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Ecological cascades following trophic rewilding: A case of study with dung beetles in the Iberá wetlands of Argentina

Yanina Tamara Bobadilla [a], Mario Gabriel Ibarra Polesel [a,b], Andrés Gómez-Cifuentes [c], Gustavo Zurita [c,d,*]

[a] Universidad Nacional del Nordeste, Facultad de Ciencias Exactas y Naturales y Agrimensura, Av. Libertad 5470, Corrientes, Argentina
[b] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Centro de Ecología Aplicada del Litoral (CECOAL), Ruta 5 Km 2.5, Corrientes, Argentina
[c] Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Av. Tres Fronteras 183, Puerto Iguazú, Misiones, Argentina
[d] Facultad de Ciencias Forestales, Universidad Nacional de Misiones, Bertoni 128, 4405 Eldorado, Misiones, Argentina

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ABSTRACT

In the context of the biodiversity crisis, trophic rewilding became an important (but controversial) management practice to restore biological interactions and ecological processes. The success of this practice relies on the richness and abundance of other organisms, mainly invertebrates. In the Ibera wetlands of Argentina, a rewilding project reintroduced large herbivores locally extinct (the Tapir and Pampas deer, among others). Taking advantage of this project, we explored taxonomic and functional changes in dung beetle assemblages associated with replacing domestic livestock with native mammals. In five replicates, we sampled dung beetles with seven different baits, estimated temperature and grass eight and described landscape composition (forest and grassland cover). Through lineal and mixed models, NMDS and ANOSIM, we compared the taxonomic and functional dung beetle structure in both areas and explored the role of environmental variables. Trophic rewilding did not change dung beetle richness and the trophic structure of assemblages; however, it strongly modified the composition of species and their functional structure. Both areas shared 40 % of species. Species associated with cow dung (such as the exotic. *D. gazella*) became rare or disappeared in rewilded areas. Roller species dominated rewilded areas, whereas livestock areas exhibited a large abundance of burying species. The trophic rewilding changed dung beetle assemblages in the Iberá partially due to changes in the diversity of available dung but also on environmental conditions. Rewilding should include the medium and long-term evaluation of other taxa and ecological processes to quantify the conservation and functional value of species reintroduction.

1. Introduction

The global or local extinction of medium and large-sized native mammals and birds became one of the most striking consequences of the global biodiversity crisis (Dirzo et al., 2014; Finn et al., 2023). This group of vertebrates usually requires large extensions of native habitats and is particularly affected by changes in land use, unsustainable hunting, and other human-related activities. A growing literature emphasizes that these local extinctions have long-term consequences on ecosystem functioning, affecting ecological cascades, biotic interactions, and changing environmental conditions and the availability of trophic resources (Culot et al., 2013; Nichols et al., 2008; Raine et al., 2018; Raine and Slade, 2019).

Recognizing the ecosystem consequences of defaunation increased the need for an active intervention to restore biodiversity and biotic interactions. Through the active reintroduction of keystone species, trophic rewilding aims to recover and stabilize ecosystem processes in the long term, enhancing biodiversity (Perino et al., 2019). The idea behind trophic rewilding is to restore ecological interactions inside food weeds to increase the resilience of native ecosystems, including predation, competition, and mutualism (Svenning et al., 2016). Whereas trophic rewilding represents a valuable tool to confront defaunation in many ecosystems, it has also been at the centre of the debate (Rubenstein and Rubenstein, 2016). The recovery of ecological interactions following reintroductions relies on the existence of other organisms involved in lower or higher levels of trophic webs; however, this

* Corresponding author at: Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Av. Tres Fronteras 183, Puerto Iguazú, Misiones, Argentina.
E-mail addresses: mario.ibarrapolesel@exa.unne.edu.ar (M.G. Ibarra Polesel), gazurita@conicet.gov.ar (G. Zurita).

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assumption has rarely been tested (Svenning et al., 2016).

Dung beetles (Coleoptera: Scarabaeibae: Scarabaeinae) are a diverse group of invertebrates with 6850 species (Schoolmeesters, 2023). Whereas the majority of species in this group use mammal dung or carrion for feeding and nesting, a large variety of feeding strategies have been described, including species feeding and nesting on fruits, leaves, fungus, and others (Raine and Slade, 2019). Whereas coprophagous dung beetles tend to prefer dung from omnivore mammals (Bogoni et al., 2014), most species are generalists and take advantage of available dung (Frank et al., 2018). Adult dung beetles usually feed on dung-rich components, primarily bacteria in the liquid. In contrast, dung beetle larvae feed on the fibres and less nutritional elements from the dung (Holter, 2016). Dung beetles have been extensively studied for their ecological role; burying large amounts of dung and carrion improves soil quality, reduces parasite incidence and contributes to secondary seed dispersal (Nichols et al., 2008). Due to their ecological role, dung beetles are essential to rewilding projects involving the reintroduction of medium and large mammals. The absence of this taxa may lead to the accumulation of dung, an increase in parasite incidence and a reduction in soil quality (Bogoni et al., 2019). However, dung beetles are rarely considered in rewilding strategies (but see Fernandez et al., 2017).

Due to the strong relationship between mammals and dung beetles (particularly coprophagous species), the defaunation process has strong consequences on dung beetle assemblages, including the local disappearance or reduction in the abundance of native species and marked changes in assemblages composition (Culot et al., 2013; Nichols et al., 2008; Raine et al., 2018; Raine and Slade, 2019; Correa-Cuadros et al., 2022). Through ecological cascades, these changes affect forest regeneration and the maintenance of soil structure and quality (López-Bedoya et al., 2022). While the consequences of the defaunation process on dung beetles assemblages were described, the opposite process of dung beetle re-assemblage following trophic rewilding has been less explored (Fernandez et al., 2017; Genes et al., 2019; Svenning et al., 2016; van Klink et al., 2015; van Klink and WallisDeVries, 2018). However, the recovery of this interaction depends on the existence of a preserved dung beetle assemblage, also called the "ecological memory" of the ecosystem (Schweiger et al., 2019).

