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REVIEW ARTICLE

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Global distribution and richness of terrestrial mammals in tidal marshes

Alejandro D. Canepuccia | **María Sol Fanjul** | **Oscar O. Iribarne**

Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar Del Plata (UNMDP) - Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Mar del Plata, Argentina

Correspondence
Alejandro D. Canepuccia, Instituto de Investigaciones Marinas y Costeras (IIMyC), CC 573 Correo Central, B7600WAG Mar del Plata, Argentina.
Email: acanepuc@mdp.edu.ar

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Abstract

Aim: Understanding the determinants of species distribution and richness is key to explaining global ecological patterns. We examined the current knowledge about terrestrial mammals in tidal marshes and evaluated whether species richness increased with the marsh surface area and/or with their proximity to the equator and whether species distribution ranges decreased with latitude.

Location: Global.

Methods: We reviewed the existing literature on terrestrial mammals in tidal marshes. We examined their ecological characteristics (e.g. habitat specialists, native or alien), predicted their variation in species richness and range size along latitude, and explored factors, such as surface area, underlying the global patterns found.

Results: We found 962 records, describing 125 mammalian species using tidal marshes worldwide, also including several alien species. Most species (95%) were not marsh specialized, and some (18%) were of conservation concern. There were information gaps in South America, Africa, Australia and Asia, and a lack of information about mammalian ecological roles worldwide. We found that species richness increased with surface area, and showed a bimodal pattern peaked between 40° and 50° latitude in each hemisphere. We found no relationship between latitude and species range size.

Main conclusions: Our worldwide findings revealed a broader range of tidal marshes inhabited by terrestrial mammals, and higher values of species richness than previously reported. The bimodal pattern of species richness was consistent with the species–area hypothesis, but it also suggested that further studies of species distribution in relation to historical and environmental factors will yield significant insights about variables driving richness in tidal marshes. Despite terrestrial mammal ubiquitous distribution in these ecosystems, there are considerable geographic gaps as regards knowledge about their functional importance and the impact of alien species on tidal marsh functioning. Consequently, extending our research efforts is key to planning the conservation of these coastal ecosystems.

KEYWORDS
coastal environments, ecological roles, ecosystems relationship, energy flow, latitudinal pattern of species richness, terrestrial mammals, tidal marshes

1 | INTRODUCTION

Tidal marshes are coastal ecosystems distributed along the coastline of all continents but Antarctica (Chapman, 1977; Mcowen et al., 2017). They are vegetated ecosystems that are regularly flooded and drained by seawater during the tidal cycles and used by both marine and terrestrial species. Coastal environments support almost 40% of the human population (Kummu et al., 2016), leading to a strong anthropic pressure (e.g. Gedan et al., 2009; Nolte et al., 2013). That pressure is also evidenced by the fact that these environments are among those most affected by the presence of alien species. This can affect species' interactions with native species, biodiversity and ecosystem function (Williams & Grosholz, 2008). During the last centuries, these facts, together with the increase in global climatic change ratios (e.g. salinization, sea-level change and extreme climatic events; Millennium Ecosystem Assessment Panel, 2005; Taillie et al., 2019), have led to the degradation or disappearance of about half of the world's tidal marshes (Costa et al., 2009; Barbier et al., 2011; Valiela et al., 2006) and could reach up to 90% if no mitigation measures are taken (Crosby et al., 2016; Giuliani & Bellucci, 2019). Along with the loss of marshes, not only the ecosystemic services they provide will be lost (i.e. carbon sequestration, Hopkinson et al., 2012; coastal protection and seawater maintenance, Barbier et al., 2011; Duarte et al., 2013; NOAA, 2017) but also its role as diversity reservoir will be compromised (Gedan et al., 2009; Greenberg et al., 2014; Hansen & Reiss, 2015; Valiela, 2006). Despite recent efforts to address the challenge of tidal marsh biodiversity conservation, their value for terrestrial species remains unknown. The lack of such basic information limits our understanding of the environmental factors driving terrestrial species distribution and diversity.

Given tidal marshes' global distribution, we would expect their species richness to vary following two biogeographic hypotheses: richness increasing as related to the surface area of marshes (Lomolino, 2000; Rosenzweig, 1995), and/or increasing in relation to their proximity to the equator (Hillebrand, 2004; Willig et al., 2003). The first one has found much support in literature with only a few exceptions reported (e.g. Dunn & Loehle, 1988). The second one has been evidenced for terrestrial plants and animals (Chaudhary et al., 2016; Gaston, 2000; Kaufman, 1995; Kinlock et al., 2018), and even for mangroves (Rog et al., 2017), which replace tidal marshes in tropical regions (Valiela & Cole, 2002). This pattern has been associated with the fact that species inhabiting temperate and Polar Regions have larger distribution ranges than tropical ones (Rapoport's rule; Stevens, 1989), which contributes to underlying the latitudinal richness gradient. However, global information on these patterns for tidal marshes is almost non-existent, particularly for terrestrial organisms. So, large-scale studies are needed to identify differences in broad-scale (geographical) spatial patterns in tidal marshes biodiversity.

As tidal marshes are highly productive (Odum, 1971), they are important sources of nutrients to coastal environments (Burden et al., 2013), providing food and refuge for a broad diversity of marine species (Foster et al., 2013; NOAA, 2017). But it can also be important for many terrestrial species such as passerine birds (e.g. Greenberg et al., 2014; Musseau et al., 2018) and mammals (Greenberg et al., 2006; Longenecker et al., 2018). However, since studies have been mainly focused on tidal marshes as aquatic ecosystems (e.g. Gedan et al., 2009; NOAA, 2017; Valiela & Cole, 2002), their role as an environment for terrestrial mammal species remains less studied. As a consequence, little is known about terrestrial mammals using these environments, their importance in tidal marsh functioning or the tidal marsh–inland relationship. As many of these mammalian species are not marsh-specialist users, they could respond to tidal marsh area loss by dispersing to neighbouring inland environments. Nevertheless, in the last century, most of the natural coastal environments have been transformed into crop fields or livestock areas (Kummu et al., 2016; Hughes & Paramor, 2004), so tidal marshes can offer suitable conditions for many non-marsh-specialist species. For tidal marsh habitat specialist species, the situation becomes even more complex because their conservation is directly related to tidal marsh area loss (Greenberg et al., 2006). Indeed, some of these species have been declared of conservation concern (Greenberg et al., 2006; IUCN, 2022; Reid & Trexler, 1992) since much of their original environment has already been lost (Kummu et al., 2016). Furthermore, the ecological roles that mammals may play in tidal marshes are poorly understood. Both habitat specialist and non-specialist species can have important ecological effects on tidal marshes' environment functioning, affecting for example, the primary productivity and plant diversity (e.g. Canepuccia et al., 2015; Elschot, 2015; Sharp & Angelini, 2019), as well as their prey population abundances and reproductive success (e.g. Buzuleciu et al., 2016). In addition, as has been seen in other coastal environments (e.g. Carlton & Hodder, 2003), non-marsh-specialized mammals could provide important ecosystem services by transferring energy from sea to land ecosystems. So, it is essential to assess our knowledge, not only about the species of terrestrial mammals present but also about the ecological roles of these species to understand the trade-offs between redundancy and diversity in the face of the accelerated loss of marsh environments. This knowledge is essential to set effective management and conservation strategies for marshes, their biodiversity and their ecosystem services.

