

## Introduced herbivores restore late pleistocene ecological functions

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5 **Title: Introduced herbivores restore Late Pleistocene ecological functions**

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35

5 **Abstract**

Large-bodied mammalian herbivores dominated Earth's terrestrial ecosystems for several million years before undergoing substantial extinctions and declines during the Late Pleistocene (LP) due to prehistoric human impacts. The decline of large herbivores led to widespread ecological changes due to the loss of their ecological functions, as  
10 driven by their unique combinations of traits. However, recently, humans have significantly increased herbivore species richness through introductions in many parts of the world, potentially counteracting LP losses. Here, we assessed the extent to which introduced herbivore species restore lost—or contribute novel—functions relative to pre-extinction LP assemblages. We constructed multidimensional trait spaces using a trait  
15 database for all extant and extinct mammalian herbivores  $\geq 10\text{kg}$  known from the earliest LP (~126,000 ybp) to the present-day. Extinction-driven contractions of LP trait space have been offset through introductions by ~39% globally. Analysis of trait space overlap reveals that assemblages with introduced species are overall more similar to those of the LP than native-only assemblages, because 64% of introduced species are more  
20 similar to extinct rather than extant species within their respective continents. Many introduced herbivores restore trait combinations that have the capacity to influence ecosystem processes, such as wildfire and shrub expansion in drylands. Though introduced species have long been a source of contention, our findings indicate that they may in part restore ecological functions reflective of the last several million years  
25 before widespread human-driven extinctions.

5 **Significance Statement**

Humans have caused extinctions of large-bodied mammalian herbivores over the last ~100,000 years, leading to cascading changes in ecosystems. Conversely, introductions of herbivores have in part numerically compensated for extinction losses. However, the net outcome of the twin anthropogenic forces of extinction and introduction on herbivore assemblages has remained unknown. We found that a primary outcome of introductions has been the reintroduction of key ecological functions, making herbivore assemblages with non-native species more similar to those that existed before LP extinctions than native-only ones. Our findings support calls for renewed research on introduced herbivore ecologies in light of paleoecological change and suggest that shifting focus from eradication to landscape and predator protection may have broader biodiversity benefits.

## 5 **Main Text**

### **Introduction**

Global extinctions and range contractions of large-bodied mammalian herbivores have occurred across the world beginning ~100,000 years ago and peaking towards the end of the Late Pleistocene (LP) (1). Emerging consensus indicates that LP losses were  
10 primarily driven by prehistoric human impacts (2, 3), either alone or synergistically with climate change (4). On the other hand, recent introductions of herbivore taxa outside their native ranges has increased species richness across much of the world, in some continents to levels approaching the LP (5).

The prehistoric declines of large-bodied herbivores led to widespread ecosystem  
15 changes, including reduced nutrient cycling and dispersal, reduced primary productivity, increased wildfire frequency and intensity, and altered vegetation structure (6-8). Likewise, introduced herbivores have been found to drive changes in vegetation structure (9), to increase water availability in deserts through grazing and disturbance (10), and to reduce fuel loads and thus wildfire (9, 11).

20 These effects emerge from the distinct ecological functions of large herbivores. Here, we define 'function' as the capacity of organisms to affect their environment, as determined by their combinations of traits, such as body mass, fermentation type, and diet (12) (SI Appendix, Fig. S1). For example, large-bodied hindgut grazers have the unique capacity to bulk-graze large quantities of low-nutrient grasses (8, 13, 14).  
25 However, the downstream ecological effects of this function vary with ecological context (e.g. precipitation, soil type, predation pressure). For example, bulk-grazing can lead to the formation of high productivity grazing lawns, but this process is shaped by interactions between soil nutrients, rainfall, and herbivore densities (15).

5           Most extant plant and animal species evolved in the context of diverse large-  
bodied herbivore assemblages, from the early Cenozoic (30-40 million ybp) until the LP  
extinctions (16). However, most research on introduced large-bodied herbivores has  
been conducted under the premise that they are ecologically novel and thereby  
disadvantage resident species (e.g. 17). The possibility that introduced herbivores may  
10 in part restore the ecological functions that characterized the last several million years  
until LP extinctions has been suggested (18-21), but has not been rigorously evaluated.

Here, we analyze how the twin anthropogenic forces of prehistoric extinction and  
recent introduction have shaped herbivore functional diversity and the extent to which  
introduced herbivores restore lost, or introduce novel, ecological functions relative to  
15 pre-extinction LP assemblages. We do so by comparing *native-only* and *inclusive*  
(native and introduced) herbivore species assemblages of the present-day to *LP*  
assemblages in terms of trait structure across the continents.

## Results

20           We compiled native-only, inclusive (native and introduced), and LP species lists  
for continental assemblages for all herbivore species  $\geq 10\text{kg}$  recorded over the last ~  
126,000 years, i.e. since the last interglacial (Data S1). Globally, LP extinctions resulted  
in a loss of 160 of 427 (35%) herbivore species  $\geq 10\text{kg}$ , particularly in North America  
(67% lost), South America (65%), Australia (64%), and Europe (56%) (Fig. 1A). Thirty-  
25 three herbivore species were introduced into new continents, replacing lost species  
richness by 50% in Australia and Europe, 46% in North America, 42% in Africa, 27% in  
South America, and 11% in Asia (Fig. 1A).

5           To understand how extinctions and introductions affected the capacity of herbivores to influence their environments, we compiled a trait dataset of body mass, fermentation type (simple gut, hindgut, foregut non-ruminant, ruminant), diet (graze, browse), habitat (aquatic, terrestrial, arboreal), and limb morphology (plantigrade, digitigrade, unguligrade) (SI Appendix, Table S1). Fermentation type was recorded in  
10 terms of fermentation efficiency, with ruminants scoring highest. Limb morphology was included as a trait due to its influences on soil disturbance (22), locomotion (e.g. cursoriality, fossoriality) and habitat constraints, which can otherwise be difficult to infer for extinct species (23-25).

          To analyze changes in trait combinations, we constructed multidimensional trait  
15 spaces using Principal Coordinates Analysis (PCoA) to describe the primary axes by which herbivores differ from each other in terms of their traits and thus encapsulate the overall functionality of herbivore assemblages. Collectively, the first four axes of global herbivore trait space accounted for 78% of interspecific trait variation (Fig. 1B, SI Appendix, SI Appendix, Fig. S2). PCoA 1 (34% of total variation) was primarily shaped  
20 by body mass ( $r = 0.87$ ) and diet (grazing  $r = 0.78$ ; browsing  $r = -0.66$ ), while PCoA 2 (28% of total variation) primarily reflected fermentation efficiency ( $r = -0.93$ ). Changes along these axes revealed that, as expected, LP extinctions of herbivores led to substantial contractions in overall trait space, shifting the balance towards smaller-bodied species with more efficient fermentation strategies (e.g. ruminants) (Fig. 1B).

25           To understand how the overall diversity of species trait combinations has changed from extinctions and introductions, we compared the *volume* of occupied multidimensional trait space for LP, native-only, and inclusive assemblages. Trait space

5 volume is a metric of functional diversity also known as *functional richness* (26). LP  
extinctions reduced the total volume of occupied multidimensional trait space by 62%  
globally, particularly in Australia (99% contraction in richness), North America (83%),  
and South America (83%) (Fig. 2A). In contrast, introduced herbivores replaced lost trait  
space volume by an average of 39% globally, particularly in Australia (100% replaced  
10 and 30% expanded over LP levels), South America (47% replaced), Europe (22%),  
Africa (18%), and North America (17%) (Fig. 2A).

