Extant native and alien herbivores and carnivores retain substantial capacity to restore late-Quaternary trophic structure

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Classifications: Biological Sciences – Ecology

Key words: Herbivores, Predators, Late Pleistocene, Food web, Recovery, Ecosystem functions, Trophic structure

Abstract:

Global ecosystem restoration seeks to recover ecological functions and trophic integrity. However, late-Quaternary extinctions and range contractions of large mammals have simplified modern ecosystems. The extent to which trophic structure can be rebuilt by surviving species remains unclear. We assess the capacity of extant native and already-introduced alien large herbivores and carnivores to restore herbivore diversity, functional potential, and food-web structure across North and South America, Europe, and Australia. Using species distribution models, trait-based functional metrics, and probabilistic predator–prey networks, we find that extant native and alien herbivores occupy limited, largely non-overlapping portions of their climatically suitable ranges. Expanding native herbivores to potential ranges could reduce herbivore diversity deficits by ~38% on average; range expansion of native and alien herbivores restores ~50% of lost herbivore diversity, with aliens contributing complementary grazing functions where native faunas are depauperated. Recovery of total herbivore biomass is nonetheless constrained by megaherbivore loss. Predator distributions strongly shape trophic structures. Only about half of alien herbivores currently co-occur with suitable predators, but carnivore expansion to potential ranges could raise this to ~90%, and recover nearly one-third of pre-extinction trophic links. Even without carnivore recovery, partial, mesoherbivore-dominated assemblages restore more functional potential and trophic connectivity than persistently defaunated systems. Together, these results show that extant native and alien herbivores and carnivores retain substantial capacity to rebuild trophic structure, with larger-bodied herbivores providing disproportionate functional gains and carnivore recovery maximizing regulation and food-web connectivity.

Significance statement: Large mammals play key roles in regulating ecosystems, yet much of the world lost its large herbivores and predators following late-Quaternary extinctions. Whether

today's surviving species can restore these lost functions remains uncertain. Using continental-scale analyses across four continents, we show that extant native and established herbivores retain substantial potential to rebuild herbivore diversity and functional composition if allowed to recover and expand into suitable habitats. Introduced herbivores provide complementary functions, especially grazing. We find that current predator distributions limit top-down control of alien herbivores, whereas predator recovery could regulate most alien populations and markedly increase food-web complexity. Together, our results show that restoring ecosystem functions requires coordinated recovery of both herbivores and large carnivores to rebuild resilient food webs.

Introduction

The Global Biodiversity Framework sets ambitious goals for the restoration of ecosystem functions and ecological integrity, with trophic structure forming a central component of ecological integrity through its regulation of energy flow, species interactions, and ecosystem stability (1). Restoring biodiversity therefore requires not only increasing species numbers, but also rebuilding the trophic complexity that sustains ecosystem processes (2).

The late Quaternary saw the extinction of most large-bodied mammals across the world, profoundly restructuring ecosystems and reducing trophic complexity (3, 4). This collapse involved not only extinctions but also widespread population and range declines among surviving wild megafauna, with genomic evidence showing >90% reductions in global abundance, biomass, and energy turnover over the past 50,000 years, largely linked to the expansion of *Homo sapiens* (5). These declines have left modern ecosystems strongly simplified, with herbivore and carnivore guilds that are functionally and spatially impoverished compared to pre-anthropogenic baselines, and the profound loss of ecosystem functional roles

related to nutrient cycling, seed dispersal, and food-web stability (6–9).

To address this deficit, trophic rewilding has emerged as a key restoration strategy aimed at reinstating top-down trophic interactions and self-regulating ecosystem dynamics through the recovery or reintroduction of large animals (2, 4). Trophic rewilding is a forward-looking approach that seeks to promote ecological functionality and biodiversity under increasingly novel biosphere conditions, rather than to reconstruct fixed historical states. It includes both the return of extirpated native species and, where appropriate, the introduction of non-native herbivores and carnivores as ecological surrogates for extinct taxa (9–12).

Accumulating evidence indicates that such alien species can contribute to restoring key ecological functions—enhancing vegetation heterogeneity, seed dispersal, nutrient cycling, and habitat creation (13–18). Especially, alien herbivores have recovered approximately 40% of the global herbivore functional trait space lost as a consequence of Late Pleistocene extinctions at a continental scale (12). Yet, the spatial and trophic dimensions of restoring lost functions remain poorly resolved. Can native and alien herbivores jointly rebuild herbivore diversity and trophic links at continental scales, or are their contributions geographically constrained and overlapping? Regional analyses indicate that alien herbivores could substantially enhance diversity in parts of the southeastern United States if allowed to expand (19), but broader patterns remain unclear.

Despite this potential, alien herbivores also raise ecological concerns. In the absence of large carnivores, some species may escape top-down control and become overabundant, leading to habitat degradation, human-wildlife conflicts, and biodiversity loss (20–22). Similarly, alien carnivores may overexploit native prey if their densities are too high. While the large herbivores whose body mass exceeds 500 kg are constrained by resource availability rather than top-down predation (23, 24), most current alien herbivores are medium-sized species (15–100 kg) (25), which are typically regulated by large predators in intact ecosystems

(26), but may be free from top-down regulation outside their native range (but see 27). Thus, understanding the spatial match between herbivores and their potential predators is critical for evaluating the feasibility and risks of rewilding with alien species.

Large herbivore loss has also disrupted food webs, led to the extinctions of multiple large carnivores, and decreased food-web stability (28–31). Moreover, surviving large carnivores now occupy highly fragmented and incomplete distributions, which may further impede the restoration of trophic interactions and constrain food-web recovery (28, 32). Recent work highlights that rewilding aims to rebuild food-web complexity and stability through trophic reassembly and rewiring, rather than simple species recovery (29, 33). The expansion of native and alien herbivores and carnivores could potentially re-establish trophic links and restore food-web dynamics, yet this possibility has been explored only in isolated case studies (e.g., 16, 34, 35), and the extent to which food-web structure can be restored through the joint expansion of herbivores and carnivores remains unknown. Trait-based modelling frameworks now allow robust estimation of trophic interactions, offering a novel opportunity to evaluate food-web rewiring across space (29).

Here, we provide the first continental-scale assessment of how surviving wild large herbivores and carnivores—both native and alien—can contribute to the restoration of herbivore diversity, functional composition, and trophic complexity, in comparison to a present-natural baseline (the state that ecosystems would exhibit today in the complete absence of human influence through time, 2) (Figure 1). We focus on four continents with massive megafauna extinctions and also ample species spatial records: North and South America, Europe, and Australia (4). Specifically, we ask four interrelated questions:

1. To what extent can extant native herbivores, if allowed to expand to their climatically suitable ranges, reduce deficits (compared to present-natural baseline) in herbivore diversity and functional composition across continents?

2. Do alien herbivores provide complementary or redundant contributions to herbivore diversity and functional restoration relative to native species, and how does this vary geographically?
3. To what degree do current and potential large-carnivore assemblages provide top-down control of alien herbivores, and how does predator recovery alter this potential regulation?
4. How do alternative restoration scenarios involving herbivore and carnivore expansion influence large-mammal food-web complexity relative to present and present-natural baselines?

To address these questions, we compare current herbivore assemblages with two expansion scenarios: (*i*) potential range expansion of native herbivores alone and (*ii*) joint expansion of native and alien herbivores across all climatically suitable areas. We then evaluate how these herbivore scenarios, combined with current and potential carnivore distributions, affect trophic regulation and food-web link density. Together, these analyses reveal the global opportunities and constraints for functionally informed trophic rewilding, highlighting where surviving species—native and alien—could most effectively rebuild the diversity and ecological complexity of herbivore guilds in the Anthropocene.

Results:

Large herbivore diversity and restoration potential

We began by comparing modern mammalian herbivore richness across the four continents (Figure 2A-B, Figure S2 in Supporting information). The current richness of native large-bodied herbivores (body mass >15kg) is generally low, averaging 0.94 (± 1.32 SD) species per 100 × 100 km grid cell across continents (Figure 2A). Among regions, mean richness is highest in Europe (1.49 on average), followed by North America (0.99), South America (0.77), and

lowest in Australia (0.48) (Figure 2A). Alien herbivores show a lower mean richness (0.46 ± 1.05) but a distinctly different spatial pattern, peaking in Australia (0.65), followed by North America (0.52), Europe (0.49), and South America (0.39) (Figure 2B). Hotspots of current native and alien richness are largely non-overlapping: native species concentrate in the Alps and Iberian Peninsula (Europe), Rocky Mountains (North America), and Andes Mountains and tropical grasslands (South America), whereas alien richness peaks in western Europe, Texas, and Pampas. In Australia, both groups are richest in southeastern Australia (Figure 2A-B).