In this study, we aimed to review the existing global scientific knowledge about terrestrial mammals using tidal marshes, their predicted distribution and richness variation around the world. We explored what was known about the role of terrestrial mammal species in tidal marshes, alien species in these environments and where there were knowledge gaps. With the generated database we tested the hypotheses of (a) the species–area relationship, by evaluating the relative importance of the area surface of tidal marshes in driving the general patterns of species richness, and (b) the latitudinal diversity gradient, by evaluating if the estimated mammal richness in tidal marshes decreases as latitude increases worldwide. In addition, we analysed one of the conceptual components of Rapoport's rule, which predict that the size of species' distribution ranges decreases with latitude, contributing to underlying the richness of latitudinal patterns.

2 | METHODS

2.1 | Criteria of the literature search

We searched scientific information published about species or subspecies of terrestrial mammals registered in tidal marshes around the world and published until 2021. We considered 'tidal marshes' as those marshes affected by astronomical tides (e.g. Miller & Egler, 1950). Defined as such, we included salt marshes and brackish marshes, but we did not include freshwater marshes that are not affected by oceanic tides.

To carry out the literature search, we used Scopus and Google Scholar databases using the terms 'salt marsh OR coastal marsh OR tidal marsh OR brackish marsh' together with the term: 'mammal' inside the 'all fields'. We evaluated all papers published in indexed scientific journals, but we did not restrict our overview to peer-reviewed articles. We also considered grey literature, including reports, databases created by governmental and non-governmental organizations, universities, institutes Conferences, Proceedings and Theses. In the case of Theses that were later published in peer-reviewed journals, we only included the journal-published information to avoid duplication of the information/report over a species. When we identified particular taxa names of species in the scientific literature reported in tidal marshes, we included them in another specific search (i.e. Alopex, Badger, Bear, Bobcats, Canid, Cannis, Capra, Cat, Ctenomys, Dasypus, Deer, Didelphis, Equus, Felids, Ferret, Fox, Grison, Guanacos, Guinea pig, Hare, Hedgehogs, Horse, Kangaroo, Lemming, Lemurs, Macropodidae, Marmot, Meadow, Microtus, Mink, Mouse, Mus, Pig, Possum, Primates, Rabbit, Raccoon, Rangifer, Rattus, Rodent, Shrew, Skunk, Small mammal, Squirrels, Sus, Talpide, Tapir, Tasmanian devil, Ungulate, Ursus, Wallabia, Weasel, Wolf, and Wolves). Given that the study aims at evaluating the role of tidal marshes as terrestrial habitats, we focused on fully terrestrial species. Consequently, we did not include species that rely on aquatic ecosystems, such as pinnipeds, muskrats or nutria. We neither included domestic mammals nor mammals under farm management (i.e. mammals with human dependence such as cattle taken to marshes for grazing), but we did include species that have become feral independently from humans (e.g. wild pigs, feral horses).

All of the studies found in the literature were examined, and their reference lists were checked for other relevant articles. Among these studies, we only included those where the authors recorded directly – by captures or sightings – or indirectly – by footprints or faeces – the presence of a species of terrestrial mammals in tidal marshes. In this sense we excluded the studies: (a) where it was not clear if mammalian species were recorded in the tidal marsh or if they were elsewhere; (b) in which the record was based on remains (e.g. bones and hair) from predators, faeces, raptor bowling or based on blood of mosquito stomachs since it is not possible to define the environment where they were captured; and (c) that carried out experiments (e.g. exclusions) but authors who never confirmed the presence of a mammal species, directly or indirectly. When authors confirmed the presence of species through scientific bibliography, we revised the referenced study/ies and evaluated them to decide their inclusion according to the previously mentioned criteria.

From each scientific study that fitted the search criteria, we compiled: (1) author/s, year of publication and publication source (peer-review Journal, Thesis, Report, or Proceedings); (2) registers to the lowest ranked taxa level (species or subspecies) of terrestrial mammals, including their current scientific name if their valid name had been changed from the date of publication; (3) methods of detection of the species; (4) the dependence of species on the marsh (habitat specialist or non-specialist species); (5) conservation status and if it was a native or an alien species (Biancolini et al., 2021; IUCN Red List, 2022); (6) trophic guild, i.e. herbivores, omnivores and predator – including insectivores and carnivores (IUCN Red List, 2022; see Table S2); (7) type and vegetation that dominated the tidal marsh; (8) location of the marsh: continent, macro-geographic region, country, locality and geographic position – latitude and longitude; and (9) topic of the study (as distribution, biodiversity, behaviour and ecology or if the species had been reported as an incidental record).

2.2 | Species distribution and richness by an overview of scientific studies

We employed the geographic positions (latitude and longitude) reported in each study to estimate the distribution of terrestrial mammalian species that were recorded in salt marshes worldwide. When the study did not provide geographic positions, we located the site/s reported in the study on Google Maps and georeferenced them as precisely as possible according to specifications given by the author/s. With the generated database, we made a map of the locations of each terrestrial mammal species registered in tidal marshes. This map was made and analysed with the statistical program R (R Core Team, 2017) using the packages *ggplot2* (Wickham, 2016) and *maps* (Becker et al., 2018).

To analyse species richness of terrestrial mammals in tidal marshes, we calculated the number of species recorded in marshes along latitudes worldwide. At different latitudes, the number of coasts is different, and therefore, we could be led to overestimate species richness at latitudes with a greater number of coasts. For example, on one extreme of this bias, at −52°S, we observe the east and west coasts of South America; and on the other extreme, at 25°N, we find the west and east coasts of North America, the west and east coasts of the African continent, the west and east coasts of Saudi Arabia, the west coast of Pakistan and the east coast of China. To standardize these estimations, we determined the value of species richness for each latitudinal degree and each coastline of each continent landmass facing a given ocean (see Table S3). After that, we grouped richness values into bands of 10° latitude for the statistical analysis. Despite data transformation, no normal distribution of data was achieved (Shapiro–Wilk test, $p < .05$). Therefore, the non-parametric analysis of variance Kruskal–Wallis was used to test differences in species richness among bands of

10° latitude (*kruskal.test* function in R Core Team, 2017), followed by post hoc comparisons (Dunn's test), to check for pairwise significant differences (Zar, 2009). We examined whether species richness was related to the surface of a tidal marsh area, or if it was related to differential research efforts carried out among world regions. We, therefore, calculated the species richness for each of those macro-geographical regions of the world as defined in Mcowen et al. (2017). Then, we assessed if the distribution data of species richness were related to the area of tidal marsh surfaces (areas of marshes were obtained from Mcowen et al., 2017), or if it was related to the number of scientific studies in each macro-geographical region. We performed a linear model which was built by using the *lm* function of the statistical software R (R Core Team, 2017) to analyse if the species richness was related to the area of tidal marsh surfaces or the number of scientific studies in each macro-geographical region.

