

SCIENTIFIC DATA



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Functional traits of the world's late Quaternary large-bodied avian and mammalian herbivores

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Prehistoric and recent extinctions of large-bodied terrestrial herbivores had significant and lasting impacts on Earth's ecosystems due to the loss of their distinct trait combinations. The world's surviving large-bodied avian and mammalian herbivores remain among the most threatened taxa. As such, a greater understanding of the ecological impacts of large herbivore losses is increasingly important. However, comprehensive and ecologically-relevant trait datasets for extinct and extant herbivores are lacking. Here, we present *HerbiTraits*, a comprehensive functional trait dataset for all late Quaternary terrestrial avian and mammalian herbivores ≥ 10 kg (545 species). *HerbiTraits* includes key traits that influence how herbivores interact with ecosystems, namely body mass, diet, fermentation type, habitat use, and limb morphology. Trait data were compiled from 557 sources and comprise the best available knowledge on late Quaternary large-bodied herbivores. *HerbiTraits* provides a tool for the analysis of herbivore functional diversity both past and present and its effects on Earth's ecosystems.

Background & Summary

Large-bodied terrestrial avian and mammalian herbivores strongly influenced terrestrial ecosystems through much of the Cenozoic—the last 66 million years of Earth history. However, many of the world's large-bodied herbivore species became extinct or experienced significant range contractions beginning ~100,000 years ago in the late Quaternary. Human impacts were the primary driver of these extinctions and declines, though possibly in conjunction with climate change^{1–3}. The world's remaining large-bodied herbivores are among the most threatened species on the planet^{4,5}, leading to urgent calls to protect these species and to better understand their distinct ecological roles⁶.

Large-bodied herbivores are unique in their capacity to consume large quantities of plant biomass and, as the largest terrestrial animals, they are uniquely capable of causing disturbance to vegetation and soils. These taxa thus exert strong top-down control on ecological communities and ecosystem processes. Prehistoric and historic losses of large herbivores led to profound changes to Earth's terrestrial ecosystems, including reductions in ecosystem productivity from reduced nutrient cycling, reduced carbon forest stocks from the loss of disturbance, increases in wildfire frequency and severity, and changes in plant communities^{7–12}. The causes and ecological legacies of late Quaternary extinctions are key topics of rapidly growing research interest^{13–18}. Likewise, the potential for introduced herbivores (either inadvertently or intentionally) to restore lost ecological processes is an important focus of research and debate today^{19–27}.

The capacity for organisms to affect the environment is driven by their functional trait combinations²⁸ (Fig. 1). As such, the availability and accuracy of herbivore functional trait data is critical for understanding the patterns and ecological consequences of the late Quaternary extinctions, the implications of modern ecological changes, and to guide conservation action. However, datasets of herbivore traits are rare and suffer from poor documentation, incomplete species lists, and outdated taxonomies. Trait datasets have been particularly scarce