The biogeographic province of Iberá in Argentina is one the most extensive South American wetlands (Cózar et al., 2005). Since the end of the Pleistocene and the early Holocene, this region has suffered the extinction of most large herbivorous mammals (Dantas and Pausas, 2022; Di Bitetti et al., 2022). More recently, the processes of local extinction and a drastic reduction in the abundance of the remaining herbivorous and carnivorous mammals were accelerated due to unsustainable hunting, the introduction of domestic cattle and an increase in the frequency and intensity of fires. Since 2007, a large-scale trophic rewilding project in the Iberá aims to reintroduce or increase the local populations of native herbivorous and carnivorous, including two species of native deers; *Ozotoceros bezoarticus* (Linnaeus, 1758) and *Blastocerus dichotomus* (Illiger, 1815), the Tapir (*Tapirus terrestris*, Linnaeus, 1758), and the jaguar (*Panthera onca*, Linnaeus, 1758), among others (Donadio et al., 2022). In the wetlands of Brazil (the "Pantanal"), Correa et al. (2019) showed that the exclusion of cattle changed the composition of dung beetle assemblages but not richness. In another study, Correa et al. (2020) found a strong decrease in dung beetle richness and abundance in the short term after cattle remotion (first ten years) and the subsequent recovery following the recolonization of native mammals. However, the ecosystem consequences of native mammal reintroductions through ecological cascades have not been explored. In this study, we examine changes in the taxonomic and functional structure of dung beetle assemblages following the replacement of exotic herbivores (mainly cows and horses) by native herbivores in the Iberá. Also, we explore the role of local conditions and landscape composition in these changes. We expected that increasing the diversity of trophic resources would increase the abundance and richness of dung beetles. Moreover, we expected a higher preference for native dung in rewilded areas than in livestock areas.

2. Methods

2.1. Study area and experimental design

We collected dung beetles in December 2018 in the biogeographic province of Iberá wetlands (28″36′00″ S, 57″49′0″ W) in the north of Argentina (Fig. 1) (Arana, 2023). The Iberá is an extensive and heterogenous wetland, including large open water extensions, grasslands, and forests. Large portions of the Iberá are under national, provincial and private protection. The average temperature is 19.8 °C and 21.4 °C, with a defined cold and hot season and a total annual precipitation reaching 1700 mm (Ferrati et al., 2003).

In the last 20 years, a large-scale rewilding project in the Iberá replaced cows and horses with native mammals in private and governmental protected areas (Donadio et al., 2022). However, in nearby sectors, native grasslands were maintained for cattle raising. Within this area, we selected five replicates of each type of management. Livestock areas: areas with cattle; rewilded areas: areas with native fauna and without cattle. Sampling sites were at least one km apart to reduce spatial dependence (Fig. 1). A detailed description of the reintroduced mammals, including the number of individuals and the data on reintroduction, can be found in Zamboni et al. (2017) and Table 1. During fieldwork, the total number of cows was 5000 in a total area of 15000 ha (0.33 cow/ha).

To describe microclimatic conditions on each sampling site, we recorded temperature and humidity at the ground level using a datalogger HOBO Pro data-loggers (Onset Computer Corporation, Bourne, MA, USA). Automatic sensors stored both variables every 5 min for six days. We estimated average temperature and humidity during the 24 h period on each replicate. To assess vegetation structure, we measured the maximum height of grasses using a measured tape on 14 independent points randomly selected on each sampling site and averaged to obtain a single average value. On each point we measured the highest grass. To describe landscape structure and composition, we calculated the cover of forest and grassland in a radius of 500 m around each sampling site using QGis (QGis.org, 2023). We obtained data from the project MapBiomas Chaco (Project MapBiomas Chaco, 2023) using a classified image of the same year of field work.

To describe dung beetle assemblages, on each replicate we established a grid of 14 pitfall traps separated by 50 m among each to reduce spatial dependence (14 traps × 10 sampling sites = 140 traps) (Larsen and Forsyth, 2005; Mora-Aguilar et al., 2023). We performed dung beetles sampling in spring (2018), time of the year with the highest dung beetles activity in tropical and subtropical ecosystems (Halffter, 1991; Hernández and Vaz-de-Mello, 2009). Pitfall traps consisted of a plastic container (12 cm depth) filled with water and salt to avoid to the decomposition of collected individuals. We randomly baited pitfall traps with seven potential trophic resources (50 g. and two traps each bait): (I) faeces of Tapir (*Tapirus terrestris*), (II) Rhea (*Rhea americana*), (III) Pampas deer (*Ozotoceros bezoarticus*), (IV), Black howler monkey (*Alouatta caraya*), (V) Cow (*Bos taurus*), (VI) Capybara (*Hydrochoerus hydrochaeris*), and (VII) decomposing chicken. We selected baits according to the reintroduced native mammals and the most abundant native species in the area. We collected the dung of the different mammals in the field, stored it in the refrigerator and used it for a maximum time of 24 h after collection. We operated traps for six days, collecting individuals and replacing the bait every 48 hs (Mora-Aguilar et al., 2023). We stored collected individuals in 70 % alcohol and identified species using taxonomic keys and a reference collection (CA-UNNE). All individuals were deposited in the entomological collection from the Universidad Nacional del Nordeste (CA-UNNE).