2.3 | Estimation of species distribution and richness

Scientific reports of terrestrial mammal species in tidal marshes were restricted to a few sites in a few regions worldwide. For this reason, we also calculated an 'estimated species richness'. For this purpose, we first generated a dataset of locations of tidal marshes from our literature search together with the dataset of worldwide locations published by Mcowen et al. (2017). With this new dataset, we generated a global map of tidal marshes (R Core Team, 2017; Wickham, 2016). Then, we estimated the presence of each terrestrial mammal species in tidal marshes worldwide by the following criteria: if a terrestrial mammal species was recorded using a tidal marsh in part of its distribution range, we inferred that it could be present wherever tidal marshes overlap or neighbour its geographic distribution (sensu Rog et al., 2017). For example, if the field mouse (*Akodon azarae*) was recorded in the Mar Chiquita (−37.747 S, −57.435 W) and Bahia Blanca marshes (−38.897 S, −62.081 W; e.g. see Canepuccia et al., 2015) and considering its reported distribution, we inferred that this species is present in all tidal marsh areas overlapping with its distribution range. In the case of tidal marsh habitat specialist species, we used information on their distribution range and overlapped it with the global database of tidal marshes. The geographical range distribution of each species was obtained from (IUCN Red List, 2022), DAMA: the global distribution of alien mammals database (Biancolini et al., 2021) and other scientific information (see Table S2 for details). With this database, and as was described for the overview of scientific studies, we estimated species richness of terrestrial mammals in tidal marshes around the world (a) along latitude, (b) grouped by 10° latitudinal bands of every coastline belonging to each continent landmass that faces a given ocean and (c) for each macro-geographic region defined by Mcowen et al. (2017). Neither normal distribution (Shapiro–Wilk test, $p < .05$) nor equality of variance (Levene's test, $p < .05$) of data was achieved by data transformation. Therefore, a non-parametric analysis of variance (Kruskal–Wallis test) was used to test differences in estimated species richness among bands of 10° latitude (*kruskal.test* function in R Core Team, 2017), followed by post hoc comparisons (Dunn's test) to check for pairwise significant differences (Zar, 2009). Then, to examine the species–area relationship (e.g. Lomolino, 2000; Rosenzweig, 1995), we analysed the relationship between species richness and the surface of tidal marsh areas for each macro-geographic region reported by Mcowen et al. (2017) by using the *lm* function (R Core Team, 2017).

To examine the latitudinal richness gradient (i.e. if species richness decrease with increasing latitude, Hillebrand, 2004; Willig et al., 2003), we analysed if variation in the distribution of the estimated species richness was related to latitude by using the *lm* function (R Core Team, 2017). To test variations in terrestrial mammal ranges with latitude, expected according to Rapoport's rules (e.g. Stevens, 1989), we calculated the amplitude of the latitudinal range of distribution for each species, and then, a latitudinal middle point for each species range. Based on latitude values of that distribution mid-point for each species, we carried out the *lm* function (R Core Team, 2017) to evaluate if the latitudinal range size of species increased with latitude. To identify vacant areas of scientific knowledge, the estimated species richness was compared with species richness recorded through the studies reviewed. Despite data transformation, no normal distribution (Shapiro–Wilk test, $p < .05$) of species richness data was achieved. Then, differences between both "species richness" along latitudinal bands were tested by a two-way permutation ANOVA test (with 10,000 permutations). This permutation-based approach is robust against violation of normality and was made using function *aovperm* in R package *permuco* (Frossard & Renaud, 2021). This was followed by post hoc comparisons (Dunn's test) to check for pairwise significant differences (Zar, 2009). Finally, we built a global map comparing variations in (a) the estimated species richness and (b) those found in the review of studies. To optimize the data visualization on the map, and better observation of vacant areas of information, both species richness was recalculated for every 5° latitude. With these new datasets, by using the *ggplot2* package, library (maps) (Wickham, 2016), we constructed a global map showing both richness.

3 | RESULTS

3.1 | Species distribution and richness by an overview of scientific studies

Our scientific search resulted in the evaluation of 3659 studies published between 1898 and November 2021. Among these studies, only 285 recorded (directly or indirectly) and reported the location of terrestrial mammal species or subspecies in tidal marshes (see Table S1). There were 962 records corresponding to a total of 125 different species of terrestrial mammals in tidal marshes. These species included 33% Rodentia, 26% Carnivora, 10% Soricomorpha, 8% Artiodactyla, 7% Lagomorpha, 7% Eulipotyphla, 3% Didelphimorphia, 3% Diprotodontia, 2% Dasyuromorphia and

2% Perissodactyla. Among the 125 species, 10 were described as habitat specialist inhabitants of these ecosystems.

However, only five of these 10 species/subspecies (i.e. rodents: *Reithrodontomys raviventris*, Dixon 1908; shrews: *Sorex ornatus sinuosus*, Grinnell 1913, *S. ornatus salicornicus*, von Bloeker 1932, and *S. vagrans halicoetes*, Grinnell 1913; and rabbit: *Sylvilagus aquaticus littoralis*, Nelson 1909) are currently accepted as valid taxa (ITIS, 2022; See Table S2 for details). The remaining 120 species were also associated with different types of terrestrial ecosystems. Nearly 40% of these species were associated with short grass vegetation (e.g. freshwater marshes, grassland and tundra), while about 19% of species were associated with forest ecosystems. The percentage of species associated with anthropic environments (urban and farms) was around 11%. Of all species recorded, 39% were carnivores and insectivores (predators), 36% were herbivores and 26% were omnivores. There was conservation status information for 85% of these species. Among these, 72% were labelled as Least Concern and 13% were Conservation Concern. Among the latest, 8% were Endangered and Critically Endangered species, 5% were Near Threatened or Vulnerable and the remaining 1% have been recorded as Extinct in the wild but reintroduced (see Table S2 for species details). The main topics of the studies were behaviour and habitat selection (26.69%), distribution and biodiversity (25.17%) and food web (11.29% diet descriptions, 5.17% as predators 2.75%, as prey 1.29%, as herbivores and 3.71% as granivores).

We found that about 61.6% of studies recording terrestrial mammals in tidal marshes were from the North American continent, where there is 34.39% of the world's marshes surface area (Table 1). On its Pacific coast, most of the studies were recorded on the coast of the Gulf of San Francisco (USA), describing *Salicornia* spp., *Atriplex* spp. and *Distichlis spicata* as the dominant vegetation. In that area, we found records of 34 species, including 3 subspecies. Most of them were small-sized species (rodents and shrews), with the presence of endangered species (Table S2). On the Atlantic coast, most studies came from the South-East and South coast of the North American continent. In these regions, tidal marshes were reported as dominated by plants of *Spartina* spp., *Juncus* spp., *Phragmites australis*, *Iva fructecens* and *Salicornia* spp. There we found a total record of 50 species (Table 1), including 15 subspecies, with habitat specialist and non-specialist species of small mammals (rodents and shrews), with the presence of endangered subspecies. Lynxes, rabbits, raccoons and mustelids were reported among medium-sized mammals, and bears, deers and canids among large ones. The presence of alien mammals, such as rats, mice, wild horses and wild pigs, was also reported (see Table S2). In the north of the North American continent (Alaska and Canada), tidal marshes are dominated by *Spartina* spp., *Carex* spp., *Plantago* spp. and *Triglochin* spp. plants. In these marshes, we found records of seven species of terrestrial mammals, most of them of large sizes, such as grey, black and polar bears as well as wolves (see Table S2). For Mexico, with 5% of the world's marsh surface, we have not found any scientific reports of terrestrial mammal species in tidal marshes.

In the Australian continent, including New Zealand, there are extensive areas of tidal marshes (25% of the world's marsh area), but here, we only found 2.7% of the studies on terrestrial mammals (Table 1). These tidal marshes are described to be dominated by *Sarcornia* spp., grasses and reeds. In this region, we recorded information on 11 species of terrestrial mammals. All of them were not marsh-specialized medium- and large-sized species, including some endangered ones (Table 1).