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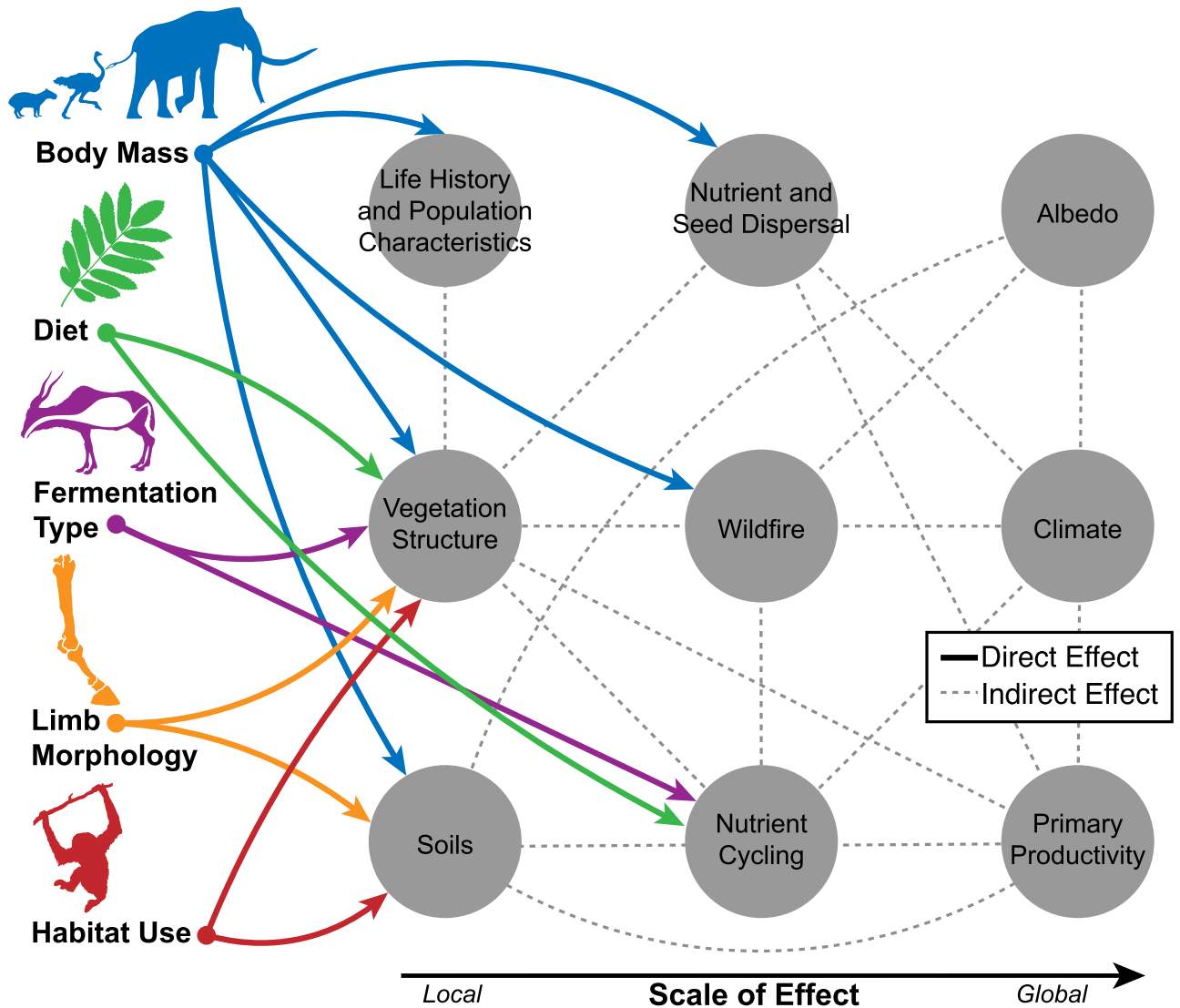


Fig. 1 Herbivores affect numerous ecological and ecosystem processes. The traits contained in *HerbiTraits* encapsulate major dimensions of herbivore ecology and its effect on the environment, from affecting local vegetation and soils to influencing global climate. Linkages indicate direct and indirect effects of traits on ecological processes or components, scaling from traits (left-hand side) to globe (right-hand side).

and/or inconsistently available for extinct species. Furthermore, there often exists a trade-off between species coverage and the resolution of many datasets. Mammalian trait datasets such as PHYLACINE²⁹ or MOM (Mass of Mammals)³⁰ include data on many late Quaternary mammal species, including carnivorous, aquatic, and flying species. These datasets thus include traits that are universal across these disparate ecological niches but in doing so lack trait data relevant to understanding herbivores and their unique ecological roles in particular. Furthermore, few datasets have considered or included avian herbivores, which can be particularly important components of large vertebrate faunas, especially on islands. The lack of a consistent and high-resolution trait dataset for late Quaternary avian and mammalian herbivores stymies efforts to understand the consequences of ecological changes that followed late Quaternary extinctions and hinders modern responses to changes in this important functional group.

