

## RESEARCH ARTICLE

# Long-term changes in functional diversity and its implications for mammalian conservation and ecological restoration in a grassland ecosystem

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**Handling Editor:** Justin Boyles**Abstract**

1. Paleontological data provide information on natural environments prior to human influence, which are useful for tracking changes in ecosystem functioning through time. During the Late Pleistocene, about 10% of terrestrial mammalian species were extinct in South America. Given the key ecological roles played by the megafauna, different approaches to ecological restoration are constantly debated. Among these, livestock has been suggested as an important factor for biodiversity maintenance and for the conservation of ecological processes, particularly in grassland ecosystems.
2. We investigated the ecological impacts of the biodiversity loss during the Late Pleistocene extinctions, focusing on terrestrial mammals from the Brazilian Pampa as a study model. To do so, we quantified and compared the functional diversity of assemblages from the Pleistocene (pre-extinction), Holocene (post-extinction) and Recent (post-extinction + introductions), and assessed whether introduced herbivores are suitable substitutes for lost species.
3. Our results show that functional loss has outpaced taxonomic decline since the Late Pleistocene. Introduced species, despite playing a role in filling some lost ecological functions, are mainly functionally redundant. Common domesticated livestock species, such as cattle (*Bos* spp.), are not functionally similar to any extinct species in this South American landscape. Conversely, some introduced species may be fulfilling ecological functions left vacant by the megafauna. From a functional perspective, we also identified current endangered species that are functionally unique and specialized.
4. This study illustrates how paleontological data may be useful for delineating and improving conservation and ecological restoration, and highlights that future conservation decisions should prioritize species important for preserving ecosystem functions.

**KEYWORDS**

alien species, extinction, livestock, megafauna, Pampa, Quaternary, South America

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## 1 | INTRODUCTION

The fossil record documents biodiversity dynamics throughout time, extending the information provided by current and historical data, as well as offering insights into terrestrial communities prior to human influence (Dillon & Pimiento, 2025; Kemp et al., 2023). A long-term perspective therefore allows for a better assessment of the consequences of species loss for the functioning of ecosystem processes, with implications for the conservation, restoration and management of living biodiversity (Barnosky et al., 2017; Dietl et al., 2015; Dillon & Pimiento, 2025). In this sense, the relatively new field of Conservation Paleobiology arises as a proposal to merge paleontological data into conservation biology (Dietl & Flessa, 2011), forming the core of the present study, which addresses ecological changes throughout the Quaternary, from the Pleistocene to the present day.

During the Pleistocene, South America was home to several megafaunal species, defined in a terrestrial context as species with body masses ranging from around 10 kg to several tons (although the definition varies among authors, with some considering values above 45 kg; see Moleón et al., 2020). These larger species were the most affected by the significant loss of global mammalian diversity that occurred at the Pleistocene–Holocene transition, 11,700 years ago (Barnosky, 2008; Owen-Smith, 1989; Smith et al., 2018; Stuart, 2015; Svenning et al., 2024). Despite its global scale, the megafauna extinction was particularly severe in South America (Barnosky et al., 2004; Stuart, 2015; Svenning et al., 2024), especially in the southern cone (Sandom et al., 2014). This loss represented about 10% of the total diversity of terrestrial mammals on the continent (Smith et al., 2018), where all mammals with body mass greater than 500 kg were extirpated (Svenning et al., 2024).

Body mass is one of the most important traits for predicting relationships and interactions with other animals, including predation and competition, their impact on the environment and for inferring biological traits such as reproduction, growth and survival (Bonner, 2011; Smith & Lyons, 2011). For instance, large herbivores can alter plant species composition and biomass (Bakker et al., 2016; Doughty et al., 2016; Pringle et al., 2023) and modulate the density and diversity of other animals through facilitation (Arsenault & Owen-Smith, 2002) or competition (Ramirez et al., 2021), with cascading effects across food webs (Malhi et al., 2016; Pringle et al., 2023). At the same time, they promote environmental heterogeneity by either creating nutrient hotspots or physically disturbing vegetation, which can have an overall positive effect on biodiversity at larger spatial scales (Trepel et al., 2024). Large herbivores can also alter the physical environment by trampling the soil, causing compaction and limiting the availability of oxygen and water in moist and dry soils, respectively (Sitters & Andriuzzi, 2019). Given their high nutritional and metabolic demands and, consequently, extensive daily movements for feeding, they contribute to ecosystem connectivity and seed dispersal (Berti & Svenning, 2020; Metera et al., 2010; Pringle et al., 2023). Their impacts can even influence

global processes, including changes in biogeochemical cycles and gas exchanges, due to characteristics inherent to their digestive physiologies (Malhi et al., 2016; Smith et al., 2023).