In the Asian continent, Russia has about 13% of the tidal marsh area of the world. However, we have not found published scientific studies recording terrestrial mammals' presence in those tidal marshes. In China, there are also extensive areas of tidal marshes, about 10% of the world's tidal marshes; however, we only found 2.3% of studies on terrestrial mammals. These marshes are dominated by grasses such as *Imperata cylindrica*, *Calamagrotis epijos* and *Spartina* spp. There we have only found records of four species of terrestrial mammals, including three small rodents and one deer that is extinct in the wild but that has been reintroduced (Table S2). We did not find registers of habitat specialist species for tidal marshes in this region.

In Europe, including Great Britain and Ireland, we found records of 8% of the tidal marsh area of the world with 14.5% of studies recording the occurrence of mammalian terrestrial species. These marshes encompass a greater variety of plants depending on the region but are mainly dominated by *Spartina* spp., *Salicornia* spp., *Limonium* spp., *Scirpus* spp., *Juncus* spp., *Festuca* spp. and *Atriplex* spp. In this region, we found records of 25 species of terrestrial mammals, including one subspecies. Most records were for small mammals like rodents, but there were medium-sized ones like mustelids and hares and large-sized mammals such as wild pigs and deer (Table S2). We did not find registers of habitat specialist species of tidal marshes in these regions.

In the South American continent, where there is about 3% of the world's tidal marsh area, we only found 5.5% of studies recording terrestrial mammal species. Most marshes are recorded in eastern Brazil, Uruguay and Argentina. These tidal marshes are dominated by plants, namely *Spartina alterniflora*, *S. densiflora* and *Sarcocornia peregnnis*. In this region, we found a record of 14 species of terrestrial mammals, including one subspecies. Most species are small rodents and marsupials, also medium-sized mammals such as felines, with the presence of an endangered deer, and also alien species such as the wild pig (Table 1). We did not find records of habitat specialist species of terrestrial mammals in tidal marshes of the South American continent.

For other regions, such as Africa (with <1% of the world's marsh area, mostly from South Africa), we only found one study that reports eight species for the north of the continent, in the Nile's estuary. For American Samoa, Guam and the Commonwealth of Northern Marianas, Puerto Rico, the US Virgin Islands, Iceland and the United Arab Emirates (each one with <0.1% of the world's marsh

TABLE 1 Summary of terrestrial mammalian species richness, the estimated terrestrial mammalian species richness and research effort (i.e. study numbers) by tidal marshes worldwide and by regions.

	Tidal marsh	Terrestrial mammal species			Scientific studies		
	Area (ha)[a] (% of total)	Richness (%)	Estimated richness[b] (%)	Species per area ($\times10^{-5}$)	Studies (%)	Studies per area ($\times10^{-5}$)	Ratio studies: Richness
Global	5,495,087 (100)	125	125	2.274	285 (100)	5.186	2.28
North and Central America							
USA[c]	1,729,289 (31.46)	74 (59.2)	75 (60)	4.279	210 (73.7)	12.201	2.851
USA (Alaska)	161,483 (2.93)	3 (2.4)	19 (15.2)	1.857	8 (3.6)	4.334	0.388
Canada	111,274 (2.02)	5 (4.0)	29 (23.2)	4.493	5 (2.3)	4.493	0.185
Mexico	272,527 (4.95)	0	19 (15.2)	0	0	0.000	0
South America							
Argentina	118,870 (2.16)	11 (8.8)	18 (14.4)	9.253	9 (4.1)	7.571	0.529
Brazil, Uruguay, Chile and Peru	37,858 (0.68)	3 (2.4)	17 (13.6)	7.924	3 (1.4)	7.924	0.214
Africa							
South Africa	6147 (0.11)	0	7 (5.6)	0	0	0.000	0
Egypt		8 (6.4)	11 (8.8)		1 (0.5)		
Madagascar	5810 (0.10)	0	0	0	0	0.000	0
United Arab Emirates	4797 (0.08)	0	3 (2.4)	0	0	0.000	0
Europe							
Mainland Europe[d]	356,947 (6.49)	25 (20.0)	41 (32.8)	7.003	32 (14.5)	8964	1.066
Great Britain	81,842 (1.48)	13 (10.4)	24 (19.2)	15.884	6 (2.7)	7.331	0.3
Ireland (Republic of)	9889 (0.17)	0	15 (12)	0	0	0.0000	0
Iceland	2617 (0.04)	0	5 (4.0)	0	0	0.000	0
Asia							
Russia	700,719 (12.75)	0	16 (14.8)	0	0	0.000	0
China	549,506 (9.99)	4 (3.2)	10 (9.3)	0.727	5 (2.3)	0.909	0.5
Oceania							
Australia	1,325,854 (24.12)	11 (8.8)	17 (13.6)	0.829	6 (2.7)	0.452	0.375
New Zealand	19,650 (0.35)	0	13 (10.4)	0	0	0	0
Guam and Northern Marianas Is.	8.2 (<0.01)	0	0	0	0	0	0
American Samoa	0.1 (<0.01)	0	3 (2.4)	0	0	0	0
Puerto Rico and US Virgin Is.	5879 (0.11)	0	0	0	0	0	0

Note: In brackets, we provide the percentage that each one represents. We also provide values for ratios of the number of species per area (ha), the number of studies per area (ha) and the ratio of studies per number of species reported for each macro-geographical region of the world. The percentage values for species richness were calculated using the total number of species recorded (n = 125) in tidal marshes.

[a]From Mcowen et al. (2017).

[b]Richness estimated by extrapolating data from this review to intersect with the geographic distribution of each mammal species with the global distribution of tidal marshes (see Section 2 for further details).

[c]Including Hawaii, Puerto Rico and US Virgin Islands.

[d]Includes 20 countries: Albania, Belgium, Bulgaria, Croatia, Cyprus, Denmark, Estonia, Finland, France, Germany, Italy, Latvia, Montenegro, Netherlands, Portugal, Romania, Slovenia, Spain, Sweden and Turkey.

area), we did not find any scientific reports on records of terrestrial mammals in tidal marshes.

From the 285 studies included in the review, we found a total of 962 geolocations for terrestrial mammals in tidal marshes (Figure 1b). These locations were distributed in 15 countries, which represent only 13.2% of all countries where tidal marshes have been reported (Figure 1a, see Table 1). The post hoc analysis after the Kruskal–Wallis test (U = 29.47, df = 14, p = .009)