Here, we present *HerbiTraits*, a comprehensive global trait dataset containing functional traits for all terrestrial avian ($n = 34$ species) and mammalian (511 species) herbivores ≥ 10 kg spanning the last $\sim 130,000$ years of the late Quaternary. *HerbiTraits* contains traits fundamental to understanding the multiple dimensions of herbivore ecology, including body mass, diet, fermentation type, habitat use, and limb morphology (Fig. 1, Table 1). These data are broadly useful for both paleo and modern ecological research, including potential conservation and rewilding efforts involving herbivores. Recent research using these data has yielded insight into the functionality of novel assemblages composed of introduced and native herbivores²⁵.

Trait	Variable Name	Variable type	Values/Unit	Notes
Mass	Mass.g	Continuous	Grams	Body mass is a continuous variable reflecting average body mass of adult, across males and females.
Diet	Three variables: <i>Diet.Graminoids</i> ; <i>Diet.Browse.Fruit</i> ; <i>Diet.Meat</i>	Ordinal	0 (insignificant, 0–9% of diet) 1 (low significance, 10–24%) 2 (moderate significance, 25–49%) 3 (high significance, 50–100%)	Graminoid, browse, and meat consumption were treated as separate ordinal variables. Fruit consumption was included with browse. Grass-seed, bamboo, and forbs (herbaceous dicots) were considered browse ³⁹ .
Fermentation type	Two variables: <i>Fermentation.Type</i> <i>Fermentation.Efficiency</i>	Categorical/Ordinal	Simple gut (Efficiency: 0) Hindgut colon (Efficiency: 1) Hindgut caecum (Efficiency: 1) Foregut non-ruminant (Efficiency: 2) Foregut ruminant (Efficiency: 3)	Fermentation type was collected as a categorical variable, following ⁴⁶ , but was ranked as an ordinal variable in terms of efficiency (0–3).
Habitat	Three variables: <i>Habitat.Aquatic</i> ; <i>Habitat.Terrestrial</i> <i>Habitat.Arboreal</i>	Binary	0 (no significant use of habitat) 1 (use of habitat)	Use of particular habitats (aquatic, terrestrial, arboreal) was given a 0 or 1, non-exclusively. This variable has also been coded categorically and includes <i>semi-aquatic, terrestrial, semi-arboreal, arboreal</i>
Limb morphology	<i>Limb.Morphology</i>	Categorical	Plantigrade Digitigrade Unguligrade	Limb morphology reflects major vertebrate postural adaptations, which govern habitat affinities, fossoriality, cursoriality, and disturbance-related effects on soils.

Table 1. *HerbiTraits* contains key traits for all late Quaternary herbivorous mammals over the last 130,000 years. Traits include body mass, diet, fermentation type, habitat, and limb morphology. These variables can be used to understand patterns and processes of ecological change.

Methods

Compilation of Species List. *HerbiTraits* includes all known herbivores over the last ~130,000 years from the start of the last interglacial period, which is ~30,000 years prior to onset of the earliest late Quaternary extinctions. The mammal species list was derived from PHYLACINE v1.2.1²⁹. Herbivorous birds ≥ 10 kg were gathered through a comprehensive review of the peer-reviewed literature, including handbooks³¹. Herbivores were selected as any species ≥ 10 kg with $>50\%$ plant in their diet, thus including several omnivorous taxa (e.g. bears). The 10 kg cut-off was chosen following Owen-Smith's³² designation of a mesoherbivore, a category paradigmatic to many herbivore ecological analyses³³ but missed by the commonly used ≥ 44 kg cutoff commonly used for 'megafauna'³⁴. Domestic species with wild introduced populations (e.g. horses *Equus ferus caballus*, water buffalo *Bubalus arnee bubalis*)²⁶ were included separately in *HerbiTraits* as their trait values (particularly body mass) can differ substantially from their extant or extinct pre-domestic conspecifics. We included the status for all species, including 'Extant', 'Extinct before 1500 CE', 'Extinct after 1500 CE', 'Extinct before 1500 CE, but wild in introduced range' and 'Extinct after 1500 CE, but wild in introduced range'. The latter two cases apply to species that are extinct in their native ranges (e.g. *Camelus dromedarius*, *Bos primigenius*, *Oryx dammah*) but which have wild, introduced populations. Species listed as Extinct in the Wild by the IUCN Red List are considered 'Extinct after 1500 CE' in the dataset.