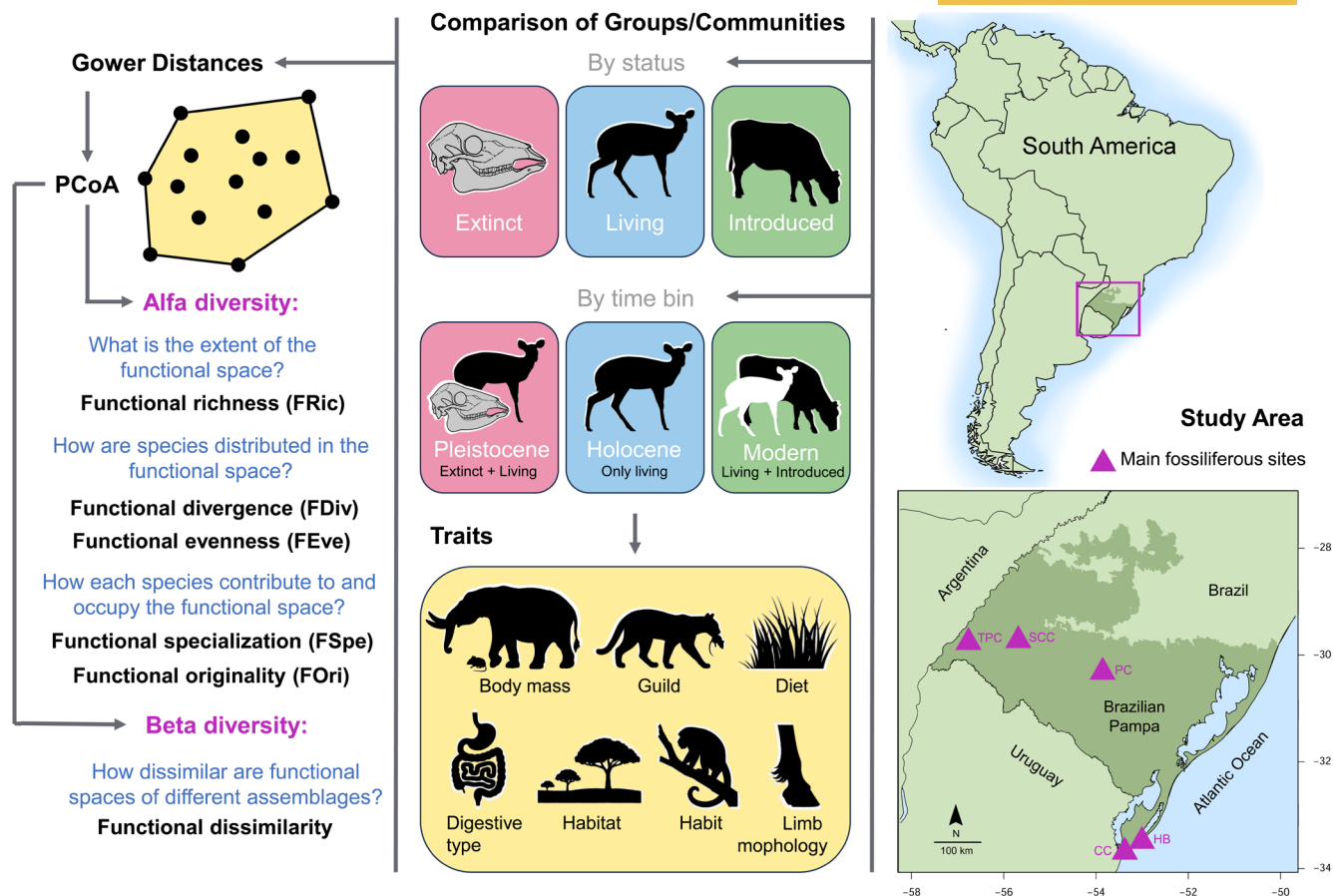
Given the loss of large herbivores (and consequently, their ecological roles), ecologists and conservationists frequently debate on the most effective approach to ecological restoration. Lundgren et al. (2020), in an integrated analysis of South America, found that alien herbivore species partially restore the ecological functions lost since the Late Pleistocene. Nonetheless, their study considered only wild populations, excluding domestic ones, despite the large and growing populations of some domestic herbivores associated with the ongoing development of human societies (Barnosky, 2008; Turvey & Crees, 2019). For example, in the Brazilian Pampa, more than 20 million head of cattle (*Bos taurus* and *B. indicus*) are raised in pastoral systems, with cattle being considered important for maintaining plant diversity and sustaining pastures (Baggio et al., 2021; Caumo et al., 2021; Overbeck et al., 2007). Still, as emphasized by Pringle et al. (2023), a few species of ungulates, mainly ruminants, may be poor substitutes for the extinct megafauna due to their less disparate traits. On the other hand, small mammals would not be able to fully substitute the ecological functions of larger ones (Pringle et al., 2023).

Here, we investigated the ecological impacts of the loss of terrestrial mammal diversity during the Late Pleistocene extinctions, specifically testing whether introduced herbivores (including domesticated ones) are suitable substitutes for the Pleistocene extinct species. To do so, we estimated the functional diversity of terrestrial mammals throughout the Late Quaternary, combining information from fossils and extant biodiversity. What we found aligns with the previous statement by Pringle et al. (2023), in which the loss of functional diversity is poorly compensated by surviving and introduced species, but wild populations of alien herbivores may play a role in fulfilling ecological functions, as suggested by Lundgren et al. (2020). From a functional perspective, our results provide relevant insights into which extant species should be prioritized to maintain modern ecosystem functioning. We also reveal valuable information that can support ecological restoration, using the natural pre-human state as a reference, in accordance with the goals of Conservation Paleobiology.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

The mammalian functional diversity of the Brazilian Pampa biome (Figure 1) was used as a study system to understand the ecological impacts of diversity loss during the Quaternary extinctions, particularly those involving the so-called megafauna. The Pampa is a biome shared with Uruguay and northeastern Argentina, characterized as a mosaic of grasses, shrubs and sparse trees, dominated by the plant families Asteraceae, Poaceae, Leguminosae and Cyperaceae (Andrade et al., 2023; Burkart et al., 2011;



**FIGURE 1** Overview of the methodological framework. The study area comprises the Brazilian Pampa, located in the southern portion of Brazil (highlighted in dark green), South America. Purple triangles indicate the main Pleistocene fossiliferous sites in this region: Touro Passo Creek (TPC), Sanga da Cruz Creek (SCC), Pessegueiro Creek (PC), Chuí Creek (CC) and Hermenegildo Beach (HB). For functional analyses, species were grouped into assemblages based on the geological epoch (Pleistocene, Holocene and Recent/Modern) or status (Extinct, Extant/Living and Introduced) for comparison purposes. Each species was then characterized by the following traits: Body mass, guild, diet, digestive type, habitat, habit and limb morphology. The main functional diversity indices and their definitions are also shown.

Orlandi et al., 2024; Overbeck et al., 2007). In its northern part, corresponding to southern Brazil, this biome is also referred to as 'Campos Sulinos' or simply 'Campos' (Allen et al., 2011), with a total area of 193,836 km<sup>2</sup> (IBGE, 2019). The climate is subtropical, with temperatures ranging from -7 to 32°C and no dry season (Wrege et al., 2012), the severity of the winters being one of the main characteristics that differentiates the Pampa from the Cerrado (the Brazilian savanna; Allen et al., 2011).