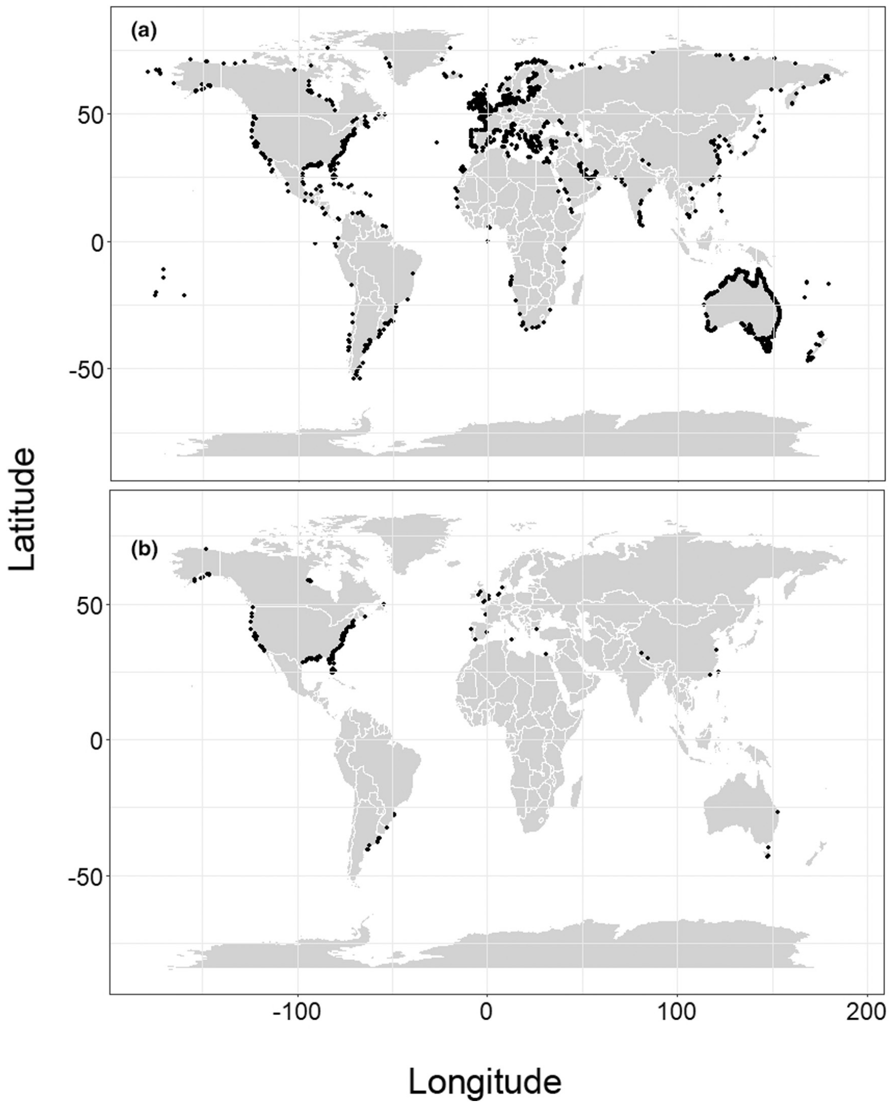

FIGURE 1 (a) Locations of tidal marshes worldwide, including 2098 tidal marshes reported by Mcowen et al. (2017) and 529 marshes recorded by the scientific publications compiled in this review. (b) Record of terrestrial mammalian ($n = 962$) in tidal marshes worldwide reported by the reviewed scientific publications ($n = 285$).

identified differences among the equatorial, temperate and cold regions, with the highest species richness of terrestrial mammals in the temperate latitudinal band of 40° to 70° in the Northern Hemisphere and between the bands of −40° and − 50° in the Southern Hemisphere (Figure 2a). The analysis of scientific records on species richness for different macro-geographic regions of the world increased (*multiple* $R^2 = .93$, $F_{(2, 17)} = 119$, $p = 1.005^{e-10}$) with the number of studies (Box–Cox transformation, $\theta = 0.1$, $b_{(studies)} = 0.56$, $p = 4.56^{e-11}$) but not with the variation in the marsh surface area ($b_{(areas)} < 0.001$, $p = .56$).

3.2 | Estimation of species distribution and richness

Tidal marshes showed a worldwide distribution throughout all continents, except on the poles (Figure 1a). In both hemispheres, the estimated species richness increased in the temperate latitudinal band of 40° to 50° in the Northern Hemisphere and between the bands of −35° and −45° in the Southern Hemisphere (Figure 3). Furthermore, when we analysed the species richness for each individual coast and within latitudinal bands of 10°, we found higher values of species richness in the temperate band of 50° to 60° for the Northern Hemisphere and the band of −40° to −50° for the Southern Hemisphere (Kruskal–Wallis; $U = 196.93$, df = 14, $p = 2.2^{e-16}$, Figure 2b). When we analysed the estimated species richness for each macro-geographic region of the world, we found that species richness increased with the surface of tidal marsh areas ($R^2 = .50$, $F_{(1, 18)} = 20.83$, $p < .001$). Latitude was a poor predictor for the range size of species ($R^2 = .002$, $p = .65$). Finally, and despite pattern similarities, we detected differences between latitudinal estimated richness and found through the record of scientific studies (interaction effects, $F = 4.86$, $p = .03$). Specifically, the values of estimated species richness for the latitudinal bands 40, 50 and 60 (Dunn tests, $p < .01$, Figure 2a,b, see also Figure 4 and Table 1) were higher than those of species richness recorded by scientific studies.

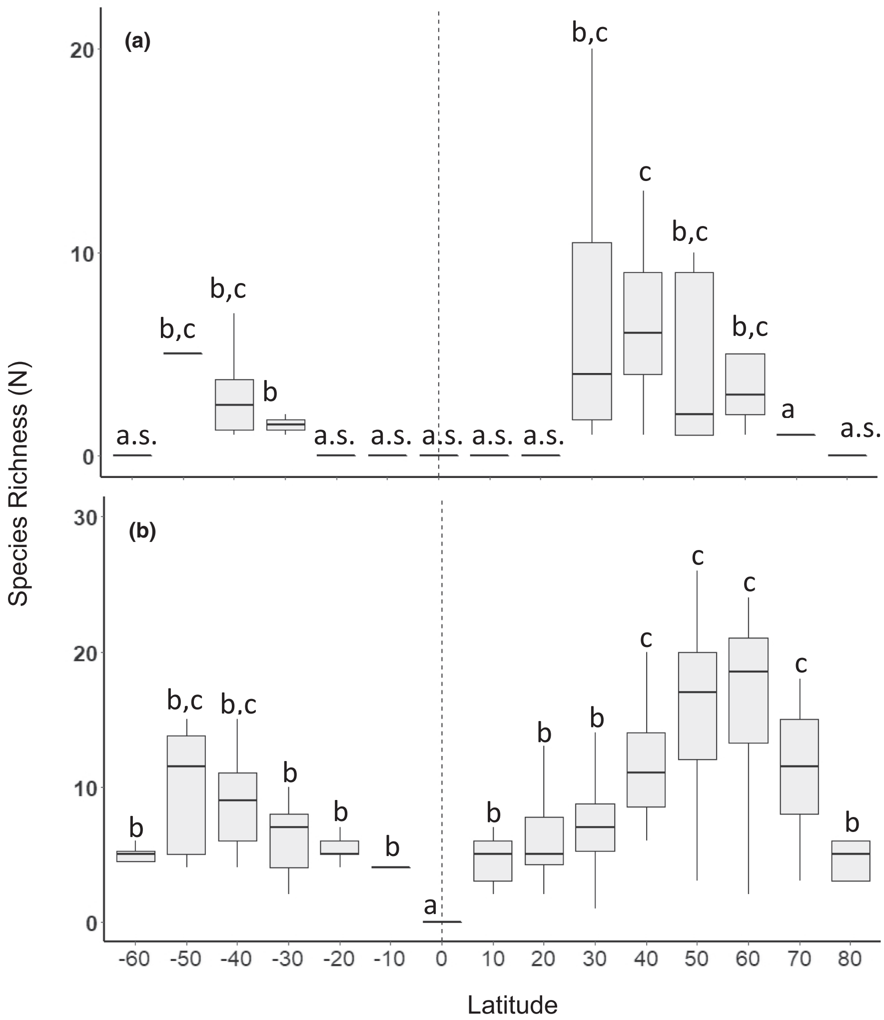

FIGURE 2 Boxplot showing the species richness of terrestrial mammals in tidal marshes grouped for each 10° latitude based on: (a) scientific studies reviewed included in this revision (n = 285) and (b) the estimated richness. The vertical dashed line indicates the separation between the Southern and Northern Hemispheres. Boxes: limits represent the 25th and 75th percentiles, whiskers are the 1st and 99th percentiles and lines within boxes are the median. a.s. indicate the absence of studies. Different letters indicate the statistical differences between latitudinal bands (Dunn test after Kruskal–Wallis test).