Functional Traits. Functional trait data were collected from a variety of peer-reviewed literature ($n = 502$ references, 91% of total references), books ($n = 28$, e.g. *Handbook of the Mammals of the World*³⁵), online databases ($n = 7$), theses ($n = 9$), and others ($n = 11$). For all taxa, multiple sources were consulted, and the most reliable source was used in trait designation. Reliability was based on the method of the source data (see Table 2 for the ranking system we employed). In cases where studies disagreed, we gave extra weight to studies with more reliable methods, larger sample sizes, and/or broader geographic and temporal coverage. We provide justification for our decision-making process in note fields.

Body mass. Body mass is strongly associated with a number of life history attributes and ecological effects, including metabolic and reproductive rates, the capacity to cause disturbance, the ability to digest coarse fibrous vegetation, and the vulnerability of herbivores to predation^{32,36} (Fig. 1). Mammal body mass (in grams) was sourced from PHYLACINE v1.2.1²⁹ and Mass of Mammals³⁰ (Table 1). Avian body masses were collected directly from the literature. We collected body mass data separately for domesticated species from AnAge: Animal Senescence and Aging database³⁷, because their body masses can vary drastically from their pre-domesticated relatives.

Given variability in mass estimation methods and their reliability, we tracked down the primary sources that the aforementioned datasets cited and coded the mass estimation method used. In general, the most reliable body mass estimates for extinct mammals were calculated with volumetric estimates (e.g. by measuring displacement of a fluid) or by allometric scaling equations. Isometric equations (which assume a simple linear relationship between morphology (e.g. tarsus length) and body mass) were ranked lower, as were cases where body masses were estimated based on similar, often closely related species (Table 2). However, we restricted metadata gathering to extinct taxa as accounts of extant species rarely report how their mass estimates were generated (though in all likelihood they are derived from a measured voucher specimen). Furthermore, the mass estimates of extinct species are the most uncertain and the most difficult to verify for users who are not familiar with extinct species or paleobiological methods of mass reconstruction. The avian mass estimates were collected by the authors directly from the peer reviewed literature.

Reliability rank	Diet	Mass	Habitat	Fermentation & Limb morphology
0	Expert opinion Imputed Inferred from ____: <i>Genus, habitat associations</i>	Expert Opinion Imputed Method unknown Method uncertain Inferred from ____: <i>relative of suggested similar size</i> <i>Extant species (method unknown, presume measured)</i>	Expert opinion Imputed Inferred from ____: <i>Family, Genus, absence of evidence, co-occurring species</i>	Proxy isotopes ____: ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$) Proxy ____ morphology: <i>craniodental, appendicular</i> Inferred from ____: <i>diet, Class, Infraclass, Order</i>
1	Functional ____ morphology: <i>craniodental, appendicular</i> Observed low sample size (1–5) ____: <i>dental bolus/coprolite</i>	Functional isometric relationship (____): <i>bone size, shoulder height, teeth size etc.</i>	Functional ____ morphology: <i>craniodental, appendicular</i> Observed low (1–5) sample size ____: <i>dental bolus, coprolite, foraging, fecal analysis, stomach-contents, DNA metabarcoding</i>	Inferred from ____: <i>Suborder, sister Families</i>
2	Proxy ____: <i>isotopes ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$, $\delta^{15}\text{N}$, etc), dental wear (mesowear, microwear)</i>	Proxy allometric relationship (____): <i>bone size, shoulder height, teeth size etc</i> , Proxy volumetric estimate	Inferred from ____: <i>habitat association, vegetation association</i>	Inferred from ____: <i>Subfamily, Family</i>
3	Observed ____: <i>Fecal analysis, stomach-contents, coprolites, foraging observations, dental bolus, DNA metabarcoding</i>	Observed measured body mass	Observed ____: <i>foraging observations, habitat use</i>	Observed ____: <i>Species, Genus</i>

Table 2. Method for assigning reliability in trait assessments for all traits. The italic text substitutes for ‘____’. At times, in cases where sources contradicted each other, or because of low source quality, reliability rank will be lower than reported here, with explanations in respective notes column. Likewise, particularly for diet, if empirical evidence was interpolated from a closely related species, the taxonomic relation is noted in parentheses following the method designation and reliability ranks are reduced.

Diet. Diet determines the type of plants herbivores consume and thus downstream effects on vegetation, nutrient cycling, wildfire, seed dispersal, and albedo (Fig. 1)^{19,33}. Diet was collected as three ordinal variables describing graminoid consumption (i.e. grazing), browse and fruit consumption (i.e. browsing), and meat consumption (including vertebrate and invertebrate) (Table 1). Grazing and browsing have distinct effects on vegetation and ecosystems and are key dimensions of herbivore dietary differentiation³³, reflecting a suite of strategies that have evolved across all major herbivore lineages. This is because grasses and their relatives (graminoids) and dicots (woody plants and herbaceous forbs) present different obstacles to herbivory. While graminoids are highly abrasive and composed primarily of cellulose, dicots are lignified and/or protected with secondary chemical compounds³⁸. Frugivory is often impossible to differentiate from browsing based on paleobiological sources of data for extinct taxa and thus was included with browsing, though known records of fruit consumption are marked in the dataset’s diet notes column. The consumption of bamboo was considered browsing despite bamboo being a grass, as its lignification makes it structurally similar to wood³⁹.

Graminoid, browse, and meat consumption ranged from 0–3, with 0 indicating insignificant consumption and 3 indicating regular or heavy consumption. In general, 0 indicates 0–9% of diet, 1 indicates 10–19%, 2 indicates 20–49%, and 3 indicates 50–100%. For example, an obligate grazer that consumes 90% graminoids would have a 0 for browse, and a 3 for graze, whereas a grazer that consumes 70% graze and 30% browse would have a 3 for graze and a 2 for browse. Likewise, if a species consumed both graze and browse equally (e.g. a mixed feeder) they would receive a score of 3 for each. While dietary estimates for extinct taxa by necessity came from broad temporal and spatial scales⁴⁰, the coarseness of our ordinal (0–3) diet designation allowed us to capture intraspecific and spatiotemporal variation, making extant and extinct species comparable.

Diets for extant species ($n = 321$) were based on records from the *Handbook of the Mammals of the World*³⁵, which represents a compiled, expert-reviewed synopsis of natural history data across mammals. However, to ensure that these diet designations were up to date, we conducted literature reviews for each species, searching for any papers published since the *Handbook of the Mammals of the World* (2009–2011 depending on taxonomic group). We also consulted region-specific handbooks, in particular Kingdon *et al.* 2013 *Mammals of Africa*⁴¹. In cases where percent diet composition was unavailable, we determined dietary values by converting textual descriptions into ordinal values (Table 3) following the methods outlined by MammalDIET⁴². Diets for extinct species were gathered from a variety of literature, as no systematic compilation of extinct herbivore diet is presently available. Discrepancies between sources were noted and described in the dietary notes field.

The methods of the original source papers for extant and extinct were designated and ranked by reliability (Table 2), which was used in assigning final dietary values. We gave priority to direct observations, including fecal or stomach content analysis, coprolites, fossilized boluses (e.g. phytoliths or other vegetation remnants in teeth), and foraging observations. This category was followed by proxy data, such as stable carbon isotopes and dental microwear and mesowear. Inferences from functional morphology, direct observations with sample sizes ≤ 5 , expert opinions, and inferences from extant relatives were considered to have the lowest reliability (Table 2).

Herbivore diets can be highly variable, particularly across seasons and regions. In most cases where primary sources differed because of geographic variation in diets (e.g. a diet heavy in grass in one location and in browse in another), we increased the value of both dietary categories to reflect the mixed feeding capacity of the species across their range. However, we tempered this in cases of unusual diets in response to starvation, such as in the

Diet Value	Interpretation	Textual description
3	The food source is a major (51–100%) and essential part of the species' diet.	"primarily consumes" "mainly consumes" "regularly consumes" "major part of the diet" "only consumes"
2	The food source is an important but not major part (21–50%) of the species diet. It is generally a non-essential part of the species diet.	"also consumes" "seasonally consumes" "may consume"
1	The food source is a relatively small (11–20%) and unimportant part of the species diet.	"occasionally consumes" "sometimes consumes" "opportunistically consumes" "has been reported to eat"
0	This food source is an insignificant part (0–10%) of the species diet.	"does not consume" "has once been seen consuming" The text does not mention the food source

Table 3. Method for converting textual descriptions to ordinal dietary values. This table is based upon the method outlined by Kissling *et al.*⁴², and shows some example key words and phrases that were used to determine dietary values.

case of severe droughts, as consumption does not necessarily mean the species has the capacity to survive on these alternative diets. In these cases, we have noted the evidence and justified our decision-making process.