We then evaluated how existing alien herbivores, as well as the potential expansion of native and alien herbivores into all climatically suitable areas, could reduce current richness deficit (the difference between current native richness and present-natural baseline, 36). Without human impacts, the present-natural richness of large herbivores is on average 17.09 (± 9.80) species per grid cell, and current richness deficit is 15.68 (± 9.63). Present-day alien herbivores offset this deficit by only 4.97% (± 14.3%) across space. If native herbivores expanded, the deficit would decline by an average of 37.5% (± 25.5%) across space (Figure 2C), with the greatest recovery in Australia (71.1%). Allowing both native and alien herbivores to expand increases recovery to 52.7% (± 26.8%), led by Australia (91.1%) and Europe (56.1%), but less in South America (44.4%), and North America (42.8%) (Figure 2D).

Notably, the potential contributions of alien herbivores are largely spatially complementary to those of native species. Alien-driven recovery is concentrated in introduction hotspots such as the southern United States, the Pampas and Patagonia, and western Europe (Figure 2D), whereas native herbivores contribute more strongly in mountainous regions, deserts, and tundra areas (Figure 2C).

Restoration of Functional composition

Beyond species richness, we quantified the functional composition of herbivore assemblages using three trait-based metrics: total body mass (sum of body mass across species, kg), total

grazing intensity (sum of species grazing level 1-4), and total browsing intensity (sum of browsing level 1-4). These metrics represent key dimensions of herbivore impacts on ecosystems and were derived from the *HerbiTraits* database (37). Although species abundance data were unavailable, we interpret summed trait values as proxies for ecosystem functional potential, consistent with evidence that herbivore effects on ecosystem processes can be additive (38, 39). Analogous to the richness analyses, we quantified current functional deficits—defined as deviations between current native functional composition and present-natural baseline—and evaluated the extent to which existing alien species and the potential range expansion scenarios could offset these deficits.

For the total body mass of herbivore assemblage (Figure 3A-C), current alien herbivores compensate for only 4.1% (± 17.3% SD) per grid cell of the deficit. Even under a scenario where herbivores could expand their distributions, restoration of total herbivore body mass compared to present-natural baseline remains limited: the expansion of native species would achieve a 16.6% recovery (Figure 3A) and allowing alien herbivores to expand further only increases restoration by 6% (Figure 3B). Most body mass recovery occurs in Australia, whereas other continents show <15% recovery (Figure 3C).

For grazing intensity of herbivore assemblages, current alien herbivores restore 5.8% (± 15.4%) of the deficit. Native expansion alone could restore 32.9% (Figure 3D), while the inclusion of alien expansion adds a further 18.3% (Figure 3E), bringing total recovery to 51.2% (± 30.2%). Thus, alien herbivores account for more than one-third of the total grazing recovery under full expansion, highlighting their important and complementary role in restoring grazing functions. Their contribution is particularly strong in Australia (20.9%) and South America (19.8%) (Figure 3F). For browsing intensity, current alien herbivores reduce the deficit by 5.7% (± 14.9%). Native expansion could restore 38.6% (± 25.3%; Figure 3G), and combined native and alien expansion increases recovery to 53.3% (± 25.9%; Figure 3H).

Together, these results show that while native species dominate global restoration potential, alien herbivores may play important complementary roles. Because citizen-science records may occasionally misclassify domestic individuals as feral, we conducted a sensitivity analysis excluding all domestic taxa (Appendix S2, Supporting Information). Excluding domestic species yielded patterns similar to the main results, with non-domestic alien herbivores contributing little to current deficit reduction but substantial potential recovery under range expansion. Native domestic species add only minor additional restoration (~2–3%), whereas alien domestic species account for a larger share (~10%) of further deficit reduction.

Predation controls on alien herbivores

We also estimated the current spatial distributions of 14 large carnivores (body mass ≥ 10kg). Most species now occupy narrow ranges, except *Canis lupus* (including wolves, feral dogs and dingoes here), which remains widespread. Using a trait-based deep learning model (29), we estimated the predation probability (0–100%) between each co-occurring herbivore–carnivore pair for every grid cell. When multiple predators overlapped with an herbivore, we retained the highest probability as its likelihood of top-down control. Currently, alien herbivores experience an average 52.3% (± 47.5% SD) chance of being subject to predation (here predation means with the existence of suitable predator) across grid cells (Figure 4A), with higher probabilities in North America (67.7%) and South America (63.9%), intermediate in Europe, and lowest in Australia (14%).

If alien herbivores expand to all suitable climates, their average predation probability decreases to 43.3% (± 46.8%), with similar continental patterns (Figure 4B). However, if all large predators also expand to their potential ranges, the mean probability of predation on large herbivores increases sharply to 90.7% (± 23.4%) per grid cell (Figure 4C). These results highlight the central role of carnivore range recovery in restoring effective top-down control of alien herbivores.

Across all scenarios, *Canis lupus* and *Puma concolor* contribute most to predation on alien herbivores (contribution calculated as the sum of predation probability to alien herbivores across grid cells), followed by *Panthera onca* and *Ursus arctos* when both predators and herbivores expand (Figure 4C). One reason for the high contribution of *Canis lupus* is that we combined wolves, feral dogs, and dingoes, as they belong to the same biological species, despite their somewhat different behaviors and ecological impacts in the field (40).

Food web complexity

Beyond just the predation on alien herbivores, we also used the trait-based deep learning model to estimate the food web structure (i.e., link density) formed by interactions between large herbivores and carnivores, under different scenarios. The food web of present-natural scenario on average has 62.2 (± 53.1 SD) links per grid cell (Figure 5, Figure S3 in Supporting information). However, current native species only have on average 0.99 (± 2.6) links per grid cell, because most areas have been lacking large carnivores, and have a limited number of large herbivores (Figure 5B). Considering alien species improves this value to 1.4 (± 3.6). Assuming native herbivores expand their ranges, the mean number of links rises to 3.17 (± 5.4), while if alien species also expand, the mean number of links grows further to 4.89 (± 8.1). If large carnivores expand to suitable climatic ranges as well, then the number of food web links increases to 21.3 (± 15.7), although it is still much lower than that estimated for the present-natural scenario (34.3% of it). This suggests that the main limiting factor shaping current food webs is carnivore distribution. The strong increase in potential predator control under carnivore expansion is especially relevant for Australia, where the dingo (*Canis lupus dingo*) represents the sole surviving large predator, and no other native or alien species currently fill this trophic role (Figure 5A).

Discussion:

Achieving the goals of global ecosystem restoration requires rebuilding the trophic interactions and functional roles that underpin ecological integrity and ecosystem resilience. This study provides a continental-scale assessment of the extent to which extant native and alien herbivores and carnivores can rebuild trophic structure in ecosystems that have been profoundly simplified by late-Quaternary defaunation. We show that, although full restoration of present-natural conditions is precluded by the loss of megaherbivores and largest apex predators, surviving mammal assemblages nonetheless retain substantial capacity to recover herbivore diversity, functional composition, and trophic connectivity. Native herbivores account for most potential gains, while alien herbivores contribute complementary functions, particularly in regions where native faunas remain depauperate. Importantly, even partial, mesoherbivore-dominated recovery restores markedly more trophic interactions and functional heterogeneity than persistently defaunated conditions. At the same time, our results demonstrate that recovery is strongly modulated by predator presence—through enhanced top-down regulation and food-web connectivity—and remains incomplete relative to present-natural baselines, underscoring both the opportunities and the limits of trophic reassembly in the Anthropocene.

Restoring herbivore diversity and functional composition by native and alien herbivores

Before the late-Quaternary extinctions, the Americas, Europe, and Australia supported exceptionally diverse large-herbivore assemblages spanning multiple major clades and ecological roles, including proboscideans, large bovids, rhinos, equids, ground sloths, and giant marsupials (4). The extinctions of those species caused losses of herbivore functions, leading to reduced seed dispersal, altered nutrient cycling, collapse of many large carnivore guilds, and woody encroachment (3, 10, 30, 41–44). Today, only a small and functionally truncated subset of this fauna remains, generally smaller-bodied and more browser-dominated (4). Moreover, most extant native species only occupy a small fraction of their potential distribution because

of population declines and extirpations in native species (45). Although reintroducing native herbivores is central to restoration efforts (46, 47), our analyses suggest that even full climatic-range expansion of natives would recover on average only ~38% of the herbivore deficit. The strongest recovery is predicted in regions that originally had relatively low herbivore diversity, such as the inland deserts of Australia, as well as in mountainous areas with relatively high current diversity (Figure 2C), highlighting both opportunities and inherent limits of native-only strategies.