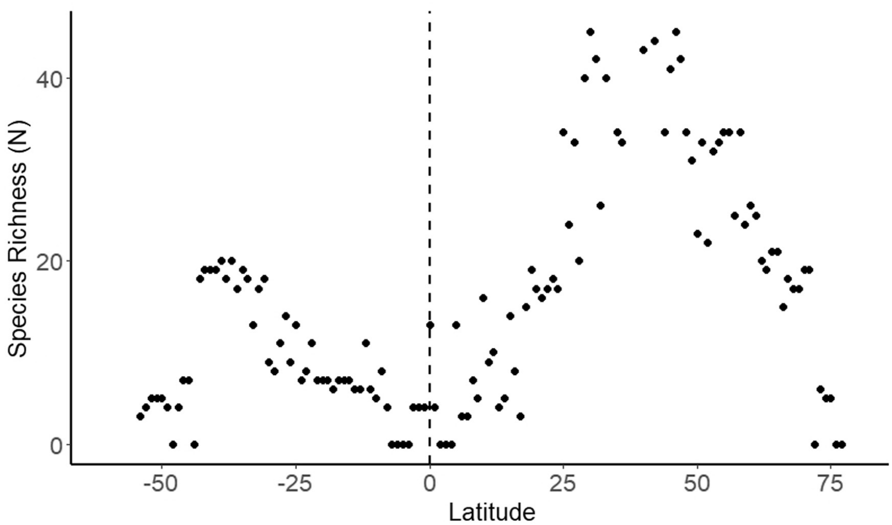

FIGURE 3 Variation in the estimated species richness of terrestrial mammals in tidal marshes along latitudes worldwide. The vertical dashed line indicates the separation between the Southern and Northern hemispheres.

4 | DISCUSSION

Our analysis integrating information from peer-reviewed articles and grey literature provides the first comprehensive assessment of global terrestrial mammal distribution in tidal marshes. Among the terrestrial mammals registered, there is a larger proportion of non-marsh-specialized than specialist species, and also several alien species using tidal marshes. Among habitat specialists, several are endangered species or close to being so, highlighting the importance of tidal marsh ecosystems and their preservation. The

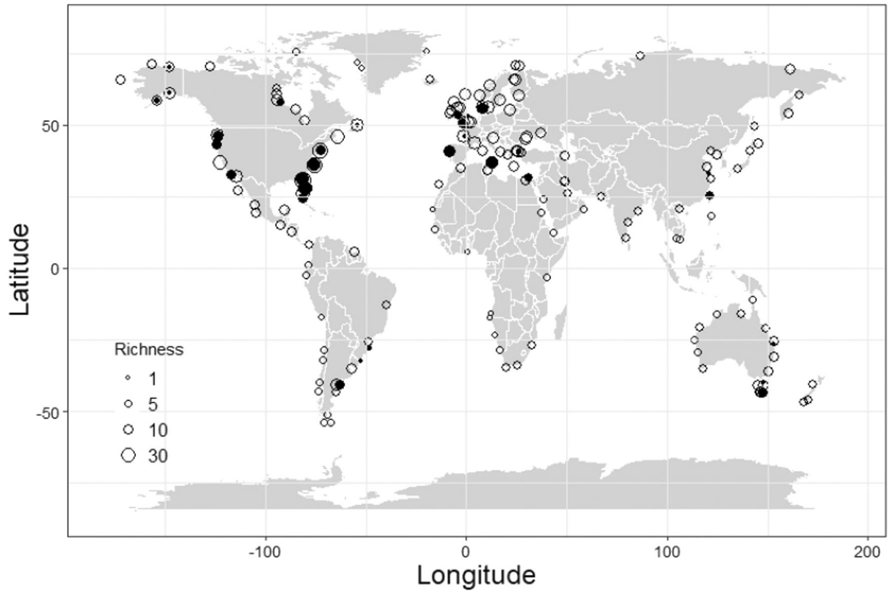

FIGURE 4 Species richness of terrestrial mammals in marshes for each 5° latitude recorded by scientific studies (by black circles) and estimated (white circles). The circle size (diameter) is proportional to the species richness value.

available scientific information is not globally homogeneous, with noticeable literature gaps for Australia, South America, Africa and Asia. Despite the existence of extensive areas of tidal marshes in those regions, scientific information about the presence, ecology, and importance of terrestrial mammals is scarce. Linguistic and cultural barriers among the scientific community could be at least partially responsible for such information gap (Amano et al., 2016; Angulo et al., 2021; Chowdhury et al., 2022) in some regions of the world. The estimated species richness was higher than that recorded by the literature search, except for the North American continent where most scientific publications come from. This highlights three facts: that marshes act as a relatively unexplored reservoir of terrestrial mammal diversity, that there is a need for further research efforts to assess these ecosystems for their biodiversity and that their functioning may be affected by the presence of alien species. Such global heterogeneity in scientific knowledge was also evidenced by the fact that species richness from macrogeographic regions increased with the research effort while the estimated richness from macrogeographic regions did with an increased tidal marsh surface area. Despite the inconsistency between estimated and observed species richness, both showed a bimodal distribution with peaks located between 40° and 50° latitude in both hemispheres, being higher in the Northern Hemisphere.

4.1 | Species characteristics

We have found records of 125 species and subspecies of terrestrial mammals for tidal marshes worldwide. Among these, only five species are habitat specialist users for tidal marshes (See Table S2). We also found that the occurrence of threatened species is concentrated in regions with high human impact and development (e.g. Hays & Lidicker, 2000; Statham et al., 2016). Since more than half of the global area of tidal marshes had been altered or degraded due to anthropic activity and climate change (Great Britain: Hazelden & Boorman, 2001; Hughes & Paramor, 2004; China: Gu et al., 2018; USA, Kennish, 2001; Zedler et al., 2001; South America: Costa et al., 2009), it is not surprising that species that specialize in using marshes were more prone to be at risk (Dirnböck et al., 2011; Wijesinghe & Brooke, 2006). In fact, subspecies such as the ornate shrew in Baja California (*Sorex ornatus juncensis*) have already been reported as locally extinct since all their original habitat along the coast has been destroyed (Maldonado, 1999). Nevertheless, a recent record would indicate that this species is not totally extinct (Camargo & Álvarez-Castañeda, 2019). Furthermore, with the loss of large areas of natural coastal ecosystems caused by agriculture and urbanization in the last centuries (Kummu et al., 2016; Tian et al., 2016), tidal marshes can offer suitable conditions for many non-marsh-specialist species. This seems to be the case for many species listed as vulnerable (IUCN) such as the European Lynx (*Lynx lynx*) in the estuary of the Guadalquivir River, Spain (Rodríguez-Ramírez et al., 2019), the south-western water vole (*Arvicola sapidus*), native of France, south-westwards through Spain and Portugal (Centeno-Cuadros et al., 2011) and the Pampas' deer (*Ozotocerus bezoarticus celer*) in a brackish and freshwater marsh in central Argentina (Vila et al., 2008). For this reason, it becomes of critical importance to know which terrestrial species are using tidal marshes and the relevance of this environment for those species. Such knowledge is key to predicting possible scenarios of how natural communities (e.g. Root et al., 2003) of tidal marshes and their neighbouring terrestrial habitat might respond to the current and future ecosystem loss.