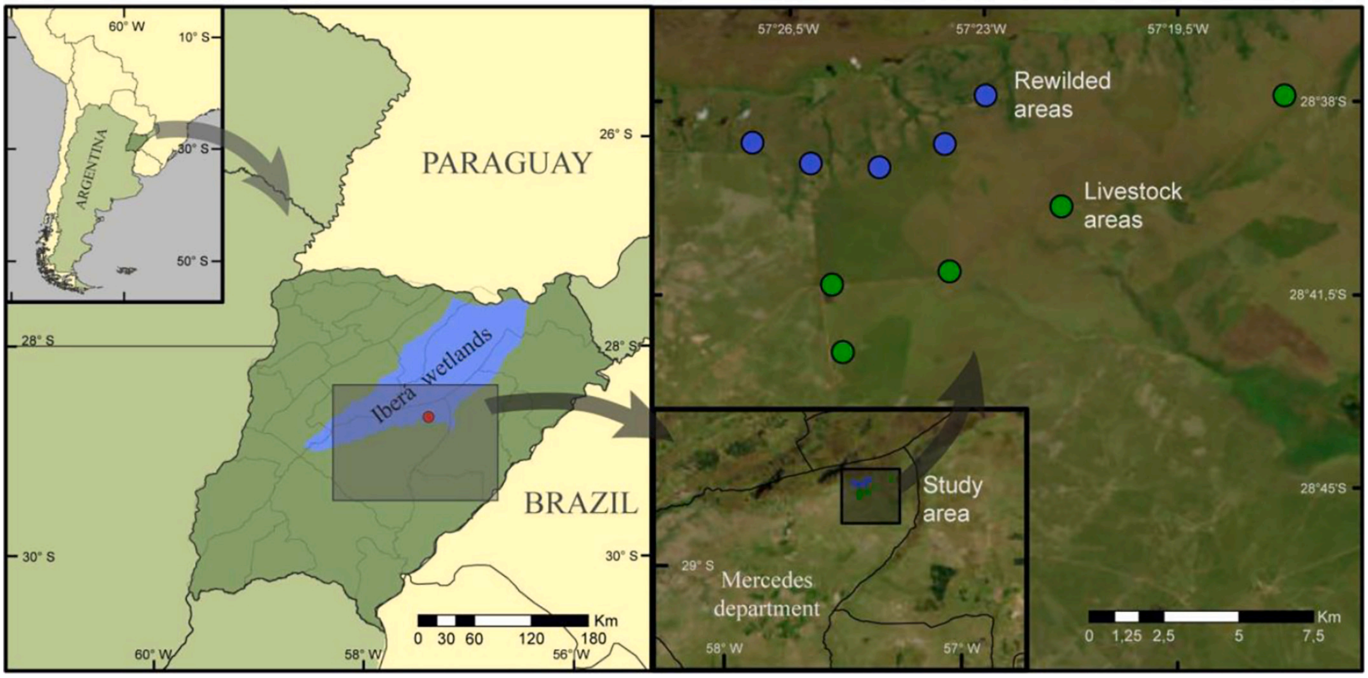

Fig. 1. Study area in the Iberá wetlands in northern Argentina. Rewilded sampling sites are marked in blue and livestock areas in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mammals reintroduced in the study area of the Iberá wetlands in northern Argentina (Zamboni et al., 2017).

Scientific name	Common name	First reintroduction (year)	Number of individuals
Myrmecophaga tridactyla	Giant anteater	2007	23
Ozotoceros bezoarticus	Pampas deer	2015	14
Dicotyles tajacu	Peccary	2015	29
Tapirus terrestris	Tapir	2017	7

2.2. Data analysis

To compare microclimatic conditions (average temperature and humidity), vegetation structure (average height of grasses), and landscape composition (forest and grassland cover) between areas (rewilded and livestock), we performed an ANOVA and Kruskall-Wallis analysis using Anova and kruskal.test functions from the stats package (R Core Team, 2021). When necessary, we explored the posthoc comparisons using the HSD.test function from the agricolae package (Mendiburu and Yaseen, 2020). To explore the completeness of our sampling protocol to describe dung beetle assemblages, we estimated the sampling coverage using the iNEXT software in both areas (Chao et al., 2016).

To compare alpha diversity, we calculated the first three orders of the Hill series (Hill, 1973); being 0D the number of species (richness), 1D, the exponential of the Shannon index representing the distribution of abundances and 2D, the inverse of the Simpson index representing the dominance. We estimated the Moran's I index to account for potential spatial autocorrelation on dung beetle taxonomic (diversity profiles) and functional (groups, see below) diversity using the Moran.test function from the spdep package (Bivand and Piras, 2015). As we did not find a spatial autocorrelation either in taxonomic or functional diversity (Table A.1), we performed a Linear Model using Generalized Least Squares (GLS) without spatial coordinates using the gls function from nlme package in both cases (Pinheiro et al., 2021). In this analysis, we compared rewilded and livestock areas, considering temperature, height of grasses and forest cover as explanatory variables. In all cases, we tested the assumptions of normality using the shapiro.test function from the stats package (Table A.2) (R Core Team, 2021).

To compare species composition, we first plotted ranking-abundance curves for each area. Then, we performed a non-parametric multidimensional scaling analysis (NMDS) to group sampling sites according to species composition (Anderson and Willis, 2003). In this analysis, we used the Bray-Curtis similarity index. We compared the composition of species between areas through an ANOSIM with a Bonferroni correction for p values (Clarke and Warwick, 2001). To compare the diversity of dung beetles caught on each bait between areas, we performed a linear mixed effects model (family = gaussian) or a generalized linear mixed effects model (family = poisson) with two fixed effects (sites and treatments) and one random effect (replicates of each area by bait, called block) using the lmer and glmer function from the lme4 package, respectively (Bates et al., 2015). To identify dung beetle species specialists and generalists of each habitat type, we performed a multinomial species classification analysis (CLAM) using the supermajority rule as the specialization threshold ($K = 0.67$, $p = 0.05$) (Chazdon et al., 2011). This analysis was performed using the clamtest function from the vegan package in R (R Core Team, 2021).

Finally, we use the classification proposed by Pessôa et al. (2017) to compare the functional structure of assemblages between areas, for which the species were classified into eight functional groups according to their daily activity (Hernández, 2002; Pessôa et al., 2017), feeding and nesting patterns (Doube, 1990; Halffter and Edmonds, 1982; Pessôa et al., 2017). Group 1 (G1): Nocturnal telecoprids; G2: Diurnal telecoprids; G3: Nesting endocoprids; G4: Small non-rollers; G5: Nocturnal nesting paracoprids; G6: Large nesting paracoprids; G7: Non-nesting paracoprids and G8: Diurnal nesting paracoprids. We obtained specific data for individual species from Pessôa et al. (2017), complemented with field observations and previous data (see Table 2). It is highlighted that the study mentioned above was carried out in the Pantanal, an area relatively close to Iberá, which is why 10 of the 11 genera collected in our study were also recorded by Pessôa et al. (2017), except *Bolbites* (Harold, 1868). As we previously mentioned, we used GLS analysis without spatial coordinates to compare the abundance of each

Table 2
The abundance of dung beetle species in rewilded (RA) and livestock (LA) areas of the Iberá wetlands in northern Argentina. The functional group (FG) proposed by Pessôa et al. (2017) is indicated for each species. Habitat specialization was calculated from a multinomial species classification analysis (CLAM).

Tribe	FG	Genus and species	RA	LA	Habitat specialization	Total
Ateuchini	G4	*Trichillum externepunctatum* Preudhomme de Borre, 1880		2	Too rare	2
Coprini	G5	*Ontherus aphodioides* Burmeister, 1874	2		Too rare	2
	G5	*Ontherus* sp. 1		1	Too rare	1
	G5	*Ontherus* sp. 2		35	Livestock	35
	G5	*Ontherus sulcator* Fabricius, 1775	110	43	Rewilded	153
Deltochilini	G1	*Anisocanthon pygmaeus* (Gillet, 1911)		39	Livestock	39
	G2	*Canthon bispinus* (Germar, 1824)	2	23	Livestock	25
	G2	*Canthon curvipes* (Harold, 1868)		4	Too rare	4
	G2	*Canthon daguerrei* Martinez, 1951	401	152	Rewilded	553
	G2	*Canthon denticulatus* Schmidt, 1922		7	Too rare	7
	G2	*Canthon mutabilis transversalis* Schmidt, 1920	5	10	Generalist	15
	G2	*Canthon ornatus thoracicus* Harold, 1868	1	4	Too rare	5
	G2	*Canthon podagricus* Harold, 1868	74	14	Rewilded	88
	G2	*Canthon quinquemaculatus* Castelnau, 1840		1	Too rare	1
	G2	*Canthon* sp. 1	1		Too rare	1
	G2	*Canthon* sp. 2		1	Too rare	1
	G2	*Canthon* sp. 3	1		Too rare	1
	G2	*Canthon* sp. 4	1		Too rare	1
	G1	*Deltochilum elongatum* Felsche, 1907	16	51	Generalist	67
	G1	*Malagoniella magnifica* Balthasar, 1939	4		Too rare	4
Onthophagini	G7	*Digitonthophagus gazella* (Fabricius, 1787)	1	9	Livestock	10
	G4	*Onthophagus hircus* Billberg, 1815	35	35	Generalist	70
	G4	*Onthophagus* sp. 1	1		Livestock	1
	G4	*Onthophagus* sp. 2	1		Too rare	1
	G4	*Onthophagus* sp. 3	2		Too rare	2
	G4	*Onthophagus* sp. 4		27	Too rare	27
Phanaeini	G6	*Bolbites onitoides* Harold, 1868	52	1	Rewilded	53
	G6	*Coprophanaeus* aff. *milon*	1	1	Too rare	2
	G6	*Coprophanaeus* sp.	1		Too rare	1
	G8	*Gromphas inermis* Harold, 1869	32	379	Livestock	411
Total abundance			744	839		1583
Total richnnes			21	21		30
Diversity of order (0D)			4.86	6.84		6.84
Diversity of order (2D)			3.01	3.98		3.98

functional group between areas. All analysis were performed in R (R Core Team, 2021).

3. Results

3.1. Microclimatic conditions, vegetation structure and landscape composition

Rewilded areas showed higher temperatures ($F = 34.51$, $p < 0.01$) than livestock areas, particularly during the day (9 to 19 h) (Fig. 2). Relative humidity was similar between areas (Chisq = 1.32, p = 0.25). Concerning vegetation structure, the maximum height of grasses was higher in rewilded areas than in livestock areas (80.3 ± 16.7 cm vs 39 ± 13.1 cm, $H = 19.25$, $p < 0.01$). At a landscape scale, both forest cover (4.5 % ± 4.4 vs 9.5 % ± 9.6) and grassland cover (95.5 % ± 4.7 vs 90.5 % ± 9.6) were similar between rewilded and livestock areas ($F = 0.87$, p = 0.38 in both cases) (Fig. 1.A).

3.2. Dung beetles diversity

We captured 1583 individuals from 30 species (Table 2). According to sample coverage, almost 99 % of species were captured in both areas (livestock = 99.4 %; rewilded = 98.7 %). Based on this result, we used the observed number of species to compare diversity between areas. A total of nine species (30 %) were only recorded in livestock areas, nine (30 %) in rewilded areas and 12 (40 %) were shared between areas. The CLAM analysis categorized six species as livestock specialists and fourth as rewilded specialists (Table 2). Regarding the GLS models, the abundance and the three levels of the Hill series (0D, 1D and 2D) were similar between livestock and rewilded areas (Table 2). Moreover, neither temperature, grass height, nor forest cover influenced the response of abundance and diversity of dung beetles (Table 3).

Whereas both areas showed similar alfa diversity, the composition of species differed. Rank-abundance curves showed different patterns of assemblage composition (Fig. 3). *Canthon daguerrei* (Martinez, 1951) was the most abundant species in the rewilded area, accounting for most captures (35 %). In contrast, *Gromphas inermis* (Harold, 1869) was the dominant species in the livestock area (26 %). Also, the rewilded area showed more rare species (with only one or two captures) than the livestock area. Consistent with these results, the NMDS and the ANOSIM clearly separated both areas ($R = 0.72$; $p < 0.01$) (Fig. 4).

3.3. Functional analysis and trophic preferences

Concerning trophic preferences, both areas showed similar structure. Tapir dung was the most attractive resource (particularly in the livestock area), capturing most species and individuals (Fig. 5), followed by carrion and monkey dung. In contrast, the other baits (Capybara, Deer, Cow and Rhea) showed low attractiveness (Fig. 5, Table A.3). Besides, we observed that the baits positively influence the total abundance and species richness (0D) of the dung beetle assemblages (*Chisq* = 93.33, $p < 0.01$); in contrast, the abundance of common (1D) and dominant (2D) species were similar between livestock and rewilded areas or baits as well as by their interaction (Table 4).

Finally, the functional structure of dung beetle assemblages, based on daily activity and nesting and feeding patterns, showed differences between areas (Fig. 6). Diurnal telecoprids (G2) were more abundant in the rewilded area compared to the livestock area. In contrast, diurnal paracoprids (G8) showed the opposite pattern. (Table A.4).

4. Discussion

Worldwide, the trophic rewilding of defaunated areas is a growing strategy to recover ecological interactions among species and increase

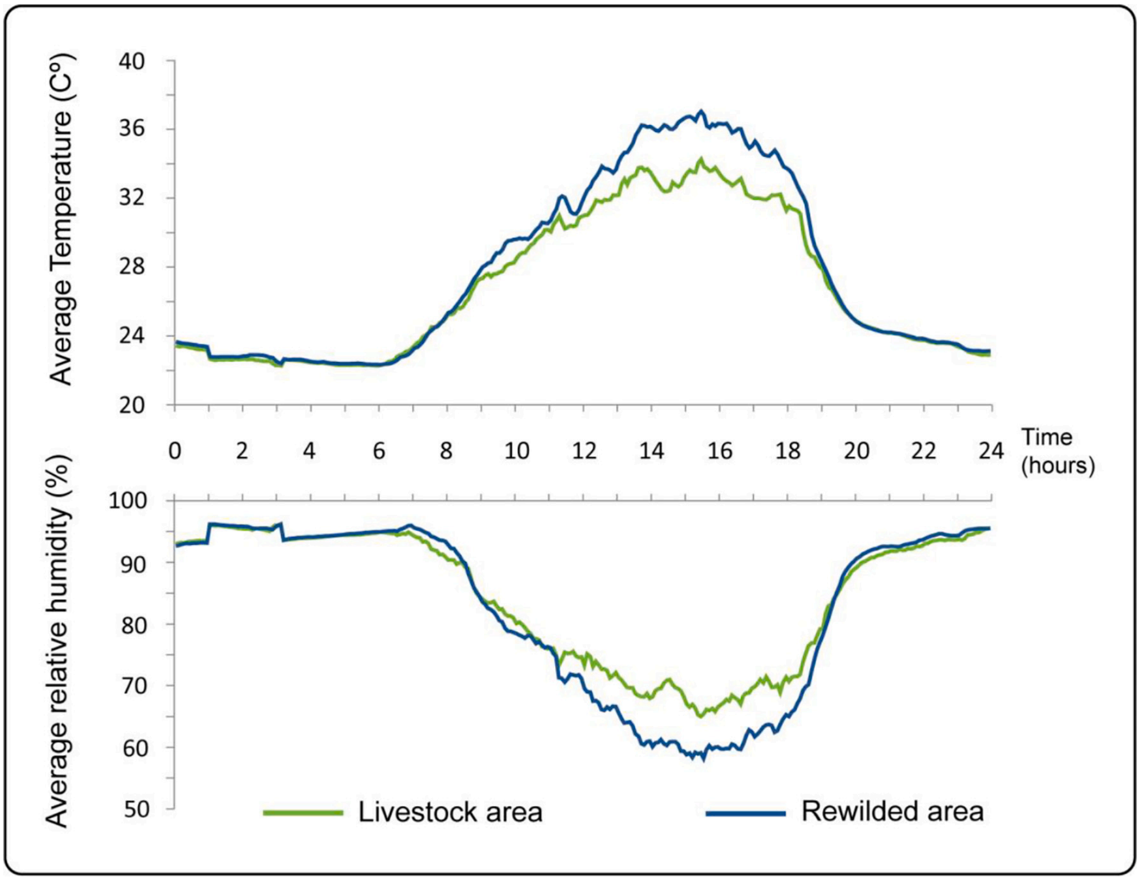

Fig. 2. The average temperature and relative humidity in livestock grasslands (green) and rewilded areas (blue) in the Iberá Wetlands in northern Argentina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Influence of microclimatic conditions and landscape structure and composition on the richness (0D) and abundance of common (1D) and dominant species (2D) of the dung beetle assemblages between the livestock and rewilded areas in the biogeographic province of Iberá. SE: Standard Error.

Richness (0D)	Value	SE	t-Value	p-Value
(Intercept)	94.76	180.13	0.53	0.62
Temp (average)	−3.06	6.66	−0.46	0.67
Grass (average)	−0.07	0.10	−0.74	0.49
Forest (%)	−0.12	0.21	−0.55	0.60
Sites	5.40	9.14	0.59	0.58

Abundance (1D)	Value	SE	t-Value	p-Value
(Intercept)	14.70	81.29	0.18	0.86
Temp (average)	−0.27	3.01	−0.09	0.93
Grass (average)	−0.08	0.04	−1.75	0.14
Forest (%)	−0.03	0.10	−0.34	0.75
Sites	3.08	4.12	0.75	0.49

Abundance (2D)	Value	SE	t-Value	p-Value
(Intercept)	−0.12	67.59	0.00	1.00
Temp (average)	0.24	2.50	0.10	0.93
Grass (average)	−0.07	0.04	−1.88	0.12
Forest (%)	−0.01	0.08	−0.18	0.87
Sites	2.07	3.43	0.60	0.57

the resilience of ecosystems to natural and human disturbances (Perino et al., 2019). Whereas trophic rewilding focuses on large species (usually mammals), this strategy success relies on other species involved in ecological cascades (Svenning et al., 2016). In this study, we take advantage of a large-scale rewilding project in wetlands of northern Argentina to explore the consequences of the replacement of livestock by native herbivores on dung beetles assemblages. Contrary to our prediction, the increase in the diversity of trophic resources (dung and carcases) did not increase the alfa diversity of dung beetles. However, the taxonomic and functional composition of species between livestock and rewilded areas was strongly influenced.

Previous studies with dung beetles showed the dependence of this taxon on large and medium mammals, either native or exotic (Correa et al., 2020); therefore, defaunation results in marked changes in the diversity and abundance of dung beetles (Culot et al., 2013; Nichols et al., 2008; Raine et al., 2018; Raine and Slade, 2019; Correa-Cuadros et al., 2022). However, the opposite process (refaunation) has rarely been tested. In one of the only studies, the reintroduction of monkeys in the Atlantic forest increased the secondary dispersion of seeds contained in faeces by dung beetles (Fernandez et al., 2017; Genes et al., 2019). In our study area, we expected the replacement of livestock by several large native mammals (such as the Pampas deer and the Tapir, among others) will increase the diversity of dung types and, consequently, the diversity of dung beetles. The similar richness found between areas may result from the two processes. First, with some exceptions, coprophagous dung beetles are trophic generalists, taking advantage of available dung, particularly from omnivorous mammals (Bogoni et al., 2014; Frank et al., 2018; Wurmitzer et al., 2017). Second, the local extinction of native large mammals in the Iberá occurred several decades ago (Zamboni et al., 2017), partially due to the large-scale introduction of cattle.