Faunal occurrences of Pleistocene extinct species were based on Lopes et al. (2020), which provides a review of fossil occurrences from predominantly Late Pleistocene sites from southern Brazil. Although the fossil record is inherently incomplete, potentially leading to an underestimation of the Pleistocene fauna, we adopted a conservative approach, considering only records from the study area. Living native species, as well as introduced species with wild populations, followed the species list for the Brazilian Pampa provided by Andrade et al. (2023). In addition to self-sustained populations of introduced herbivores, domestic herbivores were included in our analyses, given their high population densities in natural pastures (Baggio et al., 2021).

## 2.2 | Functional diversity analyses

Functional diversity can be defined as a multidimensional space, or functional space, where the axes represent traits of interest (Rosenfeld, 2002), being a synthesis of the functions performed by organisms within an ecosystem (Díaz & Cabido, 2001).

For the estimation of functional diversity metrics, species were categorized as extinct, living or introduced, and assigned to the Pleistocene (extinct + living species), Holocene (only living) and Modern (living + introduced) assemblages (Figure 1). The following functional traits were gathered from the literature: body mass (in grams and log-transformed), trophic guild (carnivore, herbivore or omnivore), diet (browse, graze, mixed feeding, invertebrates, small vertebrates, medium vertebrates or large vertebrates), habitat (forest, forest and open environments or open environments), digestive type (foregut, hindgut or simple gut), habit (aquatic, arboreal, fossorial or terrestrial) and limb morphology (digitigrade, plantigrade or unguligrade) (Supporting Information, Figure S1). Details on diet and habitat use were preferably obtained from regional studies (e.g. Carrasco et al., 2023), as some species may exhibit spatial variation

in their ecology. When data were missing, information was extrapolated based on relatives.

The first methodological step in estimating a multidimensional space is to compute the distances among species and then ordinate them using a principal coordinate analysis (PCoA, [Figure 1](#)). As the data matrix contains both continuous (e.g. body mass) and categorical data, Gower distances (de Bello et al., 2021; Gower, 1971) were calculated using the *func.dist* function from the *mFD* package (Magneville et al., 2022) in R version 4.4.2 (R Core Team, 2024). To reflect their relative ecological importance, traits were weighted so that body mass received a weight of one. Traits related to diet (trophic guild, diet and digestive type) and habitat (habitat use, habit and limb morphology) each received a weight of one-third. Consequently, body mass, diet and habitat contributed equally to the overall weighting scheme, following Hedberg et al. (2022).

The PCoA was computed up to 10 dimensions to assess the quality of the functional space following Maire et al. (2015) through the *quality.fspaces* function (*mFD* package; Magneville et al., 2022). This exploratory step resulted in the lowest mean absolute deviation (mAD) for functional spaces represented by five dimensions (mAD = 0.048; [Figure S2](#)). Functional spaces were then calculated for extinct, living and introduced species, as well as for Pleistocene, Holocene and Modern assemblages to quantify alpha and beta diversity indices using the PCoA axes one to five ([Figure 2](#), [Figure S3](#)). The relationship between PCoA axes and traits is shown in [Figure S4](#).

The trait space properties of groups divided by time or status were explored through alpha diversity indices (function *alpha.fd.multidim* from the *mFD* package; Magneville et al., 2022) of functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), functional originality (FOri) and functional specialization (FSpe, Mammola et al., 2021). Differences in FOri and FSpe between groups were assessed using the non-parametric Kruskal–Wallis test, as the assumptions of normality and homoscedasticity were not met according to the Shapiro–Wilk test of normality and Levene's test of equality of variances. This was done using R packages *car* (Fox et al., 2024) and *FSA* (Ogle et al., 2024).

Beta diversity indices were calculated based on the overlap between convex hulls of pairs of communities (Villéger et al., 2013) using the function *beta.fd.multidim* (*mFD* package; Magneville et al., 2022). The level of functional dissimilarity among groups (e.g. Pleistocene vs. Recent) was quantified through the Jaccard index decomposed into nestedness and turnover components (Baselga, 2010).

Species were also clustered based on unique shared traits to quantify the loss of functional entities (FEs) from the Pleistocene to the Holocene, applying the *sp.to.fe* function (*mFD* package; Magneville et al., 2022). For this, body mass, a continuous variable, was transformed into categorical based on quartiles, resulting in the following classification: small ( $\log_{10}[\text{body mass in grams}] < 2.5$ ), medium ( $\geq 2.5 < 4.0$ ), large ( $\geq 4.0 < 5.5$ ) and mega ( $\geq 5.5$ ).

Given that the functional space may be affected by the type of traits used, we performed additional sensitivity analyses considering diet and habitat coding as 'fuzzy traits'. This approach allows a

