Chapter 2: Introduced herbivores restore Late Pleistocene ecological functions

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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 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 database for all extant and extinct mammalian herbivores ≥10kg 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 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 before widespread human-driven extinctions.

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 are. 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.

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) (Martin and Wright 1967). Emerging consensus indicates that LP losses were primarily driven by prehistoric human impacts (Barnosky et al. 2004, Sandom et al. 2014), either alone or synergistically with climate change (Metcalf et al. 2016). 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 (Lundgren et al. 2018).

The prehistoric declines of large-bodied herbivores led to widespread ecosystem changes, including reduced nutrient cycling and dispersal, reduced primary productivity, increased wildfire frequency and intensity, and altered vegetation structure (Zimov et al. 1995, Doughty et al. 2016, Malhi et al. 2016). Likewise, introduced herbivores have been found to drive changes in vegetation structure (Werner et al. 2006), to increase water availability in deserts through grazing and disturbance (Kodric-Brown and Brown 2007), and to reduce fuel loads and thus wildfire (Werner et al. 2006, Johnson et al. 2018).

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 (Luck et al. 2012) (SI Appendix, Fig. S1). For example, large-bodied hindgut grazers have the unique capacity to bulk-graze large quantities of low-nutrient grasses (Demment and Van Soest 1985, Owen-Smith 1988, Doughty et al. 2016). 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 (Hempson et al. 2015b).

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 (Smith et al. 2018). 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. Barrios-Garcia et al. 2014). The possibility that introduced herbivores may in part restore the ecological functions that characterized the last several million years until LP extinctions has been suggested (Martin 1970, Janzen and Martin 1982, Donlan et al. 2006, Davis 2017), 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 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

We compiled native-only, inclusive (native and introduced), and LP species lists for continental assemblages for all herbivore species ≥ 10kg 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 ≥ 10kg, particularly in North America (67% lost), South America (65%), Australia (64%), and Europe (56%) (Fig. 1A). Thirty-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).

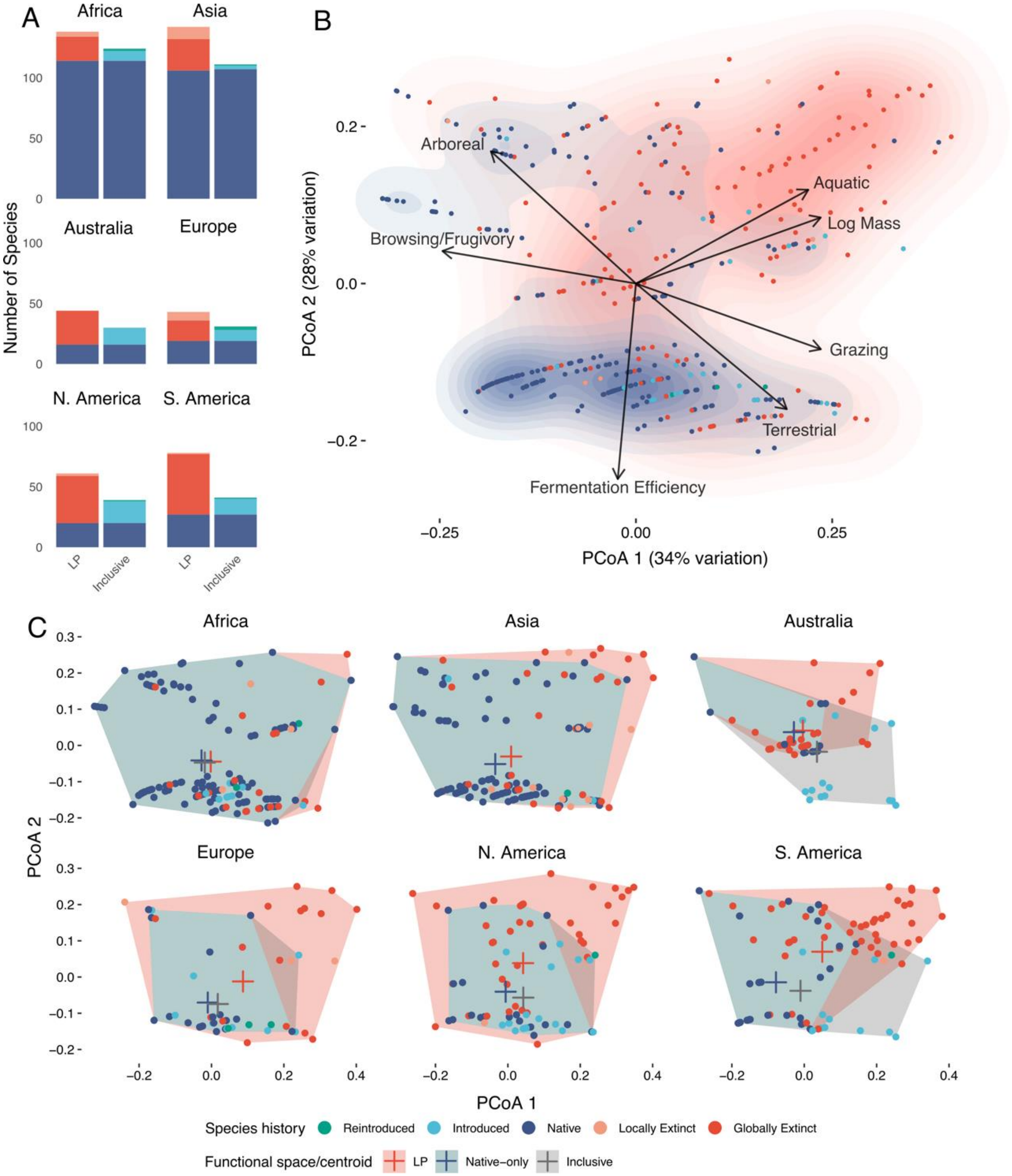

Figure 1. Trait space changes resulting from Late Pleistocene (LP) extinctions and recent introductions. (**A**) Species richness per continent. Introductions have numerically replaced lost species richness by between 11% (Asia) and 50% (Australia and Europe). Fill color indicates species fate, with 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.

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) (Table S1). Fermentation type was recorded in terms of fermentation efficiency, with ruminants scoring highest. Limb morphology was included as a trait due to its influences on soil disturbance (Cumming and Cumming 2003), locomotion (e.g. cursoriality, fossoriality) and habitat constraints, which can otherwise be difficult to infer for extinct species (Brown and Yalden 1973, Polly 2007, Kubo et al. 2019).

To analyze changes in trait combinations, we constructed multidimensional trait 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 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).

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 volume is a metric of functional diversity also known as *functional richness* (Villeger et al. 2008). 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 and 30% expanded over LP levels), South America (47% replaced), Europe (22%), Africa (18%), and North America (17%) (Fig. 2A).

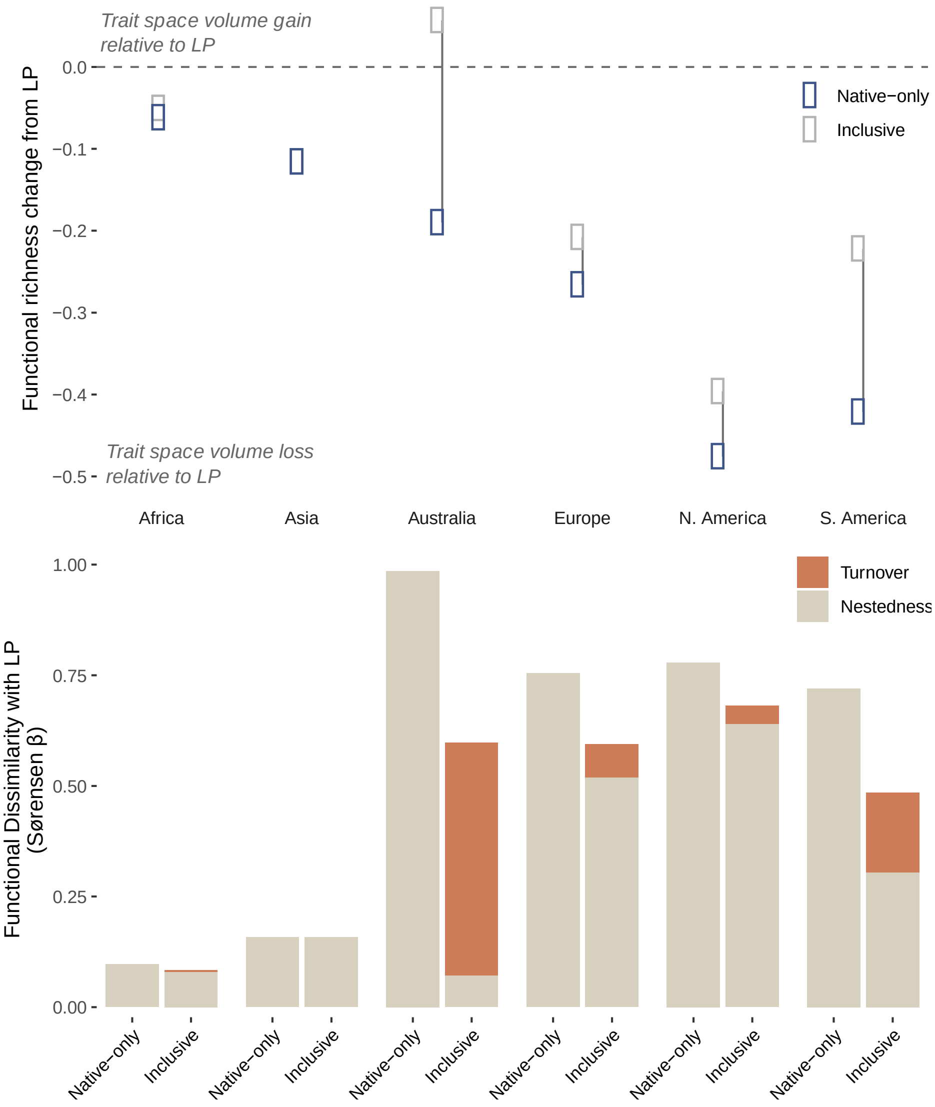

Figure 2. Change in trait space volume and functional dissimilarity (**A**) Difference between native-only and inclusive trait space volumes from the LP volume for each continent. Trait space volume is the 4-dimensional volume of each trait space (also known as functional richness). Contractions in trait 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 β) 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).

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 β) from the 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) (Baselga 2010). We found that introduced taxa make inclusive continental assemblages more 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 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 comparisons by Köppen-Geiger climate zones (Kottek et al. 2006) and by body mass bins. Body mass bins were calculated using the Sturges algorithm (Sturges 1926), which finds natural breaks points in continuous data distributions, thus reducing analytic bias.

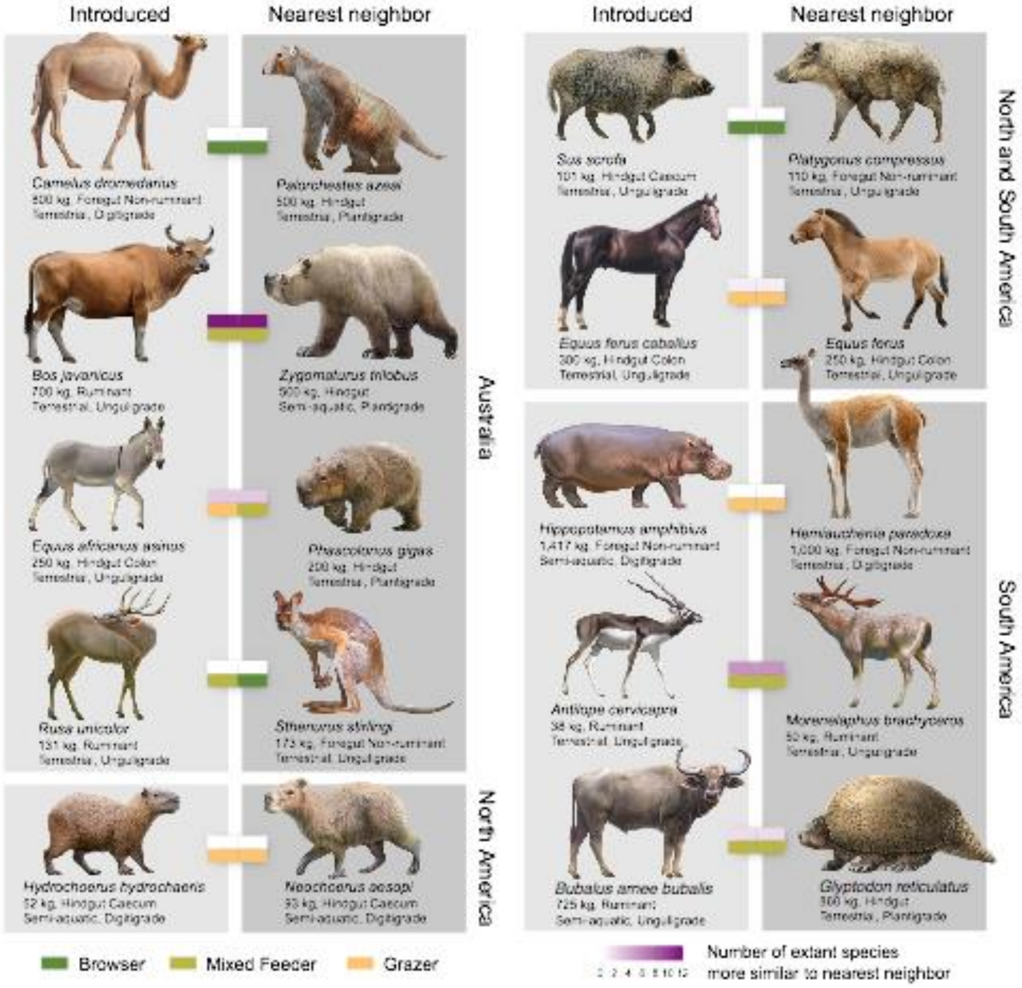

Figure 3. Select introduced herbivores and their extinct nearest neighbors in those continents most impacted by extinctions and introductions. The color of the top bar indicates the number of extant species (per body mass bin and climate zone) that are more similar to the nearest neighbor than the introduced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

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 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 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 (Doughty et al. 2016). These functions are primarily influenced by body mass and dietary guild—traits that control the *quality*, *quantity*, and *type* of vegetation consumed, with larger herbivores prone to greater dispersal distances and capable of digesting larger-quantities of fibrous, low-nutrient vegetation (Demment and Van Soest 1985, Owen-Smith 1988, Doughty et al. 2016). To understand how extinctions and introductions have affected these key metabolic functions, we categorized species into *functional groups* by combinations of body mass bins and dietary guilds.

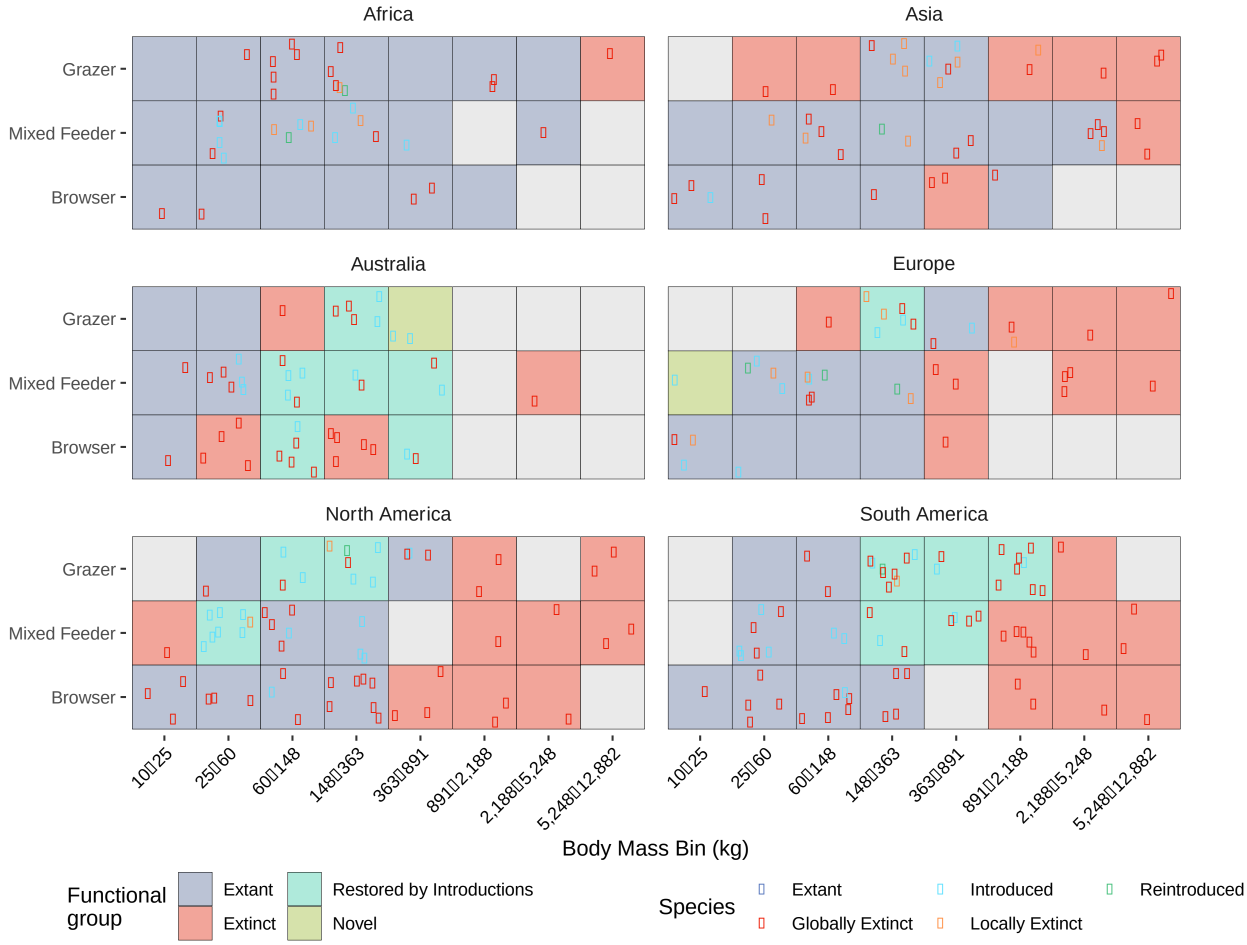

Figure 4. The loss and restoration of key metabolic ecosystem functions. Forty-four percent of introductions restore extinct functional groups, restoring 14 of 51 extinct dietary body mass groups across continents. Body mass groups were determined analytically with the Sturges algorithm, which finds 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.

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 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

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 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 promote grasslands, with implications for albedo, carbon storage, and wildfire (Cromsigt et al. 2018). Likewise, the widespread restoration of extinct large-bodied grazing functional groups, which are capable of bulk-grazing large quantities of low-nutrient grasses compared to smaller grazers, could reduce wildfire intensity (Cromsigt et al. 2018).

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. ferus*) and have restored lost trait combinations, such as large-bodied hindgut grazing. The effects of these species are poorly understood (e.g. Abella 2008) 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 to the benefit of endemic fishes (Kodric-Brown and Brown 2007) and an endangered amphibian (Bradford et al. 2004). 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 (Levin et al. 2002).

In other cases, introduced taxa are unrelated to extinct species in their new 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 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 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 (Johnson et al. 2018). Yet the extinct short-faced kangaroos (sthenurines) possessed monodactyl hoofs and an unguligrade morphology similar to 'open-plains' horses (Prideaux et al. 2009). However, rumination remains a novel trait in Australia, where macropods' non-ruminant foregut fermentation is less thorough (Hume 2002). It is therefore possible that some of Australia’s plants lack seeds capable of surviving ruminant digestive systems, which could lead to shifts in seed 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 (Orians and Milewski 2007). In a long-term experimental system in Northern Australia, seasonal bulk-grazing by introduced water buffalo (*Bubalus bubalis*) of fibrous, low-nutrient grasses, reduced wildfire and promoted tree establishment and survivorship through wildfire (Werner et al. 2006). 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 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 seemingly novel rooting behavior of wild boar (*Sus scrofa*) is thought to disadvantage native species across their extensive introduced range (Barrios-Garcia and Ballari 2012), several extinct species likely had similar foraging strategies, including *Platygonus compressus* (Koch and Barnosky 2006) in North and South America, and *Zygomaturus trilobus* (DeSantis et al. 2017) in Australia. Indeed, rooting by wild boar increases tree growth rates by mixing leaf litter into upper soil layers, enhancing decomposition rates and thus nutrient availability in eastern North American forests

(Lacki and Lancia 1986); and increases bird abundance by increasing accessibility of food resources in northern Australia (Natusch et al. 2017).

While the trait combinations of herbivores drive their functional capacity to affect ecosystems, their actual effects emerge in interaction with ecological contexts, such as predation (Wallach et al. 2015) and landscape connectivity (Boone and Hobbs 2004). Many apex predators continue to face declines (Ripple et al. 2014). Likewise, ongoing landscape fragmentation restricts herbivore movements and can lead to concentrated herbivory (Boone and Hobbs 2004). 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 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 (Smith et al. 2018). 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 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

We included all extant and extinct herbivore species ≥10 kg that lived the last 130,000 years, following taxonomy in the PHYLACINE v1.2 dataset (Faurby et al. 2018). Many analyses of LP extinctions have focused on species ≥44kg or 100kg, however, given that Australia lost all but one herbivore ≥44kg during the LP extinctions, we included herbivores ≥10kg to ensure that modern, native-only assemblages would have sufficient 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 (Smith et al. 2018) (SI Appendix, SI Text, Figs. 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. (2018), which primarily used fossil co-occurrence records to 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 (Schipper et al. 2008). Introduced species distributions, compiled from IUCN 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 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 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 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

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. (2003) and PHYLACINE v1.2 (Faurby et al. 2018) 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 (Kissling et al. 2014). While coarse, these two dietary categories remain paradigmatic to herbivore ecology in both ancient and modern systems, and reflect key evolutionary and ecological differences in herbivore dietary adaptations (Gordon and Prins 2019) (SI Appendix, Table S1, Text S1).

Fermentation type further influences the quality and quantity of vegetation herbivores consume, and the nutrient stoichiometry of resulting excreta (Demment and Van Soest 1985, Hume 2002). Fermentation type was collected as a categorical variable for five fermentation types following Hume (2002): 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 aquatic) (Table S1).

Limb morphology was included as it influences disturbance-related impacts on soils (Cumming and Cumming 2003) and is therefore frequently mentioned in relation to the non-analogy of introduced herbivores in Australia (e.g. Bennett 1999, Johnson et al. 2018). Furthermore, limb morphology is correlated with other ecological attributes such as cursoriality, fossoriality, and habitat constraints, which can otherwise be difficult to infer for extinct species (Brown and Yalden 1973, Polly 2007, Kubo et al. 2019), Limb morphology was obtained from a variety of peer-reviewed literature sources (primarily, Kubo et al. 2019) and was inferred based on family and order for extinct taxa if specific morphological studies (e.g. Janis et al. 2014) were unavailable. Limb morphology and was treated as three binary variables: digitigrade, plantigrade, and unguligrade (Table S1).

All trait data were cross-referenced with the primary literature or handbooks (e.g. Wilson and Mittermeier 2009-2019). 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 traits using the R package “Rphylopars” v. 0.2.9 (Goolsby et al. 2017) and PHYLACINE phylogeny. “Rphylopars” was run with all default parameters including a Brownian motion evolutionary model.

Analytic Methods

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 (Safi et al. 2011, Mazel et al. 2014).

We weighted traits when calculating Gower distance, with mass weighted by two; diet, fermentation, and habitat weighted by one; and limb morphology weighted half (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 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).

Multidimensional trait spaces were constructed using the function *dbFD* in the R package “FD” (Laliberté et al. 2014).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 been shown to distort functional relationships across a variety of real and simulated datasets (Maire et al. 2015). The relationship between PCoA axes and traits was determined using the R function *envfit* in the R package “vegan” with 1000 iterations (Oksanen et al. 2019).

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 present, we focused on functional richness, which is a measure of the multidimensional volume of trait space (Villeger et al. 2008). 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) (Baselga et al. 2018), which returns a Sørensen dissimilarity metric 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 (Kottek et al. 2006) climate zones to prevent comparing species with different physiological tolerances (e.g. arctic species 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* *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 (Sturges 1926), 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 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 (grazer, browser, and mixed feeder) was classified from the twin ordinal diet scores for graze and browse (see Table S1).

Supplemental Information

Species List Sensitivity

We conducted our analyses using the dataset published in PHYLACINE (Faurby et al. 2018). However, other species lists for the LP exist and can differ drastically. One such dataset, published by Smith et al. 2018 (Smith et al. 2018), contains 3 fewer total species than PHYLACINE, but 26 more extinct species and 33 fewer extant species (Fig. S4). These differences show a taxonomic signal, with Smith et al. 2018 reporting more extinct perissodactylas and diprotodons, and PHYLACINE reporting more extant cetartiodactylas and primates (Fig. S4)

To understand if discrepancies between PHYLACINE and Smith et al 2018's species lists and others could affect our results, we conducted all major analyses using the species list published in Smith et al. 2018. However, unlike Smith et al. 2018, who analyzed Europe and Asia as Eurasia, we chose to analyze our data with Europe and Asia separate, given their divergent socio-biogeographic histories since the LP.

Overall, we found strong concordance between the results using either PHYLACINE or Smith et al. 2018's datasets (Fig. S5-S7). Changes in species richness from extinction and introduction remained largely the same (Fig. S5), as did changes in functional richness (e.g. volume of trait space) (Fig. S6A and C). The functional beta diversity results (e.g. whether change in trait space reflects increasing similarity or dissimilarity) were qualitatively the same except for in Eurasia, where total dissimilarity *increases* slightly from introductions (Fig S6B and D). This is because of the absence of certain extant species in Smith et al. 2018's dataset, leading to the introduced red-necked wallabies (*Macropus rufogriseus*) falling outside of native-only functional space. Finally, the percent of introduced species most similar to extinct taxa varied only by decimal points between datasets, remaining at ~64%. This final analysis was not fully comparable between datasets as we did not have climate distributional data to constrain pairings for the Smith species list.

Trait Resolution

We chose traits that are strongly supported by empirical literature to influence the ecology of herbivores. All studies have inherent scales, meaning that the ecological patterns that emerge are dependent upon the scale chosen (Levin 1992). Our interest was to encapsulate herbivore trait variation over the last 100,000 years of Earth's history, which drives the emergent functional capacity of herbivore assemblages. Unwarranted precision in trait estimates at these broad spatiotemporal scales could lead to an artificial over-emphasis of ecological difference (e.g. every species becomes functionally unique), given the broad ranges of variation within species (Asevedo et al. 2012, Davis and Pineda-Munoz 2016, Rivals and Lister 2016). Likewise, organismal responses (e.g. of plants to herbivory) are unlikely to be so tightly coevolved with herbivore traits (e.g., lock-and-key coevolution) but rather driven by diffuse coevolution with suites of species (Jablonki and Sepkoski 1996). We therefore used categorial variables to capture fermentation type, limb morphology, and habitat use (SI Appendix, Table S1).

We collected two ordinal variables to describe diet, varying from 0-3 in importance, for browse and graze. While, diet is often treated categorically (e.g. Smith et al. 2015), our ordinal diet scores allowed a higher degree of resolution than in most studies to distinguish between obligate grazers, mixed-feeders, and browsers. Given the impossibility to separate fruit consumption from browsing among fossil taxa, frugivores were considered browsers. The consumption of bamboo was considered browsing, as its heavy lignification makes it more chemically similar to wood than to grass (Van Soest 1996). Dietary data was collected from a variety of peer reviewed sources and either collapsed into the ordinal scale from continuous data (e.g. stomach contents, isotope values) or from expert estimates (e.g. a “specialized grazer” would receive a 3 for graze and a 0 for browse). These two ordinal scores provided a high degree of resolution in dietary trait values, while still encapsulating intra-specific variation.

Grazing and browsing remain paradigmatic axes of dietary differentiation among herbivores, involving a suite of evolutionary adaptations in cranio-dental morphology, tooth-enamel hardness, and skull morphology that have appeared independently in all major herbivore lineages (Gordon and Prins 2019). Likewise, these axes of dietary differentiation control the capacity of herbivores to affect broad components of vegetation and drive downstream effects on global processes, such as climate (Cromsigt et al. 2018). The differentiation between grazers and browsers are keystone to many studies of herbivore ecology, both in extant and extinct systems (Janis et al. 2000, Hempson et al. 2015a, Cromsigt et al. 2018, Faith et al. 2019).

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