4.2 | Species distribution

More than half of mammal species reported using tidal marshes around the world, and all habitat specialists, were recorded in the North American continent. This could be not only due to the fact that the North American continent accounts for over 41% of the world's tidal marshes (Mcowen et al., 2017) but also because the

79% of the available scientific studies that record terrestrial mammals in tidal marshes come from that region. The fact that variation in species richness is related to the number of studies but not to tidal marsh area as we expected (species–area relationship, e.g. Lomolino, 2000; Rosenzweig, 1995), which seems to be the result of different knowledge gaps for certain regions of the world. These gaps are particularly important in some world regions like Oceania, South America, the Russian Federation and China; despite having extensive tidal marsh areas, there is little or no scientific information about terrestrial mammal presence or its ecology. Oceania, for example, represents only 5.7% of the land area of the earth (2021 worldatlas.com) but comprises an extensive area of tidal marshes (about 24.5% of world tidal marshes, Mcowen et al., 2017). However, here we only found information from six studies that recorded 11 non-marsh-specialized species. In Asia, as an example, China represents 6.4% of the land surface (2021 worldatlas.com) and contains about 10% of the tidal marshes of the world (Mcowen et al., 2017). A large proportion of tidal marsh has been transformed for human use (i.e. agriculture and urbanization) and is still ongoing (Jiang et al., 2015; Tian et al., 2016). However, we only found five scientific articles that record four terrestrial mammal species in that country. Furthermore, we did not find published scientific research on terrestrial mammals for tidal marshes in Russia, with 11.4% of the Earth's surface (2021 worldatlas.com) and comprising 13% of the global surface of tidal marshes (Mcowen et al., 2017). These information gaps for many areas of the world support the premise that the research effort made by studying tidal marshes as marine ecosystems has led to disregarding the importance of terrestrial components of this community.

4.3 | Importance of terrestrial mammals for tidal marshes

Mammal species can have important ecological effects on tidal marsh functioning. However, the geographically restricted information about their roles in tidal marshes is surprising. In agreement with the importance of the primary productivity of tidal marshes (Odum, 1971), there is a general prevalence in the herbivore information. For example, small mammals like meadow voles (*Microtus pennsylvanicus*), deer mice (*Peromyscus leucopus*) in New England, USA (Crain, 2008), or the wild cavies (*Cavia aperea*) in Southwest Atlantic areas, Argentina (Canepuccia et al., 2010; Pascual et al., 2017). Similar to small mammals, medium-sized mammals like hares (*Lepus europaeus*) in the Dutch sandy barrier island of Schiermonnikoog (Dormann & Bakker, 2000; Elschot, 2015) can have top-down influence, reducing growth and primary productivity and affecting tidal marsh vegetation succession and diversity. But predators can also exert top-down pressure, limiting their prey population. However, our revision shows a relative dearth of research, geographically restricted to the USA, about the effects of terrestrial mammal predators in tidal marshes. For example, predation by bobcats (*Lynx rufus*) can limit the population growth of the white-tailed deer (*Odocoileus virginianus*) in South Carolina, USA (Roberts, 2007). Meanwhile, predation by raccoons (*Procyon lotor*) can threaten the population persistence of the Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) in the Lower Keys, Florida, USA (Schmidt et al., 2010), and likewise, it may limit the nesting success of the Diamond-backed Terrapin (*Malaclemys terrapin*) (Buzuleciu et al., 2016). Accordingly, we need a better understanding of the role of consumers and their strength of top-down control to evaluate their importance for tidal marsh functioning.

Due to the fact that the number of non-marsh-specialized mammals recorded in tidal marshes categorically outnumbers the number of specialist species, we can expect transfer energy across terrestrial–tidal marsh ecosystems to be a common phenomenon. The movement of organisms between ecosystems implies an energy flow (e.g. see review by Carlton & Hodder, 2003). For example, in the western South Atlantic, wild cavies inhabit terrestrial grassland neighbouring brackish marshes (Canepuccia et al., 2010). But, when grassland productivity decreases in autumn and winter (e.g. Sala et al., 1981), they move to the marsh to feed their grasses (Canepuccia et al., 2010). This behaviour may be more common and frequent for species that inhabit impoverished terrestrial ecosystems (Carlton & Hodder, 2003), and then rely on the use of more productive (e.g. Mitsch & Gosselink, 2001; Shanholtzer, 1974) tidal marsh ecosystems for survival. The organism movement among adjacent ecosystems implies a transfer of nutrients, and this can affect food webs (Polis et al., 1997; Stapp et al., 1999), abundances and distribution of species, and the structure of the communities involved (e.g. Carlton & Hodder, 2003). For example, the over-winter survival of bears depends on fat reserves they may gain during the spring/summer season (Noyce & Garshelis, 1994), which in some areas are tightly related to their access to salt marshes and their ability to forage salmon (Rode et al., 2006). In other aquatic–terrestrial biomes, it is known that bears can lead the energy obtained from water systems towards inland forests, which they later use as refuge (Carlton & Hodder, 2003; Chi & Gilbert, 1999; Willson et al., 1998), and the same could happen between tidal marsh and inland suitable areas. Nevertheless, it is surprising how little we know about the ecological roles of terrestrial mammals in tidal marshes and their potential role in energy flow cross-neighbouring inland ecosystems. This lack of information could be due to the fact that the phenomenon of energy flow cross-ecosystems has been overlooked as it is assumed to be rare. However, our results point out that this is not the case, this is a ubiquitous phenomenon that has been ignored. For this reason, further studies should be aimed at understanding the importance of terrestrial mammals in sea–land energy flow, and the importance of marsh energy for the terrestrial environment.

Our results show a considerable amount of alien species introduced in tidal marshes, which potentially impact the structure and function of these environments. Alien species can threaten biodiversity (Clout & Russell, 2008; Vilà et al., 2021), leading to the loss of native species (see review Tedeschi et al., 2022), modifying their ecological roles (Zavaleta, 2002) and thus, the ecological processes of the environment they invade. Synanthropic alien species with a cosmopolitan distribution, such as the house mouse (*Mus musculus*), the black rat (*Rattus rattus*, e.g. Puckett et al., 2016) and the feral hogs (i.e. *Sus scrofa*; Lewis et al., 2017), are likely to be present in most tidal marshes near human settlements around the world. In the case of the feral hog, which our results registered is present in numerous marshes (mostly near human settlements; Blackburn et al., 2017), its presence and behaviour in south-eastern US coast results in a profound impact on tidal marsh vegetation cover and soil traits by altering the organic carbon, porewater and ammonium–nitrogen ratios (Hensel et al., 2021; Sharp & Angelini, 2019). Also, feral horse herbivory and trampling in Cumberland Island, USA (Turner, 1987), and North Carolina, USA (Porter et al., 2014), deeply modify the vegetation structure and sediment stability of marshes. However, despite the importance of these alien species' effects on tidal marshes functioning and conservation (Hensel et al., 2021; Sharp & Angelini, 2019), this kind of ecological information is still restricted to a few geographically concentrated species. In fact, we did not find information about the effects of alien species on the marsh–inland energy flow, as has been reported on other environments. For example, the invasive rats that prey upon seabirds can reduce forest soil fertility by disrupting sea–inland nutrient transport by these birds (Fukami et al., 2006). Similarly, the alien Arctic fox (*Alopex lagopus*) in the Aleutian archipelago, by preying on seabirds, can also reduce nutrient transport from coast to land, modifying soil fertility on grasslands and shrub ecosystems (see revision Clout & Russell, 2008; Croll et al., 2005). Similar effects between marshes and inland environments could be caused by common alien predators such as the red fox (*Vulpes vulpes*), which is potentially present in several Australian and US marshes (this study). This highlights the urgent need for assessment of how alien species are affecting tidal marsh biodiversity, its conservation and functioning. Such information could be especially important for regions in which tidal marshes are particularly threatened by human activities (see Gedan et al., 2009; Perez et al., 2022) and where we need to implement novel management and conservation plans.