While introductions substantially replaced lost trait space volume, to understand  
whether inclusive assemblages with introduced species are more or less similar to the  
LP than native-only ones, we calculated functional dissimilarity (Sørensen's  $\beta$ ) from the  
15 overlap of native-only and inclusive trait spaces with LP ones. Functional dissimilarity,  
like other beta diversity measures, is comprised of two additive components:  
nestedness, the overlap of assemblages in trait space (e.g. the degree to which one is a  
subset of the other), and turnover, the degree of non-overlap in trait space (e.g. novelty)  
(27). We found that introduced taxa make inclusive continental assemblages more  
20 functionally similar to the LP than native-only assemblages, by 39% in Australia, 33% in  
South America, 21% in Europe, and 13% in North America. However, introductions  
contribute turnover to inclusive assemblages, driven by the unique traits and trait  
combinations of some introduced taxa (Fig. 2B). Australia had the highest turnover, with  
88% of the remaining dissimilarity with the LP comprised of turnover. This is due to the



5 introduction of ruminants and larger-grazers than those present in its LP marsupial-  
dominated fauna (Fig. 2B).

To understand how introduced species relate to other taxa, we examined  
whether their nearest neighbors in trait space are extant or extinct. To avoid comparing  
species with different thermal tolerances (e.g., tropical versus arctic), we restricted  
10 comparisons by Köppen-Geiger climate zones (28) and by body mass bins. Body mass  
bins were calculated using the Sturges algorithm (29), which finds natural breaks points  
in continuous data distributions, thus reducing analytic bias.

Overall, 64% of introduced species are most similar to extinct LP species rather  
than extant species. This is most apparent in those continents with high LP extinction  
15 rates: in Australia 93% of introduced species are most similar to extinct taxa; followed  
by 86% in South America, 74% in North America, and 50% in Europe (Fig. 3, SI  
Appendix, Fig. S3). In Africa and Asia, which experienced few extinctions, 90% and  
75% of introduced taxa are most similar to extant species (SI Appendix, Fig. S2).

The similarity of introduced herbivores to extinct ones indicates that introductions  
20 have restored lost trait combinations and thus functions. To better understand which  
functions have been restored, we focused on key 'metabolic' functions herbivores  
contribute in ecosystems by consuming plant biomass and by cycling and redistributing  
nutrients (8). These functions are primarily influenced by body mass and dietary guild—  
traits that control the *quality*, *quantity*, and *type* of vegetation consumed, with larger  
25 herbivores prone to greater dispersal distances and capable of digesting larger-  
quantities of fibrous, low-nutrient vegetation (8, 13, 14). To understand how extinctions

5 and introductions have affected these key metabolic functions, we categorized species into *functional groups* by combinations of body mass bins and dietary guilds.

We found that 42% of introduced herbivores restore extinct functional groups, particularly in Australia (60% of lost functional groups restored) and in South America (42% restored) (Fig. 4). Three introduced herbivores (5%) contribute novel functional  
10 groups: two species introduced to Australia contribute a grazing functional group larger than any present in the LP (by ~200 kg), while in Europe the introduction of a small-bodied mixed-feeder (*Macropus rufogriseus*) contributes one novel functional group.

## Discussion

15 The redistribution of species through human introductions is primarily perceived as an environmental harm. However, our results indicate that one consequence of introductions has been to counteract global patterns of human-caused extinction by replacing lost functional diversity and making modern trait compositions more similar to those of pre-extinction LP assemblages. In doing so, the majority of introduced species  
20 are functional surrogates for extinct species and many restore 'metabolic' functional groups, particularly in those continents most impacted by LP extinctions.

Many of these restored functions have the potential to affect ecosystems. For example, large-bodied browsers were severely impacted by LP extinctions in Australia (Fig. 4). The restoration of these functional groups may reduce shrub cover and  
25 promote grasslands, with implications for albedo, carbon storage, and wildfire (30). Likewise, the widespread restoration of extinct large-bodied grazing functional groups,

5 which are capable of bulk-grazing large quantities of low-nutrient grasses compared to smaller grazers, could reduce wildfire intensity (30).

In some cases, introduced taxa have close phylogenetic relationships with extinct species. For example, in North and South America, introduced equids (*E. africanus asinus*, *Equus ferus caballus*) are related or conspecific to extinct taxa (*E. francisci*, *E.*  
10 *ferus*) and have restored lost trait combinations, such as large-bodied hindgut grazing. The effects of these species are poorly understood (e.g. 31) but some evidence suggests that the restoration of these trait combinations can have facilitative effects on other species. In North American desert wetlands, disturbance and grazing by wild burros (*E. a. asinus*) of fast-growing, emergent vegetation maintains open water habitat  
15 to the benefit of endemic fishes (10) and an endangered amphibian (32). Likewise, grazing by wild horses (*E. f. caballus*) in North American salt marshes favors higher diversity of foraging birds and increased crab density, while reducing fish density and diversity (33).

In other cases, introduced taxa are unrelated to extinct species in their new  
20 homes yet show strong functional similarities, although often in novel trait combinations. For example, introduced hippos (*Hippopotamus amphibius*) in South America present a chimera of multiple extinct species' trait combinations. While they are most similar to a giant extinct llama (*Hemiauchenia paradoxa*, Fig. 3) in all assessed traits bar habitat use, our analysis revealed that they are nearly as similar to an extinct semi-aquatic  
25 notoungulate (*Trigonodops lopesi*) in all traits but fermentation type. While the ecological effects of hippos in South America remain unknown, their trait combinations suggest that their ecological effects may overlap with extinct species in certain

5 ecosystem components (e.g. grazing and disturbance in riparian zones) and diverge elsewhere (e.g. direction of nutrient transport).

The apparent novelty of some introduced traits is tempered when compared to the trait compositions of the LP. For example, the disturbance-related effects of Australia's introduced hoofed ungulates on soils and vegetation appear novel (11). Yet  
10 the extinct short-faced kangaroos (sthenurines) possessed monodactyl hoofs and an unguligrade morphology similar to 'open-plains' horses (34). However, rumination remains a novel trait in Australia, where macropods' non-ruminant foregut fermentation is less thorough (35). It is therefore possible that some of Australia's plants lack seeds  
15 dispersal efficacy and possibly to vegetation structure. Australia also received two grazers larger than any LP grazing species (by ~200 kg). The introduction of large-bodied bulk-grazing may have strong effects on Australia's uniquely fire-driven ecosystems (36). In a long-term experimental system in Northern Australia, seasonal bulk-grazing by introduced water buffalo (*Bubalus bubalis*) of fibrous, low-nutrient  
20 grasses, reduced wildfire and promoted tree establishment and survivorship through wildfire (9). Whether these ecological effects are novel or overlap with those of extinct mixed feeders is unknown.

Many important traits remain unknown for extinct taxa, such as sociality, movement patterns, foraging behavior, and vulnerability to predators. All could be  
25 factors affecting similarity with LP species and thereby shaping how introduced herbivores interact with extant native species. Yet, the diversity of LP herbivores makes it likely that many of these introduced traits have precedents. For example, although the

5 seemingly novel rooting behavior of wild boar (*Sus scrofa*) is thought to disadvantage  
native species across their extensive introduced range (37), several extinct species  
likely had similar foraging strategies, including *Platygonus compressus* (38) in North  
and South America, and *Zygomaturus trilobus* (39) in Australia. Indeed, rooting by wild  
boar increases tree growth rates by mixing leaf litter into upper soil layers, enhancing  
10 decomposition rates and thus nutrient availability in eastern North American forests  
(40); and increases bird abundance by increasing accessibility of food resources in  
northern Australia (41).

While the trait combinations of herbivores drive their functional capacity to affect  
ecosystems, their actual effects emerge in interaction with ecological contexts, such as  
15 predation (42) and landscape connectivity (43). Many apex predators continue to face  
declines (44). Likewise, ongoing landscape fragmentation restricts herbivore  
movements and can lead to concentrated herbivory (43). Therefore, while introductions  
make herbivore assemblages more functionally similar to the LP, they do not  
necessarily restore ecosystems to LP conditions due to ongoing anthropogenic  
20 pressures.

Introduced species have been primarily studied in the context of recent historic  
states under the premise that their ecological functions are novel. However, presumed  
novelty yields to functional similarity when compared to the LP, a time period largely  
reflective of the last ~40-30 million years of terrestrial ecosystem evolution (16).  
25 Compared to these pre-anthropogenic conditions, introduced herbivores replace lost  
functional diversity, make modern herbivore assemblages more similar to LP ones, and  
restore key metabolic functional groups in the Earth system. Our results indicate that

5 introductions are an inadvertent counterpoint to prehistoric and historic anthropogenic defaunation and that future research on the ecologies of introduced herbivores would benefit from incorporating deep-time perspectives.

## Materials and Methods

10 We included all extant and extinct herbivore species  $\geq 10$  kg that lived the last 130,000 years, following taxonomy in the PHYLACINE v1.2 dataset (45). Many analyses of LP extinctions have focused on species  $\geq 44$ kg or 100kg, however, given that Australia lost all but one herbivore  $\geq 44$ kg during the LP extinctions, we included herbivores  $\geq 10$ kg to ensure that modern, native-only assemblages would have sufficient  
15 numbers of species for analysis. Herbivores were selected from PHYLACINE as species with  $>50\%$  plant in their diet, thereby including some carnivorans (e.g., bears). Alternative species lists for the LP exist, varying in their taxonomy of extinct and extant species. To verify that our results were robust to differences in taxonomy we conducted all analyses using the species list in Smith et al. 2018 (16) (SI Appendix, SI Text, Figs.  
20 S3-S6).

To determine how modern (native-only) and inclusive (native and introduced) herbivore assemblages compare to LP ones, we compiled three datasets of herbivore species ranges. We drew continental LP assemblages from 'present-natural' ranges of herbivores from Faurby, *et al.* (45), which primarily used fossil co-occurrence records to  
25 reconstruct modern-day herbivore ranges in the absence of anthropogenic extinction and range contraction. Native-only assemblages were drawn from spatial distributions in the IUCN Red List V6.1 (46). Introduced species distributions, compiled from IUCN

5 spatial distributions and numerous peer-reviewed sources and databases (see Data  
S1), were added to native assemblages to establish inclusive assemblages. Only self-  
sustaining populations that have been moved across continents were included (e.g.  
intra-continental introductions were excluded). Domestic herbivores were excluded from  
analysis as these populations are not necessarily ecologically viable without human  
10 intervention, and their behavior and interactions within ecosystems are heavily modified  
by human management. However, wild populations of domestic species were included.

Given different types of error in each of these scenario's distribution maps (e.g.  
ranges estimated using different methods and with different degrees of certainty) we  
used these range maps to create continental species lists for LP, native-only, and  
15 inclusive assemblages. We chose to conduct analyses at the continental scale as they  
reflect the long-term dispersal-limits of herbivores and the plants and other animals they  
interact with, thus setting the eco-evolutionary context of modern ecosystems. We  
limited our analyses to large landmasses, excluding smaller islands because they have  
unique evolutionary histories owing to their isolation. Additionally, this avoids the  
20 inclusion of small populations of functionally unique and geographically restricted  
introduced species (e.g. giraffes *Giraffa camelopardalis* introduced to a small island in  
Southeast Asia).

### *Traits*

25 We collected data for traits that drive herbivores' interactions with other species  
and the environment: body mass, diet, fermentation type, habitat type, and limb  
morphology. Body mass (kg) was collected as a continuous variable from Smith, *et al.*

5 (47) and PHYLACINE v1.2 (45) and was analyzed as log base 10. We collected dietary  
data as two ordinal variables for graminoid and browse consumption respectively from  
the peer-reviewed literature, each ranging from 0-3, following the method of  
MammalDiet (48). While coarse, these two dietary categories remain paradigmatic to  
herbivore ecology in both ancient and modern systems, and reflect key evolutionary and  
10 ecological differences in herbivore dietary adaptations (49) (SI Appendix, SI Text, Table  
S1).

Fermentation type further influences the quality and quantity of vegetation  
herbivores consume, and the nutrient stoichiometry of resulting excreta (14, 35).  
Fermentation type was collected as a categorical variable for five fermentation types  
15 following Hume (35): simple gut, hindgut colon, hindgut caecum, foregut non-ruminant,  
and foregut ruminant. However, this variable was ranked in terms of fermentation  
efficiency when constructing trait spaces, and hindgut caecum and colon were lumped  
because that degree of distinction was unavailable for some extinct taxa. Habitat use  
was collected as three binary and non-exclusive variables (arboreal, terrestrial, and  
20 aquatic) (SI Appendix, Table S1).

Limb morphology was included as it influences disturbance-related impacts on  
soils (22) and is therefore frequently mentioned in relation to the non-analogy of  
introduced herbivores in Australia (e.g. 11, 50). Furthermore, limb morphology is  
correlated with other ecological attributes such as cursoriality, fossoriality, and habitat  
25 constraints, which can otherwise be difficult to infer for extinct species (23-25), Limb  
morphology was obtained from a variety of peer-reviewed literature sources (primarily,  
23) and was inferred based on family and order for extinct taxa if specific morphological



5 studies (e.g. 51) were unavailable. Limb morphology and was treated as three binary variables: digitigrade, plantigrade, and unguligrade (SI Appendix, Table S1).

All trait data were cross-referenced with the primary literature or handbooks (e.g. 52). Diet data was unavailable for 14 extinct species (of 427 total). We imputed their diets based on their phylogenetic relationship to other species with known diets and  
10 traits using the R package “Rphylopars” v. 0.2.9 (53) and PHYLACINE phylogeny. “Rphylopars” was run with all default parameters including a Brownian motion evolutionary model.

### *Analytic Methods*

15 We calculated a Gower distance matrix that evaluated pairwise functional similarity between species. Gower distance is a flexible distance-based measure that can incorporate multiple variable types and has been widely used in analyses of community trait composition and structure (54, 55).

We weighted traits when calculating Gower distance, with mass weighted by two;  
20 diet, fermentation, and habitat weighted by one; and limb morphology weighted half (SI Appendix, Table S1). Mass was weighted by two as it is correlated with many other life history traits, such as reproductive and metabolic rate. Limb morphology was weighted half because, although it captures morphological diversity and disturbance-related effects, the relationship between it and ecosystem effects is less well established. Other  
25 weighting methods produced similar results but trait spaces were less biologically interpretable (e.g. body mass had no visible correspondence to trait space axes, see sensitivity analyses in SI Appendix, Fig. S8 & S9).

5           Multidimensional trait spaces were constructed using the function *dbFD* in the R package “FD” (56). This conducts principal coordinates analysis (PCoA) on the Gower’s distance matrix to produce synthetic traits which become the axes of the multidimensional trait space. We used the first four axes of the PCoA after reviewing axis quality (SI Appendix, Fig. S10) and because including more than four axes has  
10           been shown to distort functional relationships across a variety of real and simulated datasets (57). The relationship between PCoA axes and traits was determined using the R function *envfit* in the R package “vegan” with 1000 iterations (58).

          A number of functional diversity metrics exist to describe different attributes of the structure of trait spaces. Since we were primarily interested in the range of functions  
15           present, we focused on functional richness, which is a measure of the multidimensional volume of trait space (26). To understand if introduced herbivores restore lost LP trait combinations or contribute novel ones by introducing traits without LP analogs, we calculated trait space overlap with the function *beta.functional.pair* in the R package “betapart” (version v1.5.1) (59), which returns a Sørensen dissimilarity metric  
20           decomposed into its primary components of nestedness and turnover.

          To understand if introduced species are functionally most similar to native or extinct taxa we identified the nearest neighbor of each introduced species from the Gower distance matrix. We filtered pairs by Köppen-Geiger (28) climate zones to prevent comparing species with different physiological tolerances (e.g. arctic species  
25           with desert species). We further constrained pairs by body mass bins to prevent spurious pairings between species with identical diet and morphological traits but gross differences in body mass (e.g. without body mass filtering, the 800 kg *Camelus*

5 *dromedarius*' nearest neighbor is a 166 kg kangaroo because of convergence in all  
other traits, see SI Appendix, Fig. S11). Body mass bins were calculated using the  
Sturges algorithm (29), which finds natural break points in continuous distributions and  
reduces analytic bias. To assess the quality of functional analogy between introduced  
herbivores and their nearest neighbors, and to accommodate the intrinsic  
10 distinctiveness of certain species, we calculated the number of extant species, per body  
mass bin and climate zone, that are more similar than the introduced analog.

To understand whether introduced species restore key metabolic functions in  
their new homes we classified herbivores into functional groups, as unique  
combinations of dietary guild and body mass bins (as determined above). Dietary guild  
15 (grazer, browser, and mixed feeder) was classified from the twin ordinal diet scores for  
graze and browse (see SI Appendix, Table S1).

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25 supplementary materials.

5 **Figure 1. Trait space changes resulting from Late Pleistocene (LP) extinctions and recent introductions.** (A) Species richness per continent. Introductions have numerically replaced lost species richness by between 11% (Asia) and 50% (Australia and Europe). Fill color indicates species fate, with the legend shared with panel c. *Inclusive*=native+introduced modern assemblages. (B) Global herbivore trait space. Arrows indicate how particular traits shape trait space axes. The first two PCoA axes (~62% of variation) of trait space are shown (see SI Appendix, Fig. S1 for PCoA axes 3 and 4). Points indicate species and the fill density indicates their density distribution, with the legend shared with panel c. (C) Changes in continental trait space (PCoA 1 and 2) from extinctions and introductions. Crosses indicate centroids of the first two PCoA axes. Locally extinct species went extinct within the respective continent but survived elsewhere. *Native-only*=modern native assemblages; *inclusive*=native+introduced modern assemblages.

20 **Figure 2. Change in trait space volume and functional dissimilarity** (A) Difference between native-only and inclusive trait space volumes from the LP volume for each continent. Trait space volume is the 4-dimensional volume of each trait space (also known as functional richness). Contractions in trait space volume following LP extinctions (native-only points) have been offset by introductions in inclusive assemblages. The dashed line indicates no change from LP. *Native-only*=modern native assemblages (blue); *inclusive*=native+introduced modern assemblages (gray). (B) Total functional dissimilarity to the LP, calculated from the overlap of 4-dimensional trait spaces. Functional dissimilarity (measured as Sørensen's  $\beta$ ) is composed of two additive components: *nestedness* is dissimilarity caused by being a subset of another trait space, while *turnover* is the degree to which assemblages do not overlap (e.g. novelty).

35 **Figure 3. Select introduced herbivores and their extinct nearest neighbors in those continents most impacted by extinctions and introductions.** The color of the top bar indicates the number of extant species (per body mass bin and climate zone) that are more similar to the nearest neighbor than the introduced species is, while the lower bar color indicates dietary guild. For a full list of pairs see SI Appendix, Fig. S3.

40 **Figure 4. The loss and restoration of key metabolic ecosystem functions.** Forty-four percent of introductions restore extinct functional groups, restoring 14 of 51 extinct dietary body mass groups across continents. Body mass groups were determined analytically with the Sturges algorithm, which finds natural breakpoints in continuous distributions. Three species introduce novel groups to Australia and Europe. Points indicate species and are jittered randomly for visualization within each cell.

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