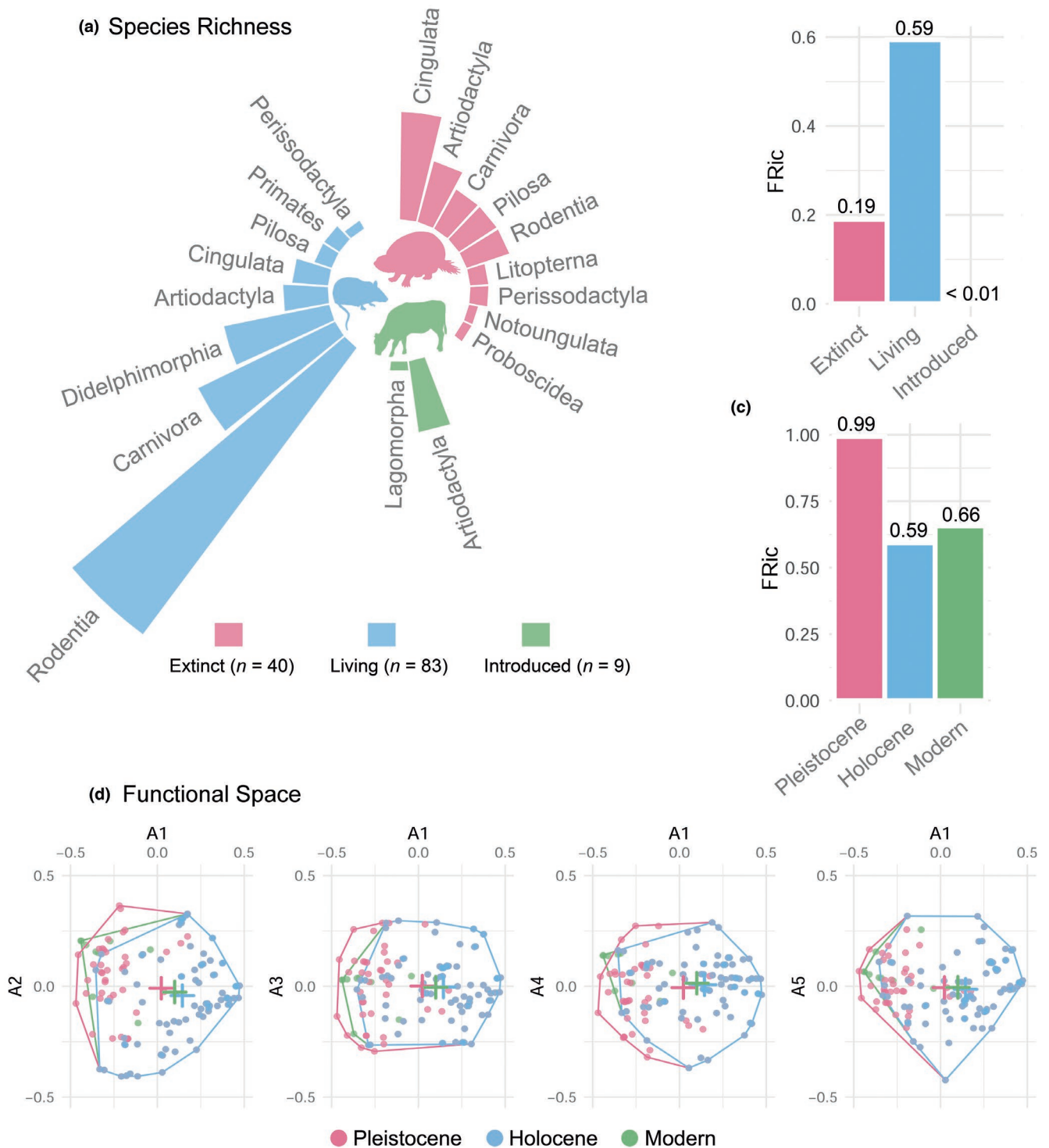
species to be assigned simultaneously to several categories instead of being placed into just one. For this, diet was decomposed into several columns: browse, graze, invertebrates, small vertebrates, medium vertebrates and large vertebrates. Predominant resources were assigned a value of 100, whereas mixed feeders received 50 for browse and 50 for graze. Similarly, habitat was decomposed into forest and open habitats, with species occurring in both (or in mesic habitats) receiving a value of 50 in each category. As the *mFD* package does not allow 'fuzzy traits' to be weighted (Magneville et al., 2022), we instead used the *gowdis* function from the *FD* package (Laliberté et al., 2015) to calculate Gower distances. The weighting scheme and the calculation of alpha and beta diversity indices followed the same steps described above, except for the number of dimensions, which was based on axes one to four.

### 2.3 | Metrics for ecological restoration and conservation prioritization

Inferences with implications for ecological restoration and the conservation of living fauna and their ecosystems were based on the nearest neighbour distance (NND; Weiher et al., 1998) in functional space and the FUSE index (functionally unique, specialized and endangered; Pimiento et al., 2020). The nearest neighbour distances are an output from the *alpha.fd.multidim* function and were calculated using the global species pool to identify extant species that are functionally similar to extinct ones. In other words, NND served as a proxy to recognize potential ecological substitutes for extinct species, whether these potential substitutes are native or introduced. Conversely, extinct species whose closest match was also extinct were interpreted as having their ecological function lost in the Modern assemblage.

The FUSE index was calculated only for extant native species to identify those with conservation priority (Pimiento et al., 2020) using the *fuse* function (package *mFD*; Magneville et al., 2022). This index combines functional uniqueness (the average distance to the five nearest neighbours) and functional specialization (the distance from the centroid of the trait space) with extinction risk. Information on extinction risk was obtained from the IUCN Red List of Threatened Species (IUCN, 2025; <https://www.iucnredlist.org/>), and the conservation status categories ([Supporting Information, Table S1](#)) were scored as numbers: 0 for Least Concern (LC), 1 for Near Threatened (NT), 2 for Vulnerable (VU) and 3 for Endangered (EN). At the time of dataset construction and analysis, no species were classified as Critically Endangered (CR). High FUSE scores mean that species are highly threatened and display unique ecological functions in their ecosystems (Pimiento et al., 2020).

Furthermore, the association between species' extinction probabilities and their functional characteristics was explored using binomial generalized linear models (GLM), performed with the *glm* R function (R Core Team, 2024). For this, IUCN categories were summarized as threatened (endangered, vulnerable and near threatened) and not threatened (least concern) to configure a binary variable.



**FIGURE 2** Main taxonomic groups (a) and functional richness (FRic; b) of extinct, living and introduced species, indicated in red, blue and green bars, respectively. Functional richness (c) and functional space (d) of Pleistocene (extinct+living), Holocene (only living) and Modern (living+introduced) assemblages are also shown, following the same colour pattern of unique species groups. Complete pairs of axes are provided in [Figure S3](#) of the [Supporting Information](#). Silhouettes obtained from [PhyloPic](#) ([phylopic.org](#)).

## 2.4 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Assemblages	Extinct 40; living 83; introduced species 9

A comprehensive overview of data matrix construction and species characteristics can be found in the [Supporting Information](#). Additional methodological details are also provided. Data and R code for analyses are available in the open repository Zenodo at the following link: <https://doi.org/10.5281/zenodo.19339296> (Carrasco et al., 2026).

## 3 | RESULTS

### 3.1 | Functional diversity indices

Overall, independently of the trait treatment used (categorical or 'fuzzy traits'), the results of functional indices showed similar trends. Here, we present the results of FRic, FDiv, FEve, FOr and FSpe from functional spaces considering diet and habitat as categorical traits. Alpha diversity results from functional spaces using 'fuzzy traits' are provided in the [Supporting Information](#) (Table S2).