Although alien herbivores expand functional trait space at continental scales (12, 48), their current contributions are spatially restricted. Their richness is concentrated in a few regions—such as the Pampas and Patagonia, Texas, southeastern Australia, and western Europe—largely shaped by colonial history, agricultural or hunting introductions, and management constraints (19, 25, 49). If expanded into climatically suitable areas, they could substantially complement native recovery, particularly by restoring grazing functions, as alien assemblages often include large grazers (e.g., horses, cattle, antelopes). However, most alien species are mesoherbivores, limiting their ability to restore total biomass, and the unique functions of true megaherbivores (>1000 kg) remain irreplaceable. Importantly, even incomplete, mesoherbivore-dominated expansions are typically preferable to persistent defaunation: mesoherbivores restore substantial biomass, trophic interactions, and ecosystem functions relative to long-term herbivore absence (50, 51). Finally, because our estimates are based on potential occurrence rather than abundance, incorporating demographic and density data would refine assessments of restoration potential in future studies.

Top-down controls on alien herbivores

A central concern with alien herbivore introductions is the risk of overabundance in the absence of predators, leading to habitat degradation and damage to agriculture (20). Top-down regulation from carnivores is therefore a critical mechanism to mitigate potential negative

impacts. There has been evidence that native predators can prey upon alien herbivores: for instance, cougar preys on feral donkeys and horses in the western United States (27, 52), and dingoes prey on wild pigs, deer, and goats in Australia (53, 54). Our analyses suggest that although most alien herbivores have ecologically suitable predators on each continent, predator distributions remain fragmented, limiting spatial overlap (Figure 4). Expanding large carnivores into climatically suitable ranges could substantially enhance potential regulation, particularly for *Canis lupus* globally and *Ursus arctos*, *Puma concolor*, and *Panthera onca* regionally. However, because we consider predator occurrence rather than abundance, effective control may be overestimated; currently many large carnivores persist at densities too low to exert strong top-down regulation (32, 55). Restoring geographic ranges alone is therefore insufficient—viable population densities are also essential.

Food web restoration

Beyond direct top-down control, the expansion of herbivores and carnivores has broader implications for food-web restoration. The late-Quaternary extinctions and range contractions of large herbivores, along with direct persecution by people, triggered cascading losses of large carnivores and dismantled complex trophic networks (3, 30, 31, 43). Our analyses show that the expansion of both herbivores and carnivores could substantially increase food-web complexity relative to present conditions (Fig. 5), helping to re-establish key ecological processes such as energy transfer, population regulation, and nutrient cycling. We emphasize, however, that the frequency and effectiveness of trophic interactions to reinstate ecosystem functions would still depend on the local abundances of predators and prey.

Although alien herbivores have more limited overall contributions than natives due to smaller potential ranges, they can partially fill vacant trophic niches left by extinct megafauna, particularly in regions where native herbivores remain scarce (56). For example, feral horses and wild pigs constitute important prey for *Puma concolor* and *Canis lupus* in parts of North

America, while red deer support large carnivores in South America (57, 58). However, it is also concerning that in some systems, subsidized predators may also exert indirect pressures on native prey via apparent competition (59). For instance, besides alien herbivores, the expansion of feral dogs, as an alien carnivore, also poses direct threats to native wildlife in some regions (60–62). Such contrasting outcomes highlight that alien species can either stabilize or destabilize food webs depending on predator assemblages, prey availability, and spatial context.

Realizing the restorative potential of food webs ultimately depends on the recovery and expansion of large carnivores (Figure 5) (32, 63). Recent recolonization of wolves and bears in Europe demonstrates that recovery is feasible under reduced persecution and improved connectivity (64, 65), but reconstructed food webs remain distant from Late Pleistocene baselines due to the extinction of many specialized apex predators (31, 35). While full trophic restoration is optimal, partial recovery still represents an ecological improvement over simplified, defaunated systems.

Conclusion

Our analyses show that extant large mammal assemblages retain substantial capacity to rebuild trophic structure in ecosystems simplified by late-Quaternary defaunation. Range expansion of native herbivores could recover a significant share of lost diversity and functions, with alien herbivores providing complementary contributions, particularly for grazing. Although the loss of megaherbivores constrains full recovery of biomass and key ecosystem-engineering roles, even mesoherbivore-dominated assemblages substantially enhance functional potential and trophic connectivity relative to persistently defaunated systems. Recovery of large carnivores further amplifies these gains by strengthening top-down regulation and food-web connectivity. Without carnivore recovery, trophic structure remains simplified and mesoherbivore dominance may pose management challenges, though such systems may still represent clear improvements on several functions over long-term defaunation.

Together, these findings suggest that substantial progress toward global ecosystem restoration goals is partly achievable through the recovery of surviving large mammals. Restoring the range and populations of extant herbivores yields meaningful ecological gains, and coordinated carnivore recovery maximizes regulation and network complexity.

Materials and Methods

Method Overview

In this study, we focused on large herbivores (≥15 kg) and carnivores (≥10kg) across four continents—North America, South America, Europe, and Australia—where late-Quaternary extinctions have been especially severe. We excluded Asia and Africa due to their relatively low extinction rates, and also the limited availability of citizen science data.

We first compiled iNaturalist records to model the current distributions of native and alien large herbivores and carnivores. We then estimated the potential distribution of alien herbivores by projecting their realized climatic niches—derived from their native ranges—to new regions. Comparing these scenarios with a present-natural baseline, we assessed the extent to which range expansions by native and alien herbivores could contribute to the restoration of herbivore diversity and ecosystem functions. To assess trophic interactions, we used a recently developed deep-learning model based on species traits (29) to predict predator–prey relationships at the grid-cell level. This allowed us to estimate: (*i*) the contribution of alien herbivores to food web restoration, and (*ii*) whether local predator assemblages are likely to exert top-down control on alien herbivores.

Species data

For herbivores, we focused on terrestrial mammalian herbivores ≥15 kg, primarily from the orders Perissodactyla and Artiodactyla, as well as Diprotodontia (in Australia) and Caviidae

(*Hydrochoerus* in South America). Analyses were limited to mainland regions of the four focal continents. For Oceania we only included Australia - New Zealand was excluded in the analyses because it lacks large mammalian herbivores before human colonization, while New Guinea was also excluded because of the low sampling effort. Established alien herbivores (species with established populations in non-native continents) were identified using the book *Introduced Mammals of the World* (25) and iNaturalist occurrence data (Table S1, Supporting information). In most cases, species listed in *Introduced Mammals of the World* had corresponding iNaturalist records within their introduced ranges. Exceptions, such as *Camelus dromedarius* and *Capreolus capreolus* in North America, were excluded following literature review indicating failed or no longer extant populations. To maintain conceptual consistency, species that were historically native to a continent but went extinct and were later reintroduced by humans, such as *Equus caballus* in North America (66) and *Ovibos moschatus* in Europe (67), were treated as alien species in our analyses.

Some species presented ambiguous establishment status, particularly when iNaturalist records were sparse (<10) and not referenced in *Introduced Mammals of the World* (25). For these cases, we followed a two-step verification: (*i*) literature searches (via Google Scholar) to check reports of self-sustaining populations; and (*ii*) contacting iNaturalist observers to determine whether sightings represented feral/wild populations. Species with unresolved status were excluded for reliability. A full list of retained species is provided in Appendix S1, Supporting information. For domestic species with extant wild ancestors, we merged records to represent the lineage as a whole (e.g., *Lama glama* merged with *Lama guanicoe***;** *Vicugna pacos* merged with *Vicugna vicugna*).

For predators, we included large terrestrial mammalian carnivores (body mass > 10 kg), including both native and alien species (i.e., *Canis lupus* (*dingo*) in Australia and South America), and excluded those species that are predominantly omnivorous (e.g., *Chrysocyon*

brachyurus). We merged North American wolves (*Canis rufus*, *Canis lycaon*) with *Canis lupus* due to taxonomic uncertainty, and also included feral dogs (*C. lupus familiaris*) and dingo (*C. lupus dingo*) within *C. lupus* because they are the same biological species, and have hybridization potential and ecological overlap (68). The final 14 predators include *Canis lupus, Canis latrans, Canis aureus, Lynx lynx, Lynx canadensis, Lynx rufus, Lynx pardinus, Panthera onca, Puma concolor, Ursus maritimus, Ursus arctos, Ursus americanus, Tremarctos ornatus, Gulo gulo*.