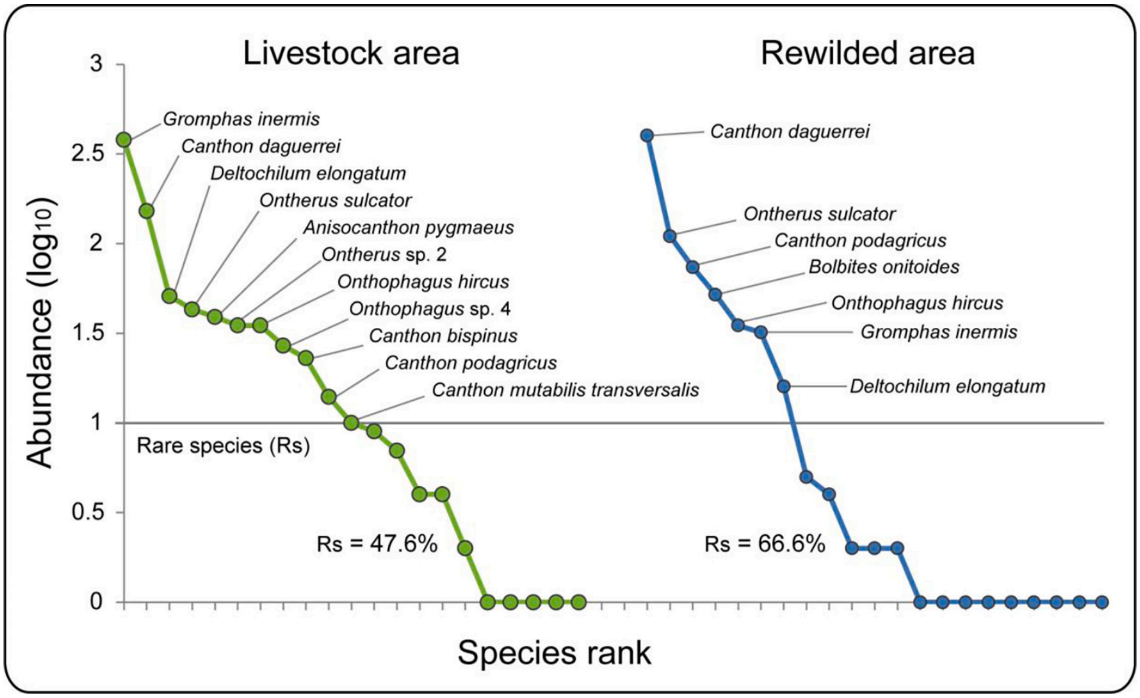

Fig. 3. Rank-abundance curves of species for the two studied areas of the Iberá wetlands in northern Argentina. The name of the most abundant species in each area is detailed, and the percentage of rare species (Re) is indicated, corresponding to all those below the horizontal line 1 of abundance (log10).

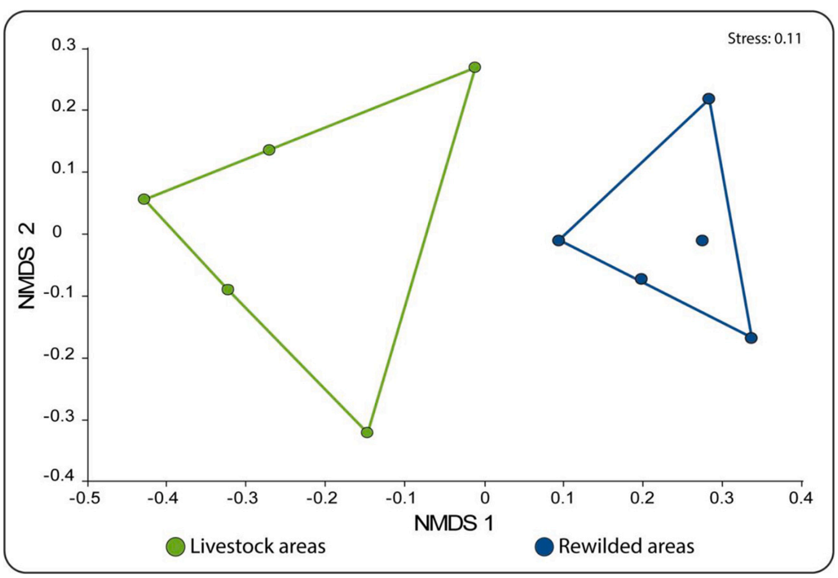

Fig. 4. Non-metric multidimensional scaling (NMDS) analysis of dung beetles in livestock (green dots) and rewilded (blue dots) areas of the Iberá wetlands in northern Argentina. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Local dung beetle assemblages may have survived using cattle dung, whereas specialised dung beetle species should become locally extinct following native mammals. Since old records or indirect evidence of dung beetle extinctions in Iberá are not available, separating these two potential mechanisms is impossible. Correa et al. (2019) in Brazilian wetlands (Pantanal) found similar results; the exclusion of cattle from grasslands did not affect dung beetle richness but changed the composition of species and the functional structure; however, these differences did not affect the ecological functions performed by dung beetles. Contrary to our results, in another study, Correa et al. (2020) found a strong decrease in dung beetles richness and abundance in the short term following cattle remotion and a subsequent recovery after ten years. These authors suggest that the slow recovery of native mammals after cattle removal may explain the recovery of dung beetle assemblages. In our study area, the active reintroduction of native mammals accelerates this process and explains the lack of differences in areas where cattle were replaced by native mammals.

Whereas rewilding did not change dung beetle diversity profiles and abundance, it strongly influenced the relative abundance of species. As a consequence, both areas exhibit clearly differentiated assemblages. Some species common in livestock areas (and identified in CLAM analysis) disappeared or became rare in rewilded areas, including *Anisocanthon pygmaeus* (Gillet, 1911), *Canthon bispinus* (Germar, 1823), *Ontherus* sp. 2 and *Gromphas inermis*. Others, like *Bolbites onitoides*

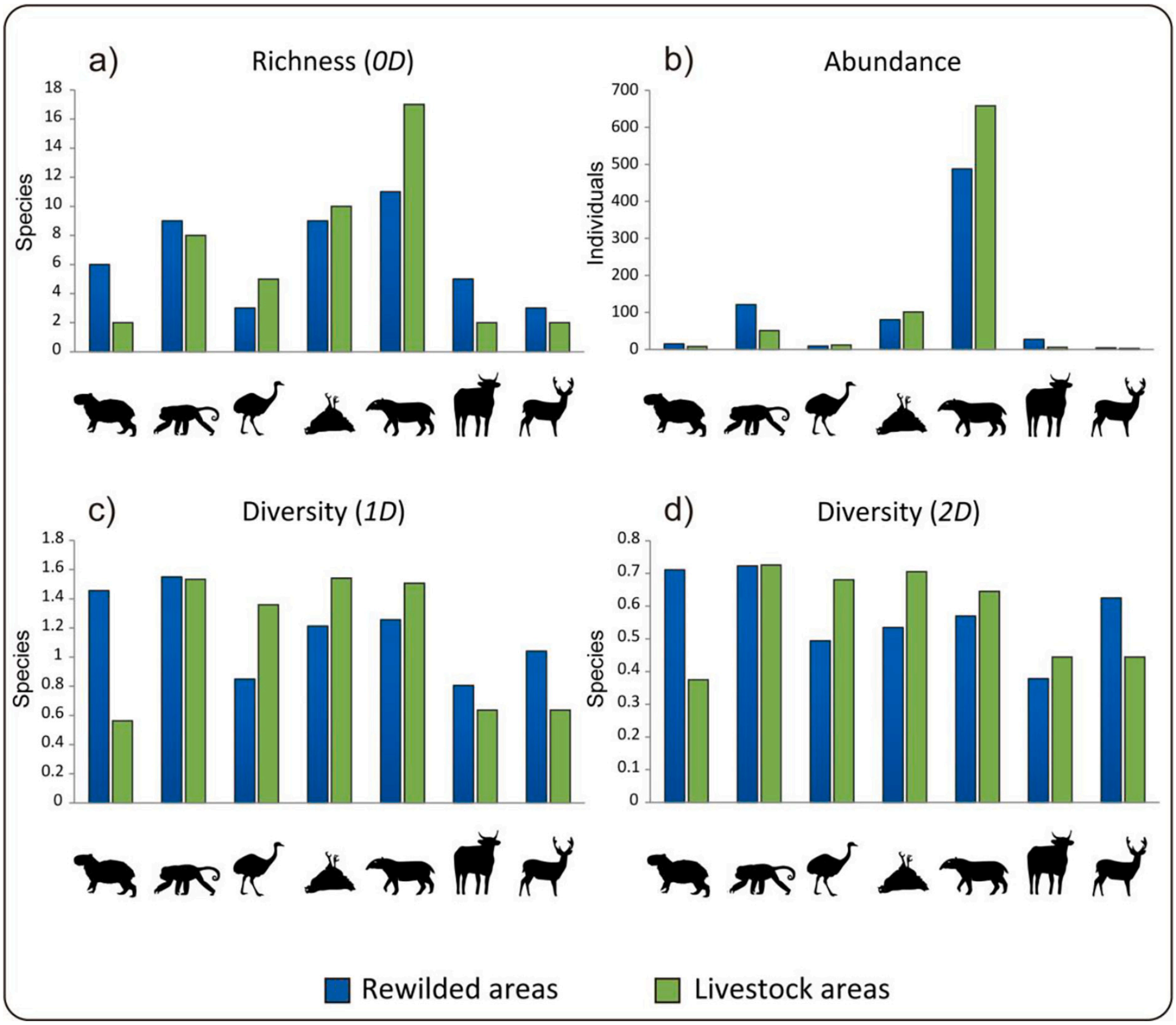

Fig. 5. Richness (a), abundance (b), diversity of order 1 and 2 (c, d) of dung beetles collected with different types of baits (Capybara, Monkey, Rhea, carrion, Tapir, Cow and Deer) in rewilded (RA) and livestock areas (LA) of the Iberá wetlands in northern Argentina.

(Harold, 1868), *Canthon podagricus* (Harold, 1686) and *C. daguerrei* showed the opposite pattern becoming more common in rewilded areas. However, these differences seem not to be related to differential dung preferences since, in both areas, the abundance and richness of species differentially attracted to the different baits were similar. Dung beetles are susceptible to changes in vegetation and soil structure and microclimatic conditions (Giménez-Gómez et al., 2020; Gómez-Cifuentes et al., 2019; Macedo et al., 2020; Noriega et al., 2021). Whereas environmental variables were not significant in statistical analysis, the higher temperature, lower humidity, and different vegetation structure in rewilded areas may have important role in explaining changes in species composition among areas. We did not measure soil conditions; however, it is expected that soil structure and composition also strongly differed among areas due to livestock activity (Lai and Kumar, 2020).

The idea that environmental conditions, rather than the availability of trophic resources, are responsible for the observed differences in species composition is reinforced by differences in the functional structure of assemblages. More than 45 % of dung beetles collected in livestock areas where diurnal nesting paracoprids; in contrast, only 4 % belonged to this functional group in rewilded areas. Paracoprids bury and nest directly under dung; as a consequence, species in this group are particularly affected by changes in soil conditions (Carvalho et al., 2021; Raine and Slade, 2019; Daniel et al., 2022); the lower temperature and higher humidity in livestock areas may favour this group of species. Diurnal telecoprids were dominant in rewilded areas (65 % of individuals) and less abundant in livestock areas (25 % of individuals). Telecoprids species roll the dung path to a variable distance from the source, allowing them to select microclimatic refuges with appropriate temperature and humidity to bury.

Tapir dung was, by far, the most selected resource, collecting >65 % of individuals in both habitats. Monkey dung and decomposing chicken (necrophagous species) were also selected baits. In contrast, Capybara, Rhea, Cow and Pampas deer showed shallow attraction. Previous studies showed contradictory results since Tapir dung was one of the least selected resources compared to monkey dung and other omnivorous mammals (Bogoni et al., 2014; Giménez-Gómez et al., 2020). Since most adult dung beetles use a filtering strategy to feed on the dung (Holter, 2016), dry dung with a low bacteria content (Capybara, Rhea and Pampas deer) is not attractive for most species. However, in the Cerrado of Brazil, Puker et al. (2013) showed that a Capybara dung attracted many dung beetles. In the case of the reintroduced Tapirs in Iberá, released individuals were supplemented with fruits and balanced feed, which probably changed the composition and humidity of natural dung and increased its attractiveness (pers. observation). A particular case is the exotic *Digitonthophagus gazella*, originally introduced in America to bury cattle dung in open pastures (Miranda et al., 2000; Noriega et al., 2020). In our study, this species was captured primarily in livestock areas and became rare in rewilded areas, probably due to its dependence

Table 4
Influence of areas (livestock vs rewilded) and baits on the richness (0D) and abundance of common (1D) and dominant species (2D) of the dung beetle assemblages between the livestock and rewilded areas in the biogeographic province of Iberá. Df: Degrees of freedom.