4.4 | The pattern of species richness

In general, it has been reported that terrestrial species richness displays a monotonic increase towards the tropics (e.g. Hillebrand, 2004; Wiens et al., 2006; Willig et al., 2003). This unimodal pattern has been associated with the mechanistic explanation that the geographical range of species increases with latitude (Rapoport's rule, Stevens, 1989). However, our results show a bimodal pattern with richness peaks in mid-latitudes in each hemisphere, and a heterogeneous pattern of range size of species along latitude. This may be the result of an underestimation of species richness in regions where there is no, or there is scarce, information available. However, we also found the same bimodal pattern for the estimated species richness and no support for Rapoport's rule. Geometric constraints of Rapoport's rule (see Gaston et al., 1998) could account for the data deviation. Many species could have smaller latitudinal ranges than those predicted just due to the defined limits of the tidal marsh and not for biological reasons. On the other hand, invasive and cosmopolitan species such as *Rattus rattus*, *R. norvergicus* and *Mus musculus* could also introduce deviations. Alien species show greater plasticity and physiological tolerance than native ones (Chown et al., 2007; Khaliq et al., 2017), as they are able to occupy larger geographical ranges (Biancolini et al., 2021). However, bimodal patterns have been suggested for several marine environments and terrestrial invertebrates (Chaudhary et al., 2016; García-Andrade et al., 2021; Orr et al., 2021). To explain this bimodal distribution, it has been proposed that species evolved through adaptation to temperature at the edge of the tropics (Brayard et al., 2005; Chaudhary et al., 2016), a fact which determined their physiological limitations facing equatorial temperatures (Molinos et al., 2015). Indeed, the fossil record seems to support this, with reduced coastal species richness values at the equator during the warm interglacial periods (e.g. Chaudhary et al., 2016; Kiessling & Aberhan, 2007). Also, for mammals, the relationship between temperature and clade richness is not always positive (Buckley et al., 2010; Willig & Presley, 2018). Clades of tropical origin may have a positive relationship with temperature, while clades of temperate origin may have inverse relationships (Buckley et al., 2010). Another key point is the species–area relationship (Lomolino, 2000; Rosenzweig, 1995). The tidal marsh area surface decreases towards the equator, where this environment is replaced by mangroves (Valiela & Cole, 2002). Then, because tidal marshes support more species the larger their area, their decline at lower latitudes may contribute to the observed decrease in species number. Accordingly, it is possible that the interaction among species traits, environmental gradients (e.g. Böhm et al., 2017; Gaston, 2000) and area availability differentially contributes to driving the global bimodal pattern found for tidal marshes along latitude.

Another peculiar aspect of the latitudinal pattern of global richness that emerges from our analysis is the asymmetry of the bimodal pattern, with a higher peak value in the Northern Hemisphere than in the Southern Hemisphere. Other global studies also report the same asymmetry of richness peaks (e.g. see review by Chaudhary et al., 2016; Powell et al., 2012). The number of coasts (then, tidal marshes and the number of studies) in the Northern Hemisphere exceed the ones in the Southern Hemisphere, which may lead to the asymmetry we found. However, the asymmetry remained after we standardized our data for the number of coasts and also after we estimated species richness in marshes worldwide. But, if the hemispheres are different, there is no reason to expect symmetry in species richness (e.g. Brown & Lomolino, 1998; Chown et al., 2004; Willig et al., 2003). The Northern Hemisphere comprehends 70% of the world's land surface and between latitudes 30° and 60° North, the ratio of water to land is about 1:1, whereas between −30° and −60° in the Southern Hemisphere, it is nearly 16:1 (Bonan, 2015; Chown et al., 2004). The hemispheric asymmetry in species richness is a known but poorly understood pattern (Chaudhary et al., 2016; Chown et al., 2004). Most accepted explanations involve historical and ecological factors that would lead to variations in species richness between hemispheres (see review Chown et al., 2004; Ricklefs, 2004). Among the ecological factors, variations in climate and energy availability are amid the most important variables explaining this hemispheric asymmetry (see Chown et al., 2004). However, evidence supporting the major factors proposed to explain this asymmetry is still mixed (Chown et al., 2004). Once again, the asymmetry could be due to differential research efforts, and the underestimation of species richness in different areas of the world. Still, this asymmetry seems to be a common issue across taxa and ecosystems (see Chown et al., 2004). Whatever the cause, our findings suggest that the underlying processes for species distribution and richness of terrestrial mammals in tidal marshes are complex. Whether the observed pattern is the consequence of the availability of habitat (MacArthur & Wilson, 1967; Simberloff, 1972), the gradient of energy, such as temperature (Ceballos & Ehrlich, 2006), or the result of geographical biases is still unclear.

5 | CONCLUSIONS

Our analysis summarizes the current knowledge of the terrestrial mammal distribution in tidal marshes and highlights greater species richness than those values inferred by the literature. Our findings also indicate substantial knowledge gaps about status, distribution and ecology of terrestrial mammals using tidal marshes, with evidence largely biased towards Europe and North America. Information gathered also shows that there are few habitat specialists of tidal marshes, some of which are currently threatened by the tidal marsh loss, but most species inhabiting marshes are not specialized users of this environment. These species can have important ecological roles in tidal marsh functioning. Among these roles, we pointed out the need to understand their importance as energy drivers across ecosystem boundaries (i.e. cross marine–terrestrial ecosystems). Also, the presence of alien species on marshes poses a threat to native biodiversity. Thus, given these threats, the consequences of those invasions should be the subject of further research. From a biogeographic point of view, our results support the hypothesis of the bimodality in species richness along latitude, and we identify some of the potential global-scale determinants for this pattern. However, studies are needed to understand whether this latitudinal pattern in species richness is a consequence of the filtering of species along physical gradients, changes in habitat availability along latitude or if it is the consequence of the knowledge gaps for many regions of the world. Understanding the underlying causes of biogeographic patterns is important to identify mechanisms that drive richness variation, and to know how the species richness peaks are related to areas that support a large number of species occurring nowhere else (e.g. habitat specialist species). Thus, and to establish a more complete picture of these ecosystems functioning, we recommend future research moving beyond viewing tidal marshes as marine ecosystems, and considering their terrestrial components in the conservation planning of these vital coastal ecosystems.

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CONFLICT OF INTEREST STATEMENT

We have no competing interests to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13683.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supplementary Information of this article.

ORCID

Alejandro D. Canepuccia https://orcid.org/0000-0002-6070-8030
María Sol Fanjul https://orcid.org/0000-0003-1890-8183
Oscar O. Iribarne https://orcid.org/0000-0001-9306-4836

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BIOSKETCHES

Alