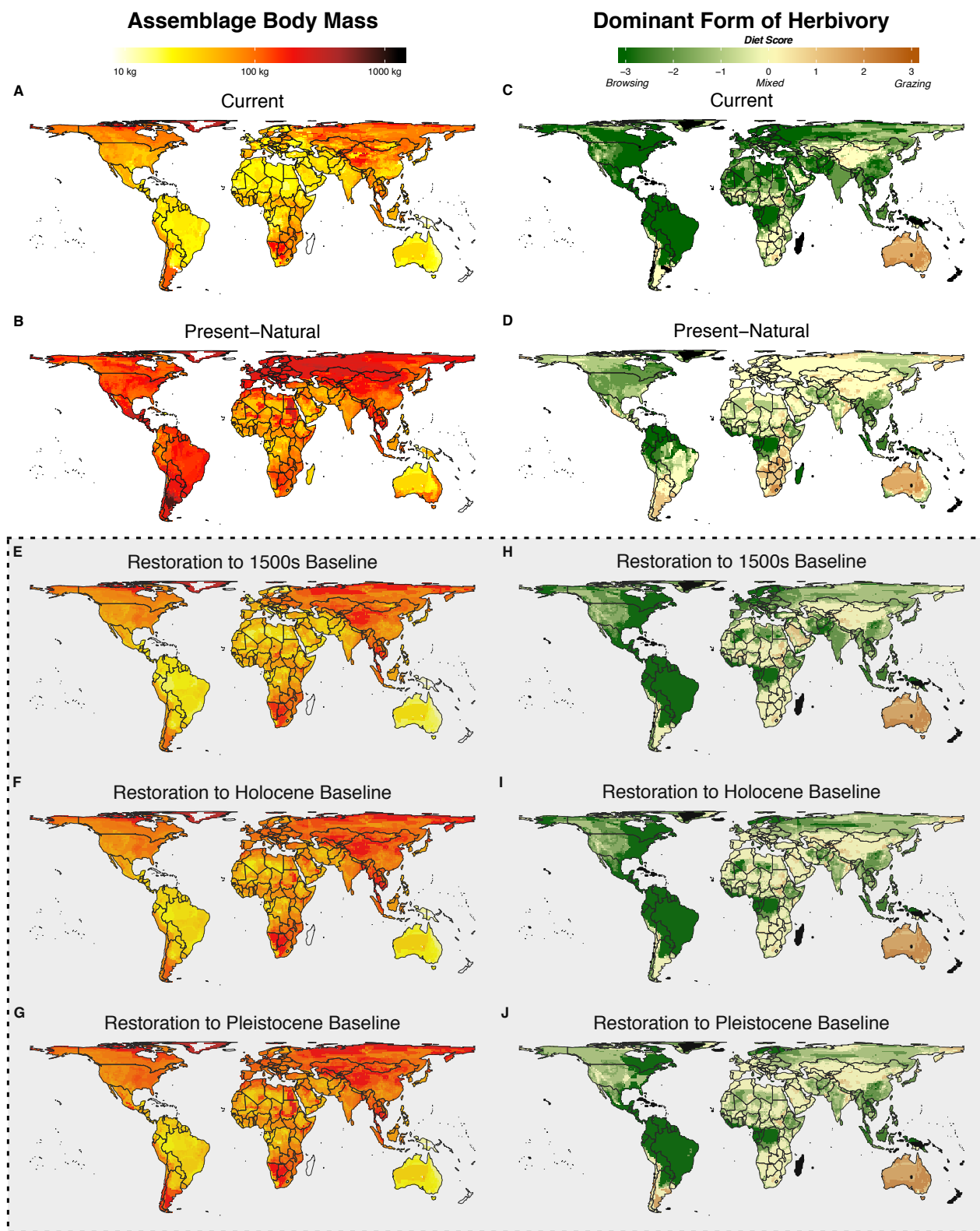


Fig. 2. Body mass and dietary structure of herbivore assemblages. **A)** median assemblage body mass of current herbivore assemblages; **B)** median assemblage body mass of present-natural herbivore assemblages; **C)** dietary composition of current herbivore assemblages; **D)** dietary composition of present-natural herbivore assemblages; **E-G)** median assemblage body mass following restoration without functional replacements, using a 1500s, Holocene, or Pleistocene baseline; **F-J)** dietary composition of herbivore

assemblages following restoration without functional replacements, using a 1500s, Holocene, or Pleistocene baseline.

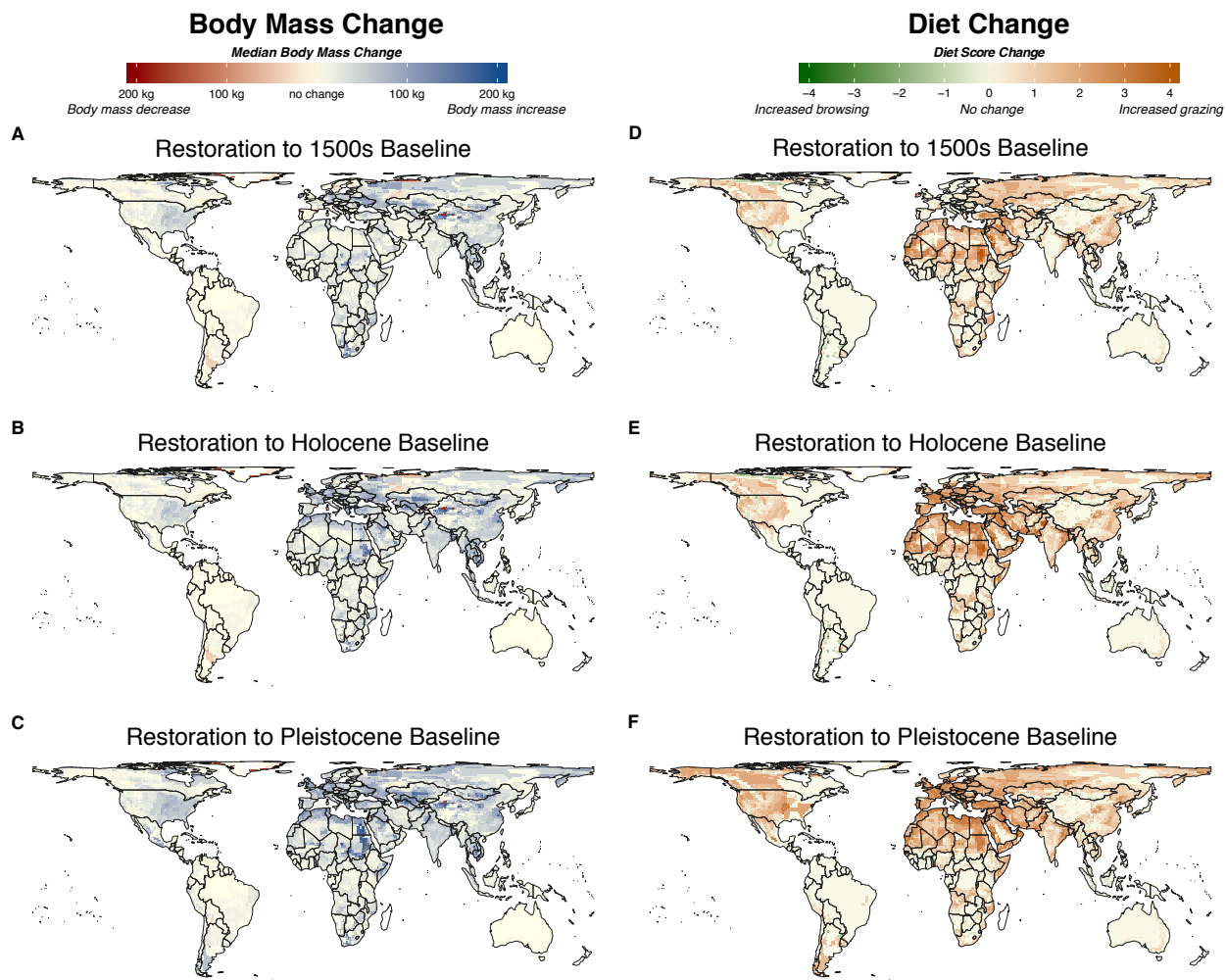


Fig. 3. Changes in the body mass and dietary structure of herbivore assemblages following rewilding without functional replacements. A-C) changes in median assemblage body mass following restoration when using a 1500s, Holocene, or Pleistocene baseline. D-F) dietary changes following restoration with herbivores when using a 1500s, Holocene, or Pleistocene baseline.