Abundance	Chisq	Df	p value
(Intercept)	0.29	1	0.59
Areas	1.27	1	0.26
Baits	1020.17	6	<0.01
Areas:Baits	60.58	6	<0.01

Richness (0D)	Chisq	Df	p-value
(Intercept)	1.27	1	0.26
Areas	0.99	1	0.32
Baits	93.33	6	<0.01
Areas:Baits	4.96	6	0.55

Abundance (1D)	Chisq	Df	p-Value
(Intercept)	7.81	1	0.01
Areas	0.01	1	0.92
Baits	0.00	6	1.00
Areas:Baits	0.00	6	1.00

Dominant (2D)	Chisq	Df	p value
(Intercept)	4.78	1	0.03
Areas	0.03	1	0.85
Baits	0.00	6	1.00
Areas:Baits	0.00	6	1.00

on livestock dung (Correa et al., 2020). Another even more notable case than the previous one was that of *G. inermis*, which in addition to being the most abundant species in livestock areas, showed a marked preference for these areas (92 % of individuals) compared to the rewilded areas. This species has a marked predilection for cow and horse manure, being abundant in livestock establishments in the region (Damborsky et al., 2015; Sánchez and Genise, 2008; pers. observation).

Both the rewilded and cattle areas located nearby; consequently, the role of climatic and geographical differences has a low influence on the observed differences. However, due to this short distance, some reintroduced mammals probably move from the rewilded to the cattle area. During fieldwork and from information provided by the organization responsible for the rewilding, the Pampas deer move between areas. However, the Tapir and the Peccaries remain in the rewilded area. Whereas dung from the Pampas deer exhibits a low attraction for dung beetles, this may have some influence on the observed results.

5. Summary

The number and magnitude of trophic rewilding projects are rapidly increasing worldwide. Whereas rewilding projects showed benefits for ecosystem functioning and resilience (Svenning et al., 2016), it also raised concern about their potential negative consequences (Rubenstein and Rubenstein, 2016). Invertebrates have been rarely considered in rewilding projects. However, the success of this strategy largely relies on the richness, abundance and functional diversity of these groups of organisms (Contos et al., 2021). On the large-scale rewilding project of the Iberá, we showed that the replacement of exotic livestock by large and medium locally extinct mammals strongly changes the composition and functional diversity of dung beetle assemblages. Moreover, trophic rewilding compensates for the potential negative consequences of cow removal on dung beetle assemblages (Correa et al., 2020). However, these changes are probably more dependent on changes in environmental conditions (soils and microclimate) than the diversification of trophic resources. This is consistent with the trophic generalism of most dung beetle species. Future studies should focus on the ecosystem consequences of these changes on ecological functions performed by dung

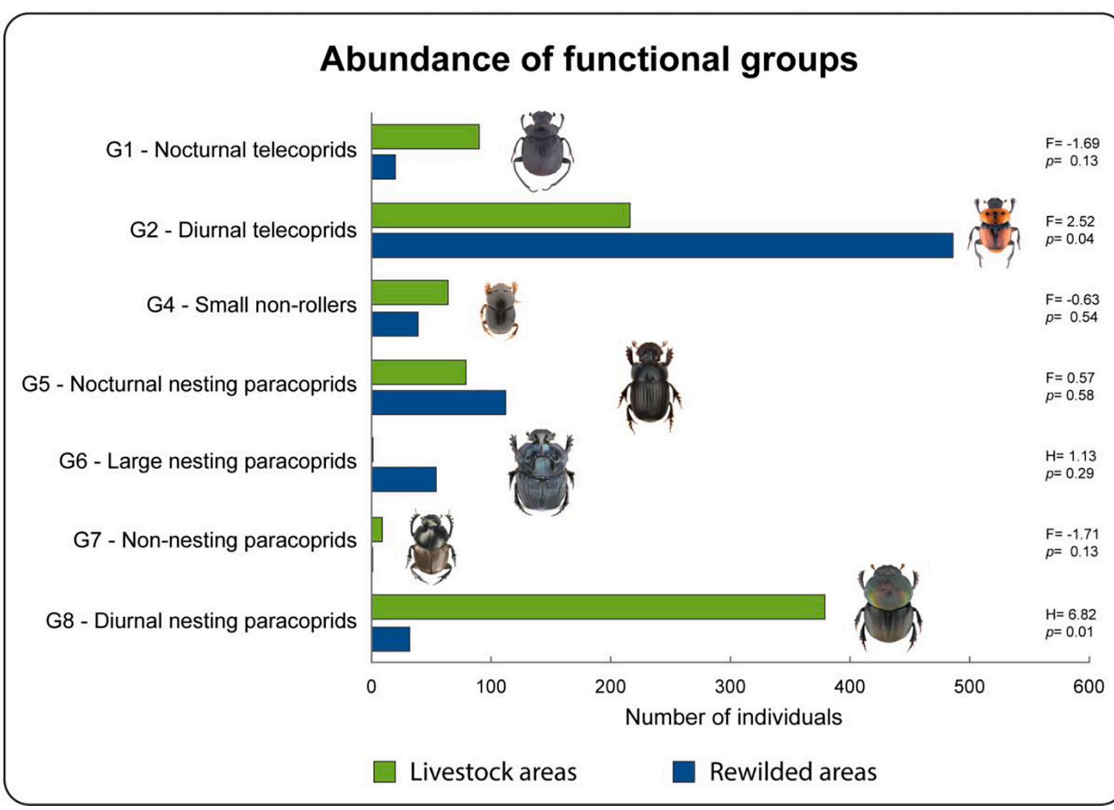

Fig. 6. The abundance of functional groups in rewilded and livestock areas of the Iberá wetlands in northern Argentina.

beetles (nutrient cycling, secondary seed dispersal, parasite control), and other related taxa. Moreover, long-term studies will provide more information on the potential re-colonization of locally extinct dung beetles and the local disappearance of species associated with cattle dung.

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CRediT authorship contribution statement

Bobadilla: Conceptualization, Methodology, Investigation, Data Curation, Writing - Original Draft. Ibarra Polesel: Conceptualization, Methodology, Formal analysis, Resources, Writing - Original Draft. Gómez-Cifuentes: Formal analysis, Resources, Writing on the revised version. Zurita: Conceptualization, Conceptualization, Formal analysis, Resources, Writing - Original Draft, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All primary data is included in the supplementary material of this article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110478.

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