Functional loss has outpaced taxonomic decline since the Late Pleistocene. The Pleistocene–Holocene extinction led to a reduction of about 30% of the terrestrial mammalian diversity, while functional richness declined by 40%. The inclusion of introduced species in the Modern assemblage resulted in a 12% increase in functional space volume (Figure 2). The level of functional dissimilarity between Pleistocene and Recent assemblages was 0.34, of which nestedness and turnover components corresponded to 0.33 and 0.0027, respectively.

There was a decline in functional divergence from the Pleistocene (FDiv=0.89) to the Holocene (FDiv=0.86), remaining unchanged in the Modern assemblage (FDiv=0.86, Figure S5). When groups are analysed separately by status, it is evident that the traits of introduced species are more concentrated near the center of their respective functional trait space (FDiv=0.70; Figure S5), compared to those of extinct (FDiv=0.81) and living species (FDiv=0.86). Furthermore, the observations in the introduced group are more clustered and irregular (FEve=0.54) than in the living (FEve=0.65) and extinct (FEve=0.76) ones. Similarly, the Pleistocene fauna had a more uniform distribution of observations in functional space, although introduced species have contributed to a slight increase in regularity in the Modern assemblage (FEve\_Pleistocene=0.70, FEve\_Holocene=0.65, FEve\_Modern=0.66). Functional originality and functional specialization did not differ significantly between Pleistocene, Holocene and Modern assemblages ( $p > 0.05$ ). However, extinct, living and introduced groups differ regarding the mean distance to the nearest neighbour (FOr,  $p = 0.048$ ; Figure S6). The post-hoc Dunn test shows that such differences are more pronounced between extinct and living groups ( $p = 0.021$ ).

When analysing functional diversity grouped by functional entities, our results indicate a loss of 31 groups with unique combinations of traits following the Late Quaternary extinctions (FE\_Pleistocene=87, FE\_Holocene=56), a loss that was only poorly compensated by introduced species (FE\_Modern=62, Figure S7, Table S3). Among the gains of functional entities in the Modern assemblage, two functional types lost during the Pleistocene were directly replaced by introduced taxa, represented by the alien spotted deer (*Axis axis*) and domesticated horses (*Equus ferus*). However, four categories represent entirely new functional entities, not present among either extinct or living native faunas, including common domesticated livestock species (*B. indicus*, *B. taurus*, *Bubalus bubalis*, *Capra aegagrus* and *Ovis aries*), the European brown hare (*Lepus europaeus*) and the wild boar (*Sus scrofa*) (Table S3).

### 3.2 | Functional substitutes and conservation priorities

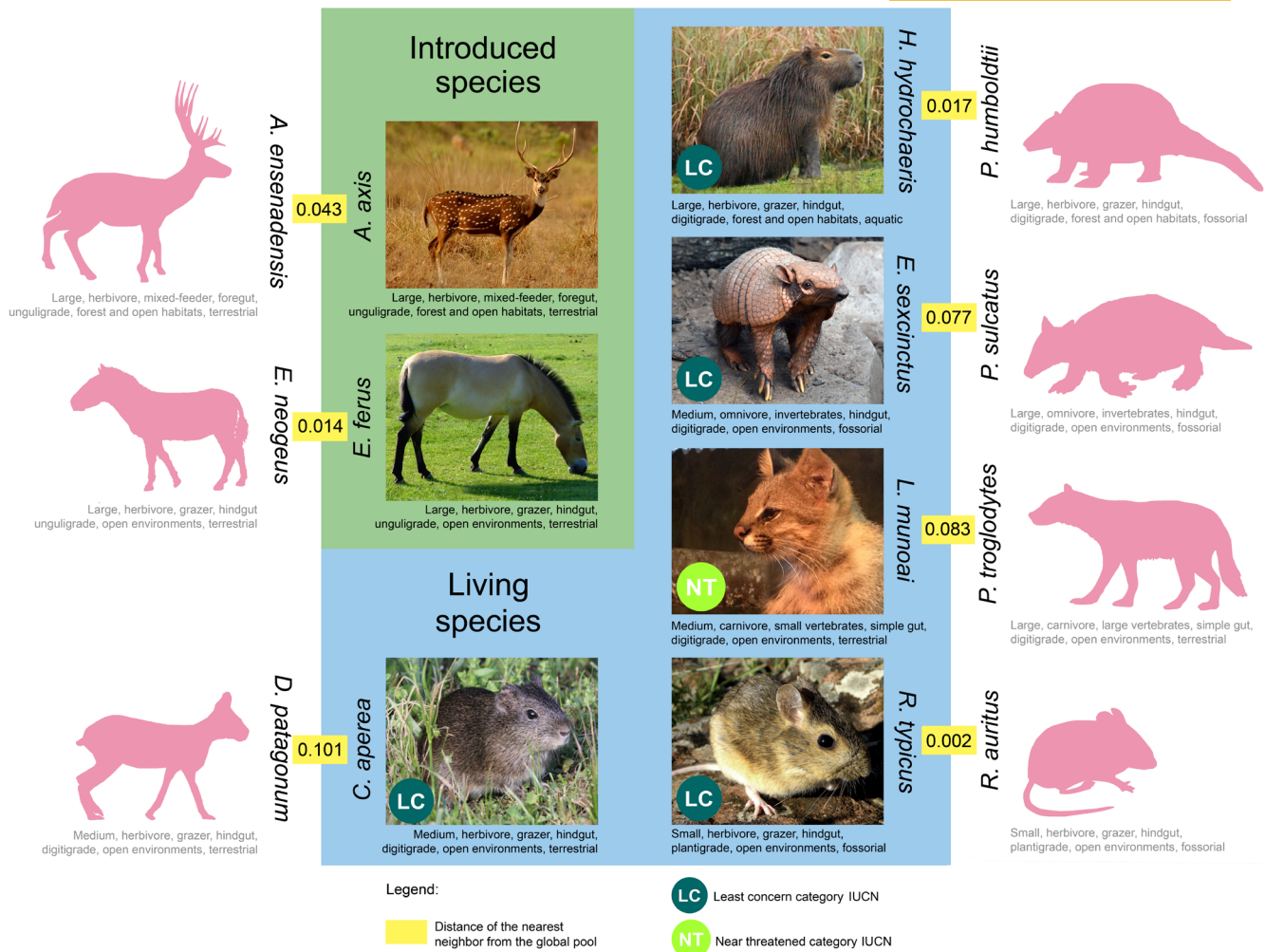
The distance to the nearest neighbour aligns with the results based on functional entities. Of the 40 species that went extinct during the Late Quaternary, five extinct species are most functionally similar to extant native species (Figure 3), while 33 are functionally similar to other extinct species, implying that their ecological functions were lost in the Holocene and Modern assemblages. Two extinct species (the deer *Antifer ensenadensis* and the extinct horse *Equus neogeus*) had an introduced species (*A. axis* or *E. ferus*, respectively) as their nearest functional neighbour. We classified extant or introduced species as potential ecological substitutes for extinct ones only if they emerged as closest neighbours in both analytical approaches (categorical traits and 'fuzzy traits'), resulting in the relationships presented in Figure 3.