In cases where no dietary data were available ($n = 26$ species), we imputed diet values based on a posterior distribution of 1,000 equally-likely phylogenies for mammals ≥ 10 kg from PHYLACINE v1.2.1^{29,43}. We used the R package "Rphylopar" v0.3.0 with a Brownian motion evolutionary model and took the median value from the 1,000 phylogenetic trees^{44,45}. This model accounted for both the evolutionary correlation of the individual dietary values across the full phylogeny as well as the probability of diet values based on other traits, as some trait combinations (e.g. arboreality and grazing) are very rare. Given that this imputation was conducted across full mammal phylogenies (≥ 10 kg), we used life history traits from PHYLACINE v1.2.1^{29,43}, so that imputation for species only distantly related to other herbivores (e.g. bears) would be robust.

Ordinal diet scores were further used to categorize species into two types of dietary guild classifications, one herbivore-specific which contained browsers (graze = 0-1, browse = 3), mixed-feeders (graze = 2-3, browse = 2-3), and grazers (graze = 3, browse = 0-1), and another guild containing omnivores (any species with meat consumption ≥ 2). Users can easily derive finer-scale dietary guilds (e.g. mixed-feeder preferring browse) from the ordinal scores if desired.

Fermentation type. Digestive physiology controls the quantity and quality of vegetation (e.g., fiber and nutrient content) that herbivores consume. Fermentation type therefore shapes effects on vegetation, gut passage rate, seed and nutrient dispersal distances, water requirements, and the resulting stoichiometry of excreta^{19,46–49} (Fig. 1). Following Hume⁴⁶, fermentation type was collected as a categorical variable consisting of simple gut, hindgut colon, hindgut caecum, foregut non-ruminant, and ruminant (Table 1). These variables capture the range of fermentation adaptations across avian and mammalian herbivores. Based on these classifications and Hume⁴⁶, we also ranked fermentation efficiencies (0–3) on an ordinal scale to these various digestive strategies, to facilitate quantitative functional diversity analyses (Table 1).

Fermentation types show strong phylogenetic conservatism at the family level. Therefore, for the most part, if direct anatomical evidence was not available, we inferred fermentation types from extant relatives. However, some extinct herbivores possess no close modern relatives and may have been functionally non-analog (e.g. 23 extinct ground sloths, 3 notoungulates, 4 diprotodons, 16 glyptodonts, and 12 giant lemurs). In these cases, closest living relatives, expert opinions, and craniodental morphology were used to determine the most likely fermentation system. For example, notoungulates, an extinct group from South America, possess no close relatives yet their craniodental and appendicular morphology resemble extant hindgut fermenting taxa (rhinos), and hindgut fermentation is widely considered to be ancestral in ungulates⁵⁰. In all cases, we describe our justification and the state of the debate in the current literature.

Habitat use. Habitat use determines the components of ecosystems that herbivores interact with and is central to understanding their effects on vegetation, soils, and processes like nutrient dispersal (e.g. moving nutrients from terrestrial to aquatic environments⁵¹). We classified habitat with three non-exclusive binary variables (0 or 1) for the use of arboreal, terrestrial, and aquatic environments. We further classified this variable categorically as semi-aquatic, terrestrial, semi-arboreal, and arboreal. Defining habitat use is challenging as many terrestrial species use aquatic or arboreal environments opportunistically, and percentage habitat use data is unavailable for most species. To ensure habitat designations were consistent for extant and extinct species, we classified taxa on the basis of obligate habitat use across their geographic range and/or the possession of specialized adaptations (e.g. climbing ability) that would be evident in the morphology of fossil specimens. Further proof of habitat use by extinct species was inferred from close relatives or isotopic proxy data, when relevant. In cases where no specific information was available, we inferred habitat use from absence of evidence (e.g. there is no specific data regarding aquatic or arboreal habitat use by gemsbok *Oryx gazella*).

Limb morphology. Limb morphology is broadly associated with herbivore habitat preferences, locomotion (e.g., cursoriality, fossoriality, climbing), anti-predator responses, and rates of body size evolution^{52–54}. Limb morphology also controls disturbance-related trampling effects on soils, with hoofed unguligrade taxa having stronger influences on soils than those with other morphologies⁵⁵. Trampling has important effects on soils, hydrology, albedo, and vegetation^{7,56} and is often considered an essentially novel aspect of introduced herbivores in Australia and North America (e.g.^{10,57,58}). Limb morphology was collected as a three-level categorical variable consisting of plantigrade (walking on soles of feet), digitigrade (walking on toes), and unguligrade (walking on hoof). For example, plantigrade species are more likely to be fossorial or scansorial in habit, digitigrade species are likely to be saltatory or ambulatory (e.g. extant kangaroos), while unguligrade species are often adapted for rocky, vertiginous terrain or cursoriality^{53,54}. Limb morphology shows high phylogenetic conservatism across herbivore lineages and thus was primarily collected at the genus or family level from primary and secondary literature.

Data Records

HerbiTraits consists of an Excel workbook containing metadata (column names and descriptions), the trait dataset, and references as three separate sheets. The dataset is open-access and is hosted on Figshare⁵⁹ as well as on GitHub (<https://github.com/MegaPast2Future/HerbiTraits>).

Technical Validation

The majority of functional trait data were collected from primary peer-reviewed literature (1,733 trait values from 456 articles), secondary peer-reviewed literature (1,294 values from 46 articles), or academic handbooks (1,099 trait values from 27 resources). Twenty-eight remaining resources consisted of theses ($n = 39$ trait values), databases (44), websites (39), conference proceedings (9), and grey literature (5). For transparency, justifications for trait designations (particularly relevant for extinct species) are described in the Notes columns and the highest quality evidence is ranked in trait-specific Reliability columns. Contradictions between sources have been noted and values have been based on the most empirically-robust methods or by averaging values across studies (see above). All data designations have been cross-checked (by EJJ, SDS, JR, MD, and OM). We aim to maintain *HerbiTraits* with the best available data. We urge users to report errors or updates on newly published data for integration into *HerbiTraits* by filing an Issue on our GitHub (<https://github.com/MegaPast2Future/HerbiTraits>) repository page, or by emailing the corresponding authors. Furthermore, the GitHub (<https://github.com/MegaPast2Future/HerbiTraits>) page includes an incomplete trait file, which contains other ecologically relevant traits, such as adaptations for digging and free water dependence⁶⁰. These traits remain unavailable for many taxa, but provide a starting point for further data collection and analysis.

Usage notes

Please cite this publication when using *HerbiTraits*. As the taxonomy and phylogeny is derived from PHYLACINE v1.2.1, that data is compatible with PHYLACINE v1.2.1's phylogeny and range maps and with the IUCN Red List Version 2016-3 (2016), with the exception of domestic mammals and birds. All source references are cited in the main text^{14,29,61–601}. Where possible, we have coded trait data in duplicate ways to facilitate different types of analysis. For example, diet, fermentation, and habitat use, are coded both as categorical variables and as ordinal/binomial variables for use in functional diversity analyses.

Code availability

The authors declare no custom code necessary for the interpretation or use of dataset.

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E.J.L. and S.D.S. contributed equally and share first authorship. S.D.S., E.J.L., O.M., J.R., S.C.S., A.D.W., D.R., C.J.S., J.C.S. devised the idea. S.D.S., E.J.L., O.M. and J.R. collected the data. S.D.S., R.Ø.P., E.J.L. and J.R. did the analysis. E.J.L., S.D.S., O.M., M.D., R.Ø.P., D.R., C.J.S., J.C.S., A.D.W. and J.R. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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