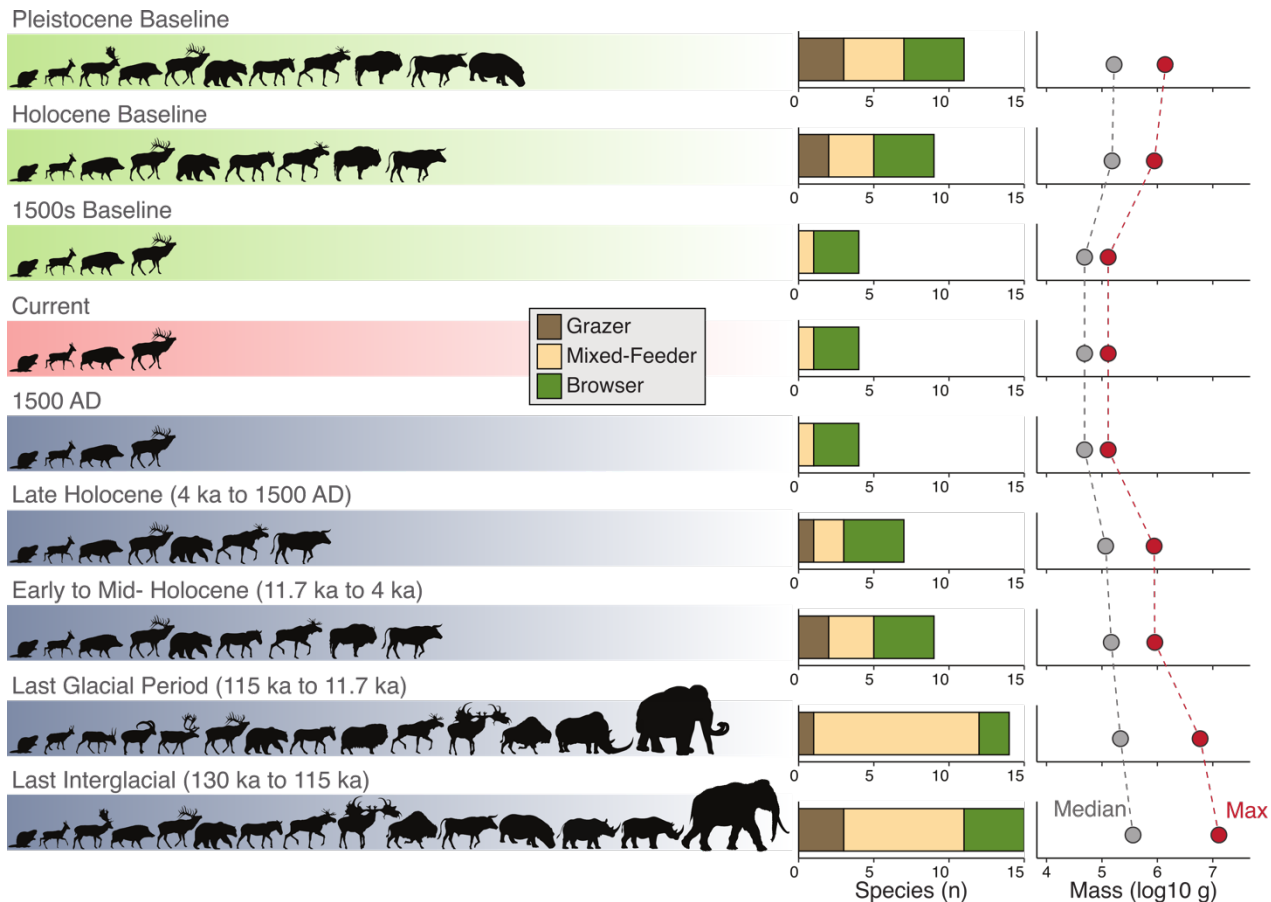


Fig. 4. Changes in the body mass and diet structure of a western European herbivore assemblage. Schematic showing changes in the body mass and diet structure of a western European herbivore assemblage during the late Quaternary and the consequences on assemblage trait structure when reinstating herbivore species using different restoration baselines. The animal silhouettes illustrate the species present at different time points in the past (blue bars) or in different future scenarios (green bars).



Fig. 5: Relative Body Mass. Boxplots and density plots showing distribution of the median and maximum body mass of herbivore assemblages, expressed as percentages relative to the median and maximum of corresponding present-natural assemblages. The different panels show the distributions of current herbivore assemblages and rewilded assemblages using a 1500s, Holocene or Pleistocene baseline respectively. The printed values show the maximum and median value respectively.