Species distribution modelling

We used georeferenced iNaturalist records (www.inaturalist.org) to estimate the distributions of large herbivores and predators. Large mammals are generally conspicuous and of high public interest, making them well-represented in citizen science platforms such as iNaturalist (69). To ensure data accuracy, we removed any records with location uncertainty greater than 10 km. Alien herbivore species with <50 records per continent (Appendix S1) were excluded from current distribution models but retained for potential distribution predictions, as their current ecological impact is limited and too few records do not support robust model training, and they also have limited impacts on introduced ecosystems. In sum, 22 alien herbivore species (33 in total) and 48 native species (57 in total) were included in current distribution analyses (Appendix S1, Supporting information).

We built species distribution models (SDMs) at 100 × 100 km resolution (so comparable with PHYLACINE) using presence-only records and four climatic predictors from WorldClim (1970–2000): *annual mean temperature, annual precipitation, precipitation of the driest quarter, and temperature seasonality* (70, 71). These variables represent the mean and variation of temperature and precipitation that could influence species distributions at large spatial scales, and we also excluded the climate variables with high correlation (Pearson's correlation > 0.8) to avoid collinearity problems. To correct spatial sampling bias, background points were drawn

proportional to iNaturalist record density using the '*sample_background()*' function from the FLEXSDM R package (72, 73). Models were fitted using random forest algorithms and evaluated via five-fold cross-validation, using *Area Under the Receiver Operating Characteristic Curve* (AUC) and *True Skill Statistic* (TSS) metrics. To address the potential overestimation of species' current distributions, we also generated range maps by buffering each presence point with a 100 km radius for each species, which captures the area accessible to our study species (74). Presence probabilities outside these buffered range maps were set to zero to better reflect current range limits.

To estimate potential distributions of alien herbivores, we compiled global iNaturalist occurrence data (native + introduced ranges) and calibrated SDMs using the same modelling framework. This approach better captures species' full realized climatic niches (75). Background points were sampled within each species' native continents only, because species absences outside their native geographic ranges are often strongly influenced by dispersal barriers and introduction history (e.g., the absence of white-tailed deer from much of Europe despite suitable climate). In this analysis, Eurasia and Africa were considered a single source region due to the lack of a biogeographic barrier, and North and South America were similarly grouped. The potential distributions of alien carnivores (only feral dogs and dingoes in South America and Australia) were also estimated in the same way.

For native herbivores and predators, we used present-natural range maps from PHYLACINE 1.2 (36) to represent potential distributions. This avoids underestimation for species with fragmented modern ranges and limited observation data.

Community-level richness and functions of herbivores

To quantify herbivore assemblage features, we converted continuous SDM outputs (occurrence probability) to binary presence/absence using the TSS-maximizing threshold. We then calculated species richness per grid cell for native, alien, and total herbivore assemblages. To

assess functional contributions, we extracted trait data from the HerbiTraits database (37), focusing on three traits: body mass (kg), grazing level and browsing level (scored 0–3; adjusted to 1–4 to avoid zeros). For each grid cell, we calculated three functional metrics based on species with predicted presence: (*i*). Total body mass – sum of species' body mass values across species; (*ii*). Total grazing intensity – sum of grazing scores; (*iii*). Total browsing intensity – sum of browsing scores. We used the sum values to represent community-level functional features because the functional roles of large herbivores are partially additive (38), and mean trait values can be strongly influenced by individual species given many grids only have one / two herbivore species. We did not calculate functional richness, as it requires at least three species per cell (76), a condition not met in many high-latitude regions in this study.

Comparing with present-natural baselines

To evaluate the extent to which native and alien herbivores could restore lost diversity and functional composition, we compared current and projected assemblages to a present-natural baseline from PHYLACINE 1.2 (36). This dataset includes the present-natural distributions of 5,831 known mammal species that existed from the last interglacial (~130,000 years ago) to the present, accounting for species that have since gone extinct since the Late-Pleistocene. Present-natural ranges refer to the potential species distributions under modern climate if they had not been subject to strong anthropogenic pressures (methodological details in Faurby et al. (36)). According to PHYLACINE 1.2, there were 193 large herbivore species, and 48 large carnivores in the four continents.

For each continent, we compared four scenarios of herbivore richness and functional composition with the present-natural baseline: *i) Current native herbivores only*; *ii) Current native + current alien herbivores*; *iii) Potential native herbivores* (native species occupying their full present-natural ranges, as per PHYLACINE 1.2) + *current alien herbivores*; *iv) Potential native and potential alien herbivores* - both native and alien species occupying their

full potential ranges. For each scenario, we calculated species richness, functional composition (total body mass, total grazing intensity, and total browsing intensity) for each grid cell. To estimate current richness / functional deficits (termed the 'current native deficit'), we subtracted the values in scenario ***i*** from the present-natural baseline. We then calculated the deficit restoration percentage for each scenario (*ii* – *iv*) as: Restoration % = (current native deficit - scenario deficit) / current native deficit × 100%. Values >100% were truncated to 100% to avoid skew from outliers.

Because some large herbivores have both domestic and feral populations, and citizen-science records may occasionally misclassify domestic individuals as feral, we conducted a sensitivity analysis excluding all domestic taxa (Appendix S2, Supporting information). This analysis allows us to evaluate the restoration potential of non-domestic extant species alone and assess the robustness of our results to possible reporting errors. Full details on species classification and sensitivity analyses are provided in the Supporting Information.

Estimating the predation relationship and food web metrics

To quantify trophic interactions, we estimated the probability of predation between co-occurring predator and herbivore species in each grid cell using the model developed by Fricke et al. (29). Predation probability between each carnivore–herbivore pair was estimated using a deep learning model trained on global predator–prey data, incorporating body mass, diet, habitat, and activity traits for both species. Body mass was included as a continuous predictor to capture the well-established scaling of predator–prey interactions with size ratios, ensuring ecologically realistic predictions of potential top-down control.

We extracted trait data from Fricke et al. (29) and used the model to predict predation probabilities for every co-occurring carnivore–herbivore pair across grid cells in this study. Specifically, twenty-one morphological and life-history traits (sourced from Soria et al. (77)) were used as predictors. We trained a multilayer perceptron (MLP) implemented in R via the

tidymodels framework (78) with Keras as the backend. The resulting model exhibited high predictive performance (AUC = 0.93), outperforming traditional logistic and phylogenetic approaches. We then calculated two sets of metrics across grid cells:

i. **The probability of predator control over alien herbivores**. For each grid cell, we quantified the probability that alien herbivore species were under potential predator control. When multiple predators overlapped with a given herbivore, we retained the highest predation probability to represent the likelihood of top-down regulation. We then averaged these probabilities across all alien herbivores within each grid cell. Three scenarios were compared: (i) both predators and alien herbivores restricted to their current distributions; (ii) alien herbivores expanded to all climatically suitable ranges while predators remained in current ranges; and (iii) both groups expanded to their potential ranges. Under each scenario, we also quantified the overall contribution of each predator species as the sum of predation probability to alien herbivores across grid cells.

ii. **Food-web link number.** To assess overall food-web complexity, we binarized predation probabilities using a 0.5 threshold and counted the total number of realized predator–prey links per grid cell. We compared six scenarios: (1) present-natural baseline; (2) native herbivores with carnivores in current ranges; (3) all current herbivores (native + alien) with carnivores in current ranges; (4) native herbivores expanded while alien herbivores and carnivores remained in current ranges; (5) all herbivores expanded while carnivores remained in current ranges; and (6) all herbivores and carnivores expanded.