The functionally unique, specialized and endangered (FUSE) index identified the giant otter (*Pteronura brasiliensis*), the marsh deer (*Blastocerus dichotomus*), the white-lipped peccary (*Tayassu pecari*), the lowland tapir (*Tapirus terrestris*) and the giant anteater (*Myrmecophaga tridactyla*) as the five species with the highest scores (FUSE > 0.50) among living species from the Brazilian Pampa and, therefore, as conservation priorities (Figure 4). Based on a binomial GLM, high extinction probabilities are associated with large body mass, use of open habitats and a strict carnivore diet (Figure S8).

## 4 | DISCUSSION

### 4.1 | Are introduced species functional substitutes for the Pleistocene megafauna?

Through the lens of Conservation Paleobiology, we provided a basis for biodiversity management and restoration based on a pre-human state (the Pleistocene epoch), testing the hypothesis that domesticated species are suitable substitutes for extinct megafauna in the Modern assemblage. Our results highlight a significant reduction in functional richness associated with a loss of mammalian biodiversity throughout the Late Quaternary. The



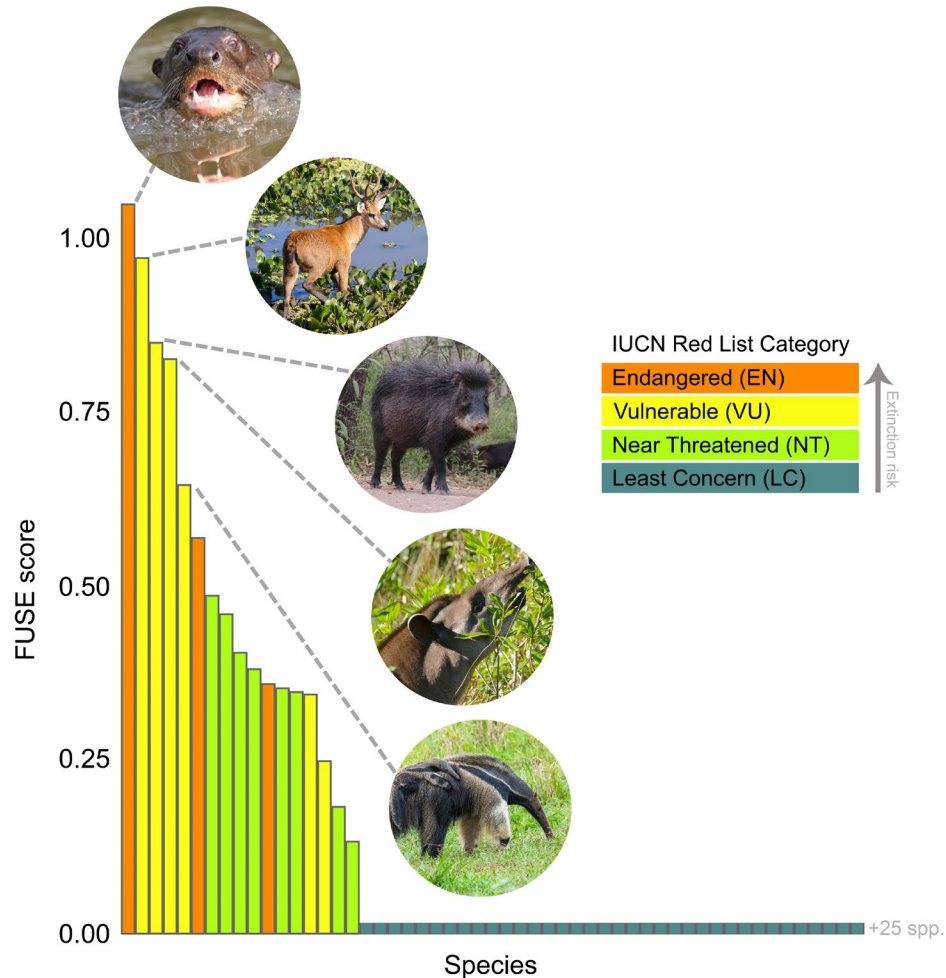
**FIGURE 3** Extinct species and their extant nearest neighbours, based on distances in the functional space. From up to bottom: Spotted deer, *Axis axis* (photo by Shankar Raman, CC BY-SA 4.0), domesticated horse, *Equus ferus* (photo by Charles Miller, CC BY 2.0), wild guinea pig, *Cavia aperea* (photo by Leyo, CC BY-SA 3.0 CH), capybara, *Hydrochoerus hydrochaeris* (photo by Ezequiel Racker, CC BY 4.0), yellow armadillo, *Euphractus sexcinctus* (photo by Vassil, CCO), obtained from Wikimedia Commons, Muñoa's Pampas cat, *Leopardus munoai* (photo by Flávia Tirelli), *Reithrodon typicus* (photo by Ricardo Roth), used with permission. Silhouettes obtained from PhyloPic ([phylopic.org](http://phylopic.org)).