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Figures

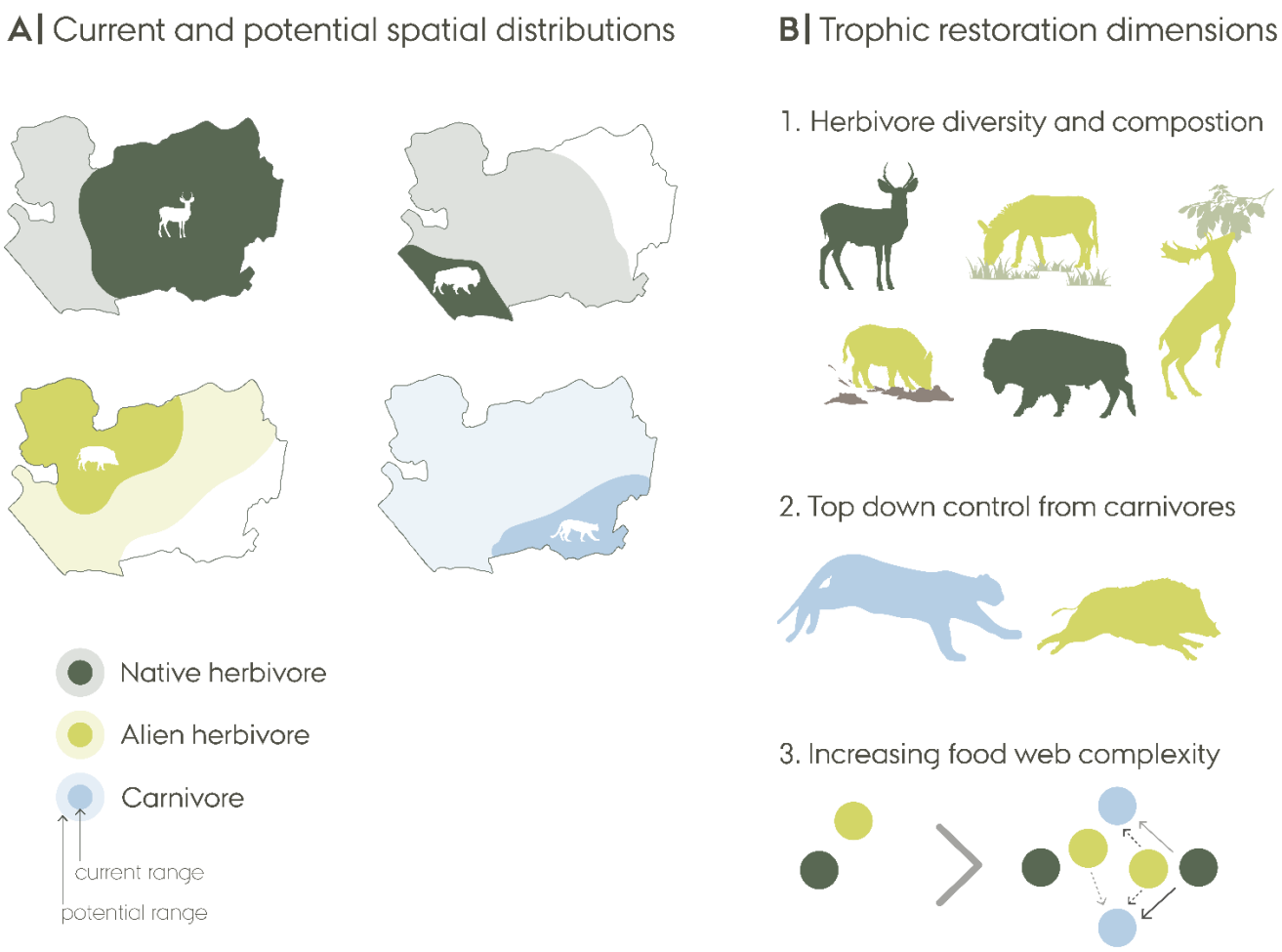


Figure 1. Conceptual diagram of this study. (A) We estimate the current and potential spatial distributions of large native and alien herbivores, and carnivores. Darker shading indicates current distributions; lighter shading represents potential distributions based on climatic suitability. (B) We assess three dimensions of trophic restoration: (B-1) the extent to which native and alien herbivores currently contribute—or could contribute under range expansion—to restoring herbivore diversity and functional composition; (B-2) the degree to which carnivores could regulate alien herbivores across regions, and (B-3) the potential for alien herbivores to restore food web complexity. In (B-3), dashed lines indicate carnivore predation on alien herbivores, while solid lines represent predation on native herbivores; black lines represent predation under current scenario of herbivore distribution, while grey lines represent range expansion scenario.

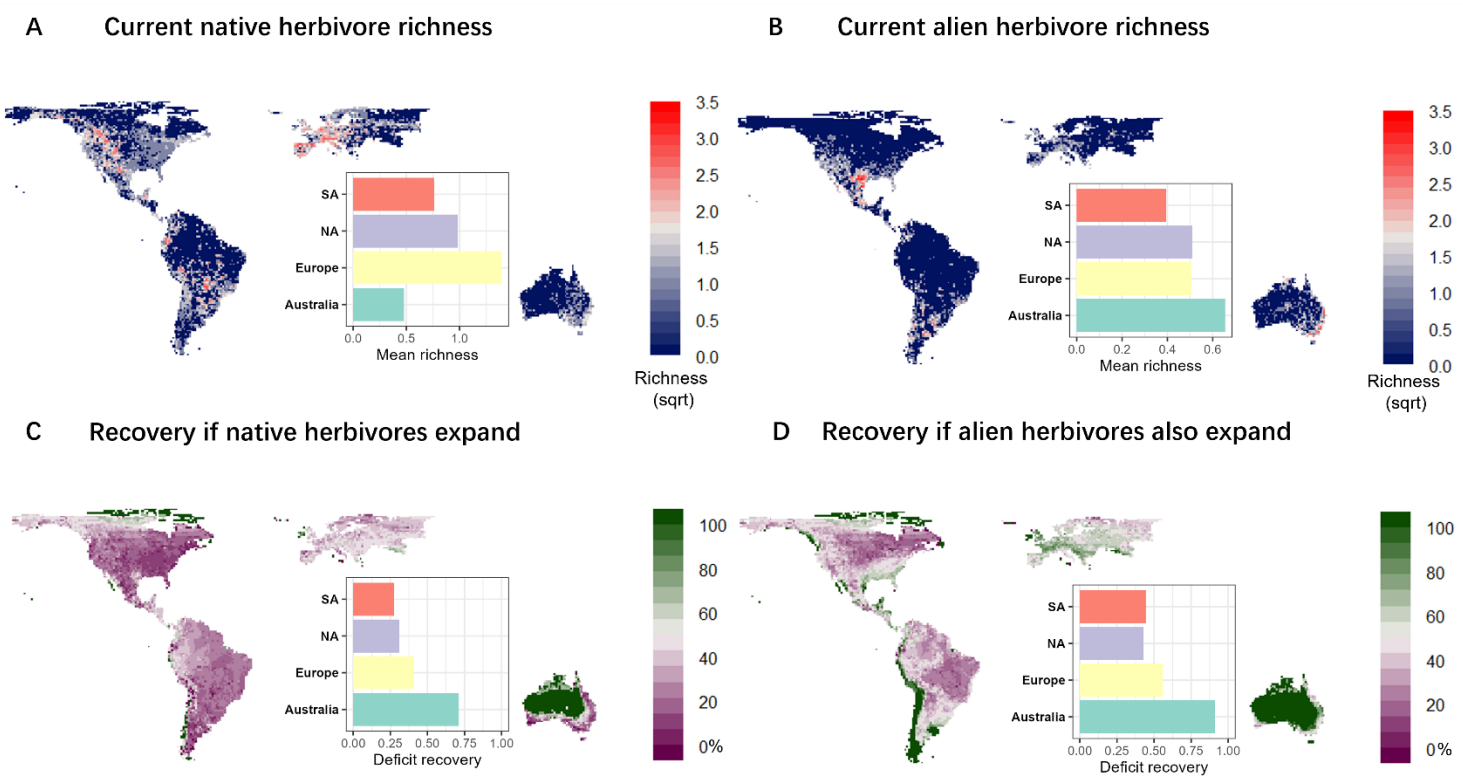
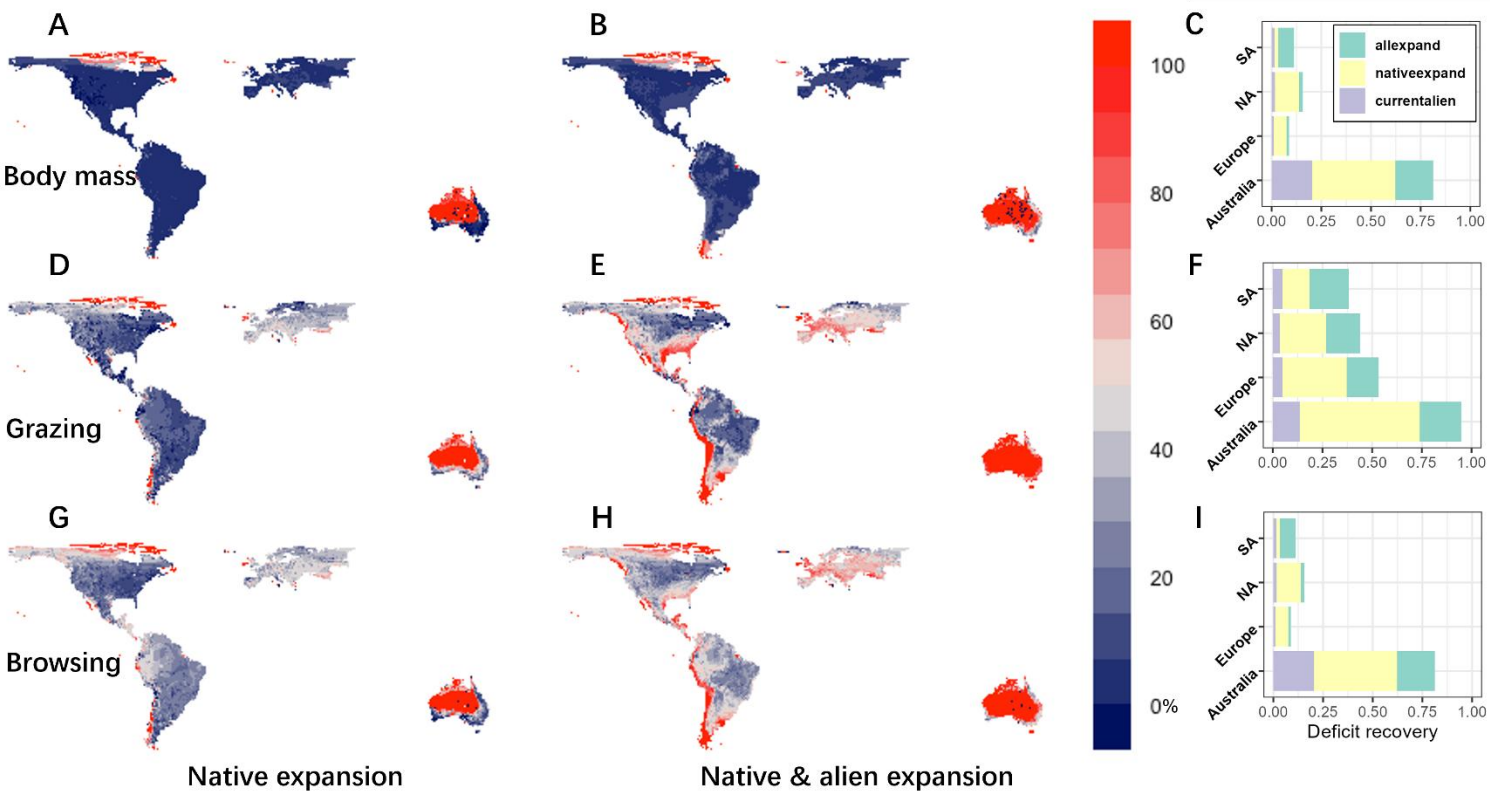


Figure 2. Current species richness pattern of native (A) and alien (B) large herbivores (square-root transformed to improve visual differentiation). Bar plots show the mean richness per 100 × 100 km grid cell for each continent. Recovery of richness deficits under two scenarios: native herbivores expand to their potential ranges (C); both native and alien herbivores expand to their full potential ranges (D). Greener colors indicate greater recovery of lost diversity (100% represents full recovery). SA refers to South America, and NA refers to North America.



713 **Figure 3.** The restoration of the functional deficits of herbivore assemblages (sum of body mass:
714 A-C; sum of grazing level: D-F; sum of browsing level: G-I) under two scenarios – if native
715 herbivores expand (left column), and if both native and alien herbivores expand (middle
716 column). The average deficit restoration per grid cell was also compared between continents
717 (right column): 'currentalien' represents the contribution of current alien herbivore distributions;
718 'nativeexpand' represents the scenario if native herbivores expand, 'allexpand' represents the
719 scenario if both native and alien herbivores expand. SA refers to South America, and NA refers
720 to North America.

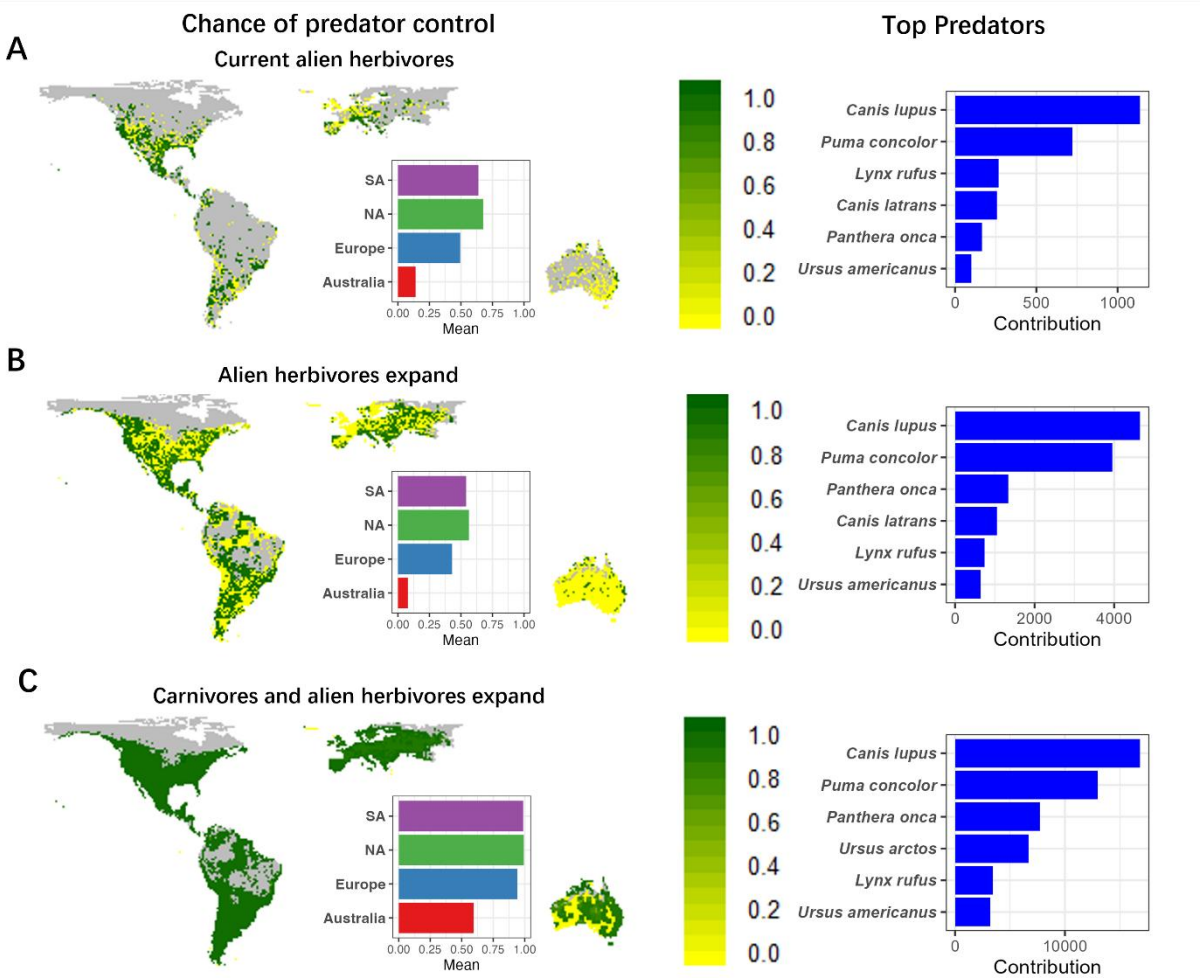


Figure 4. The mean probability that alien herbivores have a suitable predator (left column), and top six predators (right column) under different scenarios: (A) current scenario; (B) future scenario if alien herbivores expand but carnivores do not; (C) future scenario if both alien herbivores and carnivores expand. SA refers to South America, and NA refers to North America. Grey in the maps represents no distributions of alien herbivores. Predator contributions were calculated as the sum of predation probability to alien herbivores across grid cells (top six species kept).

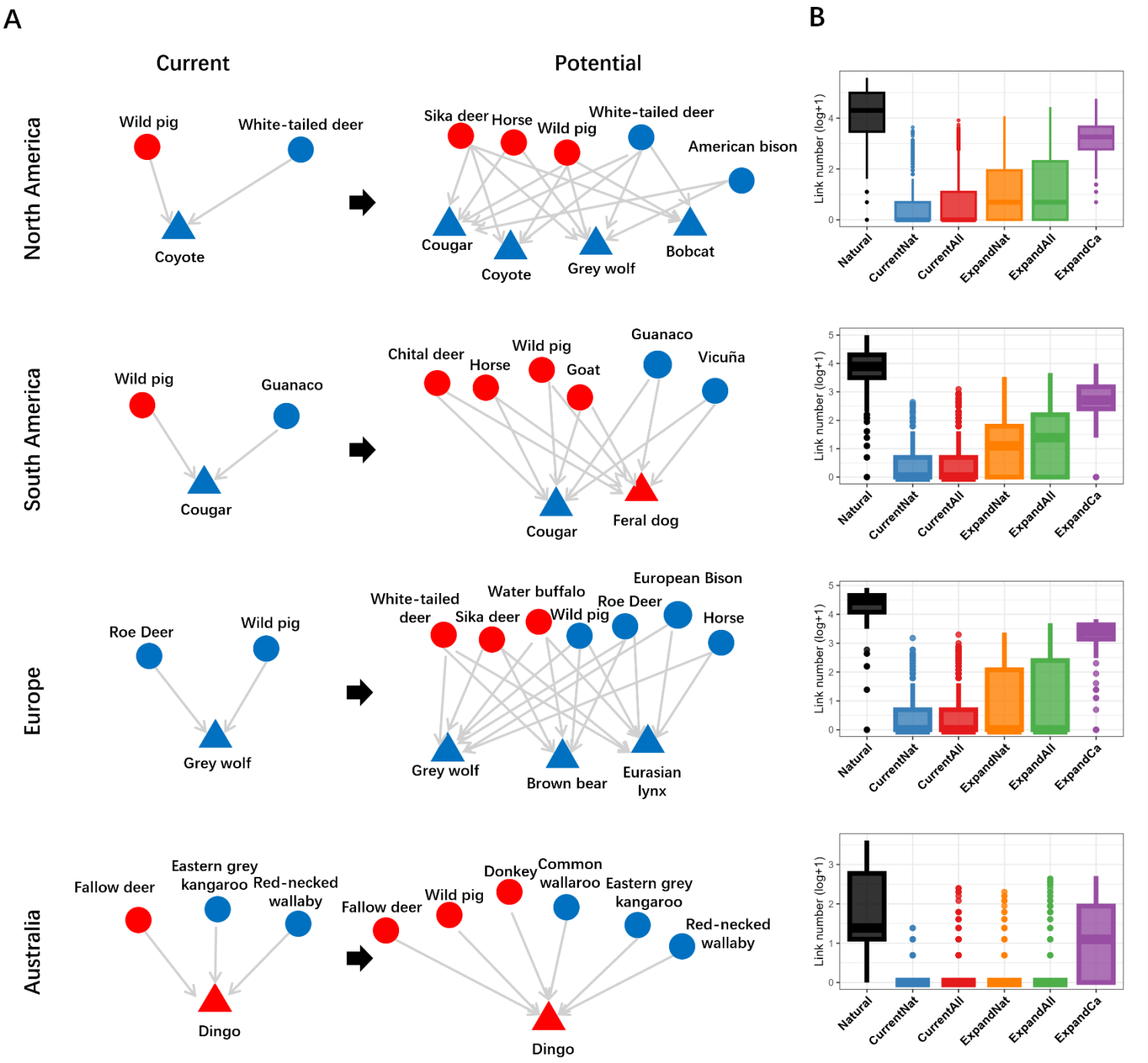


Figure 5. Food-web changes under different restoration scenarios. (A) Representative examples of current and potential large-mammal food webs if both herbivores and carnivores expand to their suitable climatic ranges. Examples are shown for four regions (a randomly chosen 100 × 100 km grid cell in each of four regions): eastern United States (North America), Patagonia (South America), western Europe, and southeastern Australia. Dingo is shown separately for ecological clarity, although dingo, feral dog and wolf records were pooled as *Canis lupus* in the analyses. (B) Changes in the number of food-web links (log-transformed) across five scenarios from left to right: (1) present-natural baseline, (2) current native herbivores with current carnivores, (3) all current herbivores (native + alien) with current carnivores, (4) native herbivores expanded with current alien herbivores and current carnivores, (5) all herbivores expanded with current carnivores, and (6) all herbivores and carnivores expanded.

Supporting information

Appendix S1. List of native and alien herbivores

Table S1: List of native and alien herbivore species included in this study. Species names in bold indicate those included in the *current* distribution modelling; other species were excluded from current models due to insufficient occurrence records, but were included in the potential distribution estimation.

Continents	Native herbivores	Alien herbivores
Europe	***Alces alces, Bison bonasus, Bos taurus, Capra caucasica, Capra ibex, Capra pyrenaica, Capreolus capreolus, Capreolus pygargus, Cervus elaphus, Rangifer tarandus, Rupicapra pyrenaica, Rupicapra rupicapra, Saiga tatarica, Sus scrofa, Equus caballus, Equus asinus, Dama dama,*** *Capra cylindricornis, Equus hemionus*	***Ammotragus lervia, Cervus nippon, Odocoileus virginianus, Ovis aries, Ovibos moschatus****, Camelus bactrianus, Lama guanicoe, Axis axis, Bubalus bubalis*
North America	***Odocoileus hemionus, Rangifer tarandus, Cervus canadensis, Alces alces, Oreamnos americanus, Bison bison, Ovis canadensis, Ovis dalli, Ovibos moschatus, Antilocapra americana, Odocoileus pandora, Mazama temama, Odocoileus virginianus, Pecari tajacu, Tayassu pecari***	***Ovis aries, Bos taurus, Capra hircus, Sus scrofa, Equus caballus, Equus asinus, Axis axis, Dama dama, Oryx gazella, Boselaphus tragocamelus, Antilope cervicapra, Ammotragus lervia, Cervus nippon, Oryx dammah, Rusa unicolor****, Tragelaphus angasii, Rucervus duvaucelii, Kobus leche, Aepyceros melampus, Hemitragus jemlahicus, Phacochoerus africanus*
South America	***Blastocerus dichotomus, Hippocamelus antisensis, Hippocamelus bisulcus, Lama guanicoe, Mazama americana, Mazama gouazoubira, Mazama nemorivaga, Mazama rufina, Ozotoceros bezoarticus, Tapirus terrestris, Tapirus pinchaque, Hydrochoerus hydrochaeris, Hydrochoerus isthmius, Odocoileus virginianus, Mazama temama, Pecari tajacu, Tayassu pecari****, Catagonus wagneri, Tapirus bairdii, Mazama jucunda, Mazama nana, Mazama chunyi*	***Antilope cervicapra, Axis axis, Bos indicus, Bos taurus, Bubalus bubalis, Capra hircus, Cervus elaphus, Ovis aries, Sus scrofa, Equus caballus, Equus asinus****, Rusa unicolor, Hippopotamus amphibius, Dama dama*
Australia	***Macropus fuliginosus, Macropus giganteus, Notamacropus rufogriseus, Osphranter robustus, Osphranter rufus,*** *Osphranter antilopinus, Osphranter bernardus*	***Axis axis, Bos taurus, Bubalus bubalis, Camelus dromedarius, Capra hircus, Cervus elaphus, Dama dama, Ovis aries, Rusa timorensis, Rusa unicolor, Sus scrofa, Equus caballus, Equus asinus****, Axis porcinus, Bos indicus, Bos javanicus*

Appendix S2. The contribution of domestic herbivores to the diversity and function pattern

Our analyses of large-herbivore diversity and functional properties include feral populations of domesticated taxa, specifically *Bos taurus, Bos indicus, Bos javanicus, Equus caballus, Equus asinus, Capra hircus, Ovis aries, Bubalus bubalis, Camelus bactrianus, Camelus dromedarius, Lama glama, Vicugna vicugna,* and *Capra aegagrus*. Because citizen-science observations may occasionally misclassify domestic individuals as feral, we conducted an additional sensitivity analysis excluding all domestic taxa. This complementary analysis also allows us to assess the extent to which non-domestic extant species alone could restore the diversity and functional roles of large herbivores.*Sus scrofa* was not included because wild pigs / boars were apparently different from domestic pigs.

Patterns excluding domestic species closely mirror those obtained when all species are included (Figure S2 vs Figures 2–3 in main text). Under current distributions, non-domestic alien herbivores contribute little to deficit (current natives compared to present-natural scenario) reduction, decreasing deficits by only 1.2% (richness), 4.1% (total body mass), 1.7% (total grazing), and 2.1% (total browsing). If current non-domestic species were to fully occupy their potential ranges, deficits would be reduced by 34.8%, 16.6%, 29.7%, and 37.0%, respectively. Allowing non-domestic alien herbivores to also expand further increases deficit reduction to 39.4% (richness), 22.7% (body mass), 34.7% (grazing), and 41.7% (browsing). Comparisons with analyses (Figure 2-3 in main text) including all taxa indicate that domestic native species contribute only modestly (~2–3%) to additional deficit reduction if expanded, whereas domestic alien species account for a larger share (~10%) of further functional restoration if expanded. These results suggest that while feral domestic species can enhance functional recovery, the dominant signal is driven by the distributional expansion of non-domestic extant herbivores.

Figure S1. **The restoration (%) of the richness and functional deficits of non-domestic herbivore assemblages** (first row - richness; second row - sum of body mass; third row - sum of grazing level: fourth row - sum of browsing level) under three scenarios – current native and alien distributions (left column); if native herbivores expand (middle column), and if both native and alien herbivores expand (right column).

Appendix S3. The richness pattern under different scenarios

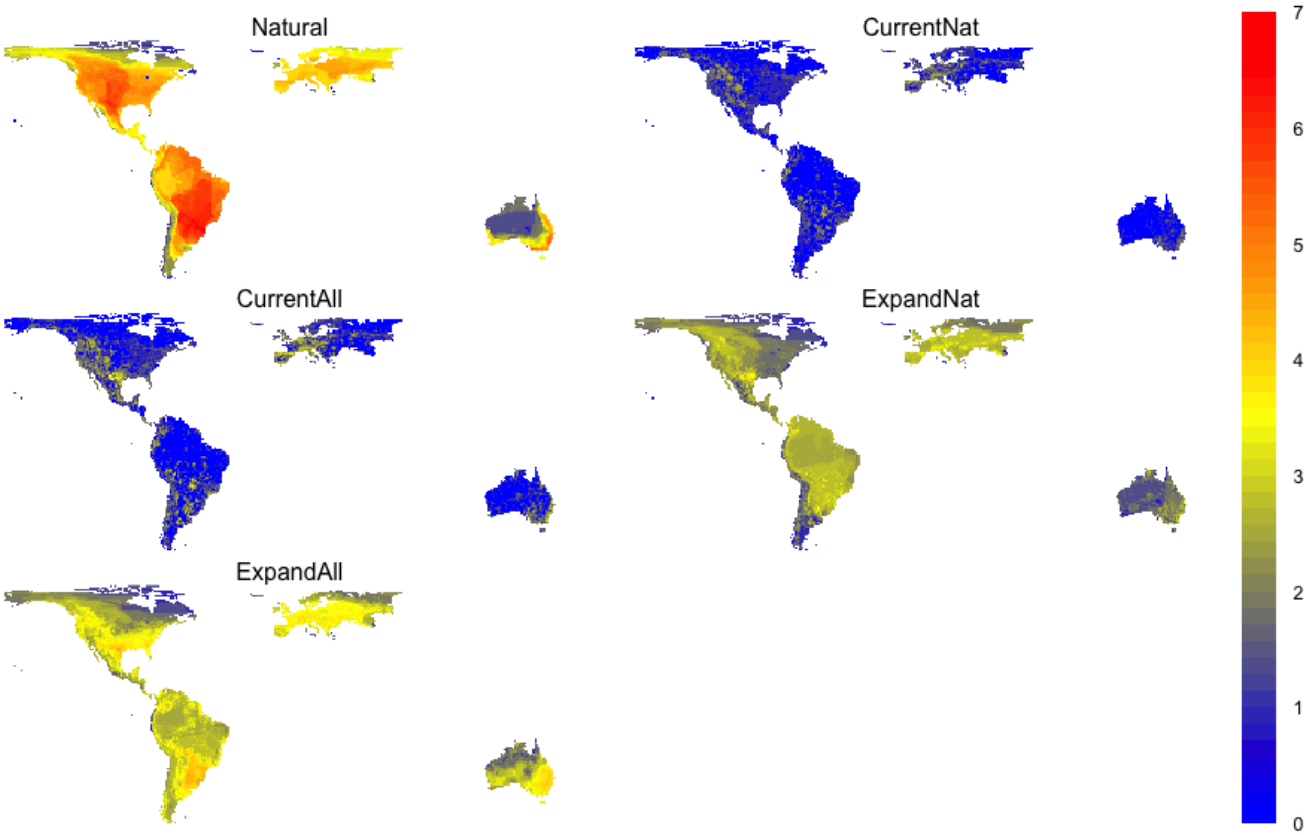


Figure S2. Herbivore richness (square root) of different scenarios: (1) 'Natural': present-natural baseline, (2) 'CurrentNat': current native herbivores without alien herbivores, (3) 'CurrentAll': all current herbivores (native + alien), (4) 'ExpandNat': all herbivores expand to suitable climate areas while alien herbivores kept in current distributions, and (5) 'ExpandAll': all herbivores expanded to suitable habitat areas.

Appendix S4. The food web links under different scenarios

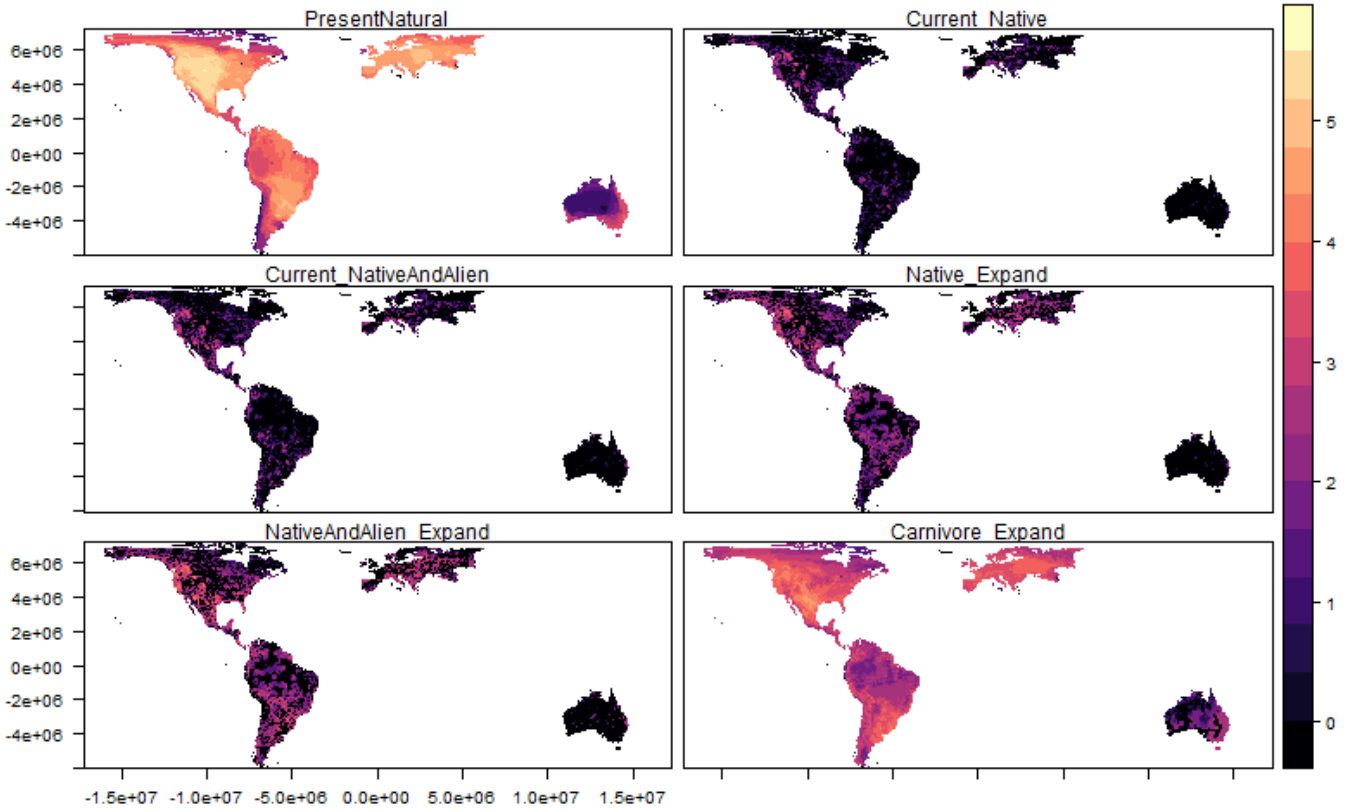


Figure S3: The link number (log_e-transformed) of food web under different scenarios: (1) 'Natural': present-natural baseline, (2) 'CurrentNat': current native herbivores with current carnivores, (3) 'Current_NativeAndAlien': all current herbivores (native + alien) with current carnivores, (4) 'Native_Expand': native herbivores expand to suitable climate areas while alien herbivores and carnivores in current distributions, (5) 'NativeAndAlien_Expand': all herbivores expand to suitable climate areas while carnivores in current distributions, and (6) 'Carnivore_Expand': all herbivores and carnivores expand to suitable habitat areas.