Pleistocene mammalian assemblage, besides occupying a larger functional space, was characterized by trait combinations more evenly distributed within the space, which may be linked to a higher degree of niche differentiation and, thus, ecological functions (Mason et al., 2005). Conversely, Holocene and Modern assemblages have less uniform functional compositions. The introduced fauna contributed only to a small increase in the overall functional space, due to their less diverse ecological and morphological traits.

Of the nine introduced and domesticated species that are raised on Pampa natural pastures, two were responsible for replacing the ecological functions of extinct megafauna species: the alien spotted deer (*A. axis*) and the domesticated horse (*E. ferus*). The spotted deer has been included in population control programs (SEMA Ordinance No. 109/2022) due to its geographical expansion (e.g. Foster et al., 2021) since its introduction in Uruguay in the 1930s for hunting purposes (Pereira-Garbero et al., 2013). While the ecological

impacts of invasive species are frequently a cause for concern (Clout & Russell, 2008; da Rosa et al., 2017), this species may be fulfilling an important ecological role left vacant by the megafauna extinction, particularly the deer *A. ensenadensis*. However, we emphasize the importance of broadly assessing the ecological role of *A. axis* and its impacts on native species, particularly across other South American biomes, to better inform conservation decisions. Although investigating the functional traits of mammals provides insights into their ecosystem functioning, detailed ecological research is still needed to understand the extent to which extant species can replace the ecological role of extinct ones (Schowanek et al., 2025).

The domesticated horse has a longer history of introductions, having been brought to the Pampa by Jesuits in the 17th century (Pillar & Quadros, 1999). It shares several functional traits with *E. neogeus*, an extinct closely related species. Due to the genetic and hereditary components, phylogenetic relationships determine in many ways the characteristics of organisms (McKinney, 1997). Thus,



**FIGURE 4** Functionally unique, specialized and endangered (FUSE) scores of living species. Bar colours indicate the IUCN Red List category (orange: endangered, EN; yellow: vulnerable, VU; light green: near threatened, NT; turquoise: least concern, LC). Note that more than 25 species of the least concern category and with FUSE score equal to zero were omitted from the graph. From left to right: Giant otter, *Pteronura brasiliensis* (photo by Alastair Rae, CC BY-SA 2.0), marsh deer, *Blastocerus dichotomus* (photo by Diogo Luiz, CC BY-SA 4.0), white-lipped peccary, *Tayassu pecari* (photo by Tomás Tamagno, CC BY 4.0), lowland tapir, *Tapirus terrestris* (photo by Bernard Dupont, CC BY-SA 2.0), giant anteater, *Myrmecophaga tridactyla* (photo by Emily Nelson, CC BY 4.0), obtained from Wikimedia Commons.

it is not surprising that close phylogenetic taxa may show strong functional similarities.

Native species also play a central role in filling some ecological gaps left by the Late Quaternary extinctions. Based on nearest neighbour distances, it was possible to identify five ecological analogues that may functionally replace extinct taxa. Nevertheless, these species coexisted with the extinct ones, as observed through the fossil record (e.g. Lopes & Buchmann, 2011) and presumably had distinct ecological functions—different enough to allow for their coexistence. It is possible that ecological release (a scenario in which a species experiences an expansion of its ecological niche and an increase in population size when it encounters a reduction or absence of competitors; Herrmann et al., 2021) is one of the mechanisms responsible for the restoration of lost ecological functions in the face of extinctions.

The real impact of megafaunal extinction on plant communities remains unclear (González-Guarda et al., 2025), but one example of

an ecological function partially restored by surviving species is seed dispersal. Several Neotropical plant species exhibit traits shaped by evolutionary interactions between megafauna and the plant community, a case of anachronism known as the ‘megafaunal dispersal syndrome’ (Janzen & Martin, 1982). Although the megafauna became extinct more than 10,000 years ago, these plants still persist, possibly due to dispersal by scatter-hoarding rodents such as agoutis (*Dasyprocta* spp.), which are capable of dispersing seeds over distances greater than 100 m (Jansen et al., 2012).

## 4.2 | The role of cattle

While horses and deer may restore lost ecological functions, cattle represent a new functional entity that was not present in a pre-extinction scenario and may reflect novel ecological functions within this ecosystem. Even though that foregut ungulates reached

the South America more than 2.5 million years ago during the Great American Biotic Interchange (Cassini et al., 2016; Webb, 1991, 2006), the introduction of bovids at the end of the 16th century (Sluyter, 2023) marked the emergence of new functional entities of large to mega-grazers with preference for open habitats. This means that modern Pampa natural pastures are likely experiencing different impacts caused by herbivores other than those in Pleistocene ecosystems. Moreover, the densities of domestic and semi-domestic herbivores often surpass those of their native counterparts, as observed in current husbandry practices (Oesterheld et al., 1992). While livestock production is generally based on a few domesticated species maintained at very high population densities, Pleistocene megafauna comprised a broader diversity of species, each likely occurring at comparatively lower densities, especially during interglacial periods. In this sense, livestock systems are characterized by a low functional diversity, with ecological impacts concentrated in a few highly abundant species. As a consequence, overgrazing (i.e. excess of herbivory by large mammals; Mysterud, 2006) is one of the most negative effects related to livestock that may lead to other ecological impacts, such as erosion and desertification due to soil exposure and degradation (Overbeck et al., 2007).

Regarding biotic interactions, even in cases in which livestock did not directly compete with native herbivores, focusing on different types of vegetation, wild populations tend to avoid areas used by cattle (Chaikina & Ruckstuhl, 2006). By changing the vegetation, the livestock consequently influences food quality and quantity, as well as shelter and nesting availability (Schiltz & Rubenstein, 2016). In the Brazilian Pampa, bird species, particularly endangered ones, are more abundant in areas of cattle exclusion or with a reduced intensity of grazing (Marque & Kasper, 2024), but the impacts on mammalian richness and abundance need to be further investigated.

Despite the overall ecological impacts of livestock in the Pampa biome, economic and social factors should be considered in sustainable management and conservation efforts. In addition to animal husbandry, socioeconomic activities in the Pampa are characterized by soybean cultivation and silviculture. In recent years, there has been an increase in these agricultural activities, transforming the landscape from grasslands to monocultures (Mengue et al., 2020). Although cattle pastures also occupy vast areas, the impacts of soybeans exceed those of livestock, not only due to the destruction of natural areas and loss of biodiversity but also because of harvesting and transportation activities (de Oliveira et al., 2017; Fearnside, 2001). In this context, the Pampa could benefit from moderate livestock, which could contain the expansion of monocultures while promoting an acceptable balance between conservation and socioeconomic activities, especially when associated with protected areas.

### 4.3 | Conservation prioritization

Rather than focusing on taxonomic identities, conservation priorities should be defined based on functional attributes that

contribute to maintaining ecosystem properties within acceptable limits (Hooper et al., 2002). In this context, the index FUSE was used to identify species of conservation priority, among which the giant otter (*P. brasiliensis*), the marsh deer (*B. dichotomus*), the white-lipped peccary (*T. pecari*), the lowland tapir (*T. terrestris*) and the giant anteater (*M. tridactyla*) were identified as the five mammal species with the highest scores. A high FUSE score indicates that these species play a central role in sustaining the community's functional diversity. Although the giant otter is considered part of the Brazilian Pampa current biodiversity (Andrade et al., 2023), it has disappeared from the southernmost regions of its original distribution, including southern Brazil, Uruguay and Argentina (Garbino et al., 2022; Noonan et al., 2017). In Argentina, occasional observations have been reported (Leuchtenberger et al., 2023), giving hope to its populational recovery. However, there are no viable populations in southern Brazil, implying that its ecological function was already lost.

Despite their high importance for ecosystem functioning, large-bodied animals are also those at greatest risk of extinction in the short term, as shown by our GLM results. Body mass associated with high extinction probability follows a tendency reported worldwide since the Late Quaternary, a pattern related to the extinction of the megafauna itself (Smith et al., 2018; Turvey & Fritz, 2011). The increasing susceptibility with body mass is driven by a combination of both intrinsic and extrinsic factors (Cardillo, 2003; Cardillo et al., 2005; Chichorro et al., 2019). Among intrinsic factors are low population densities, low reproductive rates and large geographic ranges (González-Suárez et al., 2013). For instance, large home ranges may push species to increase contact with people in fragmented habitats, also increasing their hunting vulnerability (Cardillo et al., 2005). Conversely, under the influence of perturbations, whether environmental or anthropogenic, small-bodied species can quickly recover due to their fast population growth (Johst & Brandl, 1997). Nevertheless, small mammals are sensitive to habitat loss, such as areas converted to monoculture (González-Suárez et al., 2013).

The Pampa holds about 9% of the Brazilian species diversity, in an area that represents 2% of the country (Andrade et al., 2023). However, only 1% of the Pampa is currently under protection, being the most poorly preserved biome in Brazil (Metzger et al., 2019). Protected areas provide several benefits for human populations such as clean air and water, healthy soils, disease and pest regulation, as well as cultural services (Mace et al., 2012). From a functional perspective, protected areas may serve as a refuge for wild species that contribute to maintaining ecosystem processes and functioning.

## 5 | CONCLUSIONS

Even though the ecological functions of the extinct megafauna might be partially compensated for by surviving species, introduced ones exhibit less diverse functional traits, as they mainly consist of

grazing ungulates. Nearest neighbour distances in functional space suggest that common domesticated livestock species are not functional substitutes for any species of the extinct megafauna in this South American ecosystem. Indeed, such species may contribute to new ecological functions and impacts that could pose a threat to native species. On the other hand, some introduced species may be acting as ecological substitutes for extinct deer (*A. ensenadensis*) and extinct horses (*E. neogeus*). Among these is the alien spotted deer (*A. axis*), which is currently included in population control programs, and the domesticated horse, *E. ferus*. This study illustrates how paleontological data may be useful for delineating and improving conservation and ecological restoration, and highlights that future conservation decisions should prioritize species important for preserving ecosystem functions.

#### AUTHOR CONTRIBUTIONS

Thayara S. Carrasco and Pedro L. Godoy conceived the ideas. Thayara S. Carrasco collected and analysed the data and led the writing of the manuscript. Catalina Pimiento, Tiago B. Quental and Pedro L. Godoy contributed to the methodological design, the interpretation of the data and critically revised the manuscript. All authors gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data and R code for analyses are available at Zenodo online repository: <https://doi.org/10.5281/zenodo.19339296> (Carrasco et al., 2026).

#### STATEMENT ON INCLUSION

The geographical distribution of the authorship team broadly represents the main region of interest in the meta-analysis. Data from local peer-reviewed studies were prioritized for the ecological characterization of all species.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Methodological details, and supplementary figures and tables.

**Figure S1.** Proportional distribution of traits related to body mass (a–c), guild (d–f), diet (g–i), digestive type (j–l), habitat (m–o), habit (p–r) and limb morphology (s–u) in extinct, living and introduced species of Brazilian Pampa.

**Figure S2.** Quality of functional spaces A1 to A5 according to the mean absolute deviation.

**Figure S3.** Functional space for extinct (red), living (blue) and introduced (green) species (top) as well as Pleistocene (red), Holocene (blue) and modern (green) groups (bottom) by pairs of axes A1 to A5.

**Figure S4.** Relationship between PCoA axes and traits used for functional diversity analysis.

**Figure S5.** Functional divergence (FDiv; top) and functional evenness (FEve; bottom) based on time (Pleistocene, Holocene and modern) and status (extinct, living and introduced).

**Figure S6.** Functional specialization (FSpe; a, b) and functional originality (FOri; c, d) based on status (on the left, extinct, living and introduced) and time (right, Pleistocene, Holocene and modern).

**Figure S7.** Number of species per functional entity for Pleistocene (top) and Modern (bottom) scenarios.

**Figure S8.** Interaction between traits and extinction probability, based on binomial GLM.

**Table S1.** IUCN status of native species from the Brazilian Pampa. LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; DD, data deficient.

**Table S2.** Alfa diversity results from functional spaces based on diet and habitat as fuzzy traits.

**Table S3.** List of lost and new functional entities, showing the species belonging to each functional entity.

**Data S1.** Traits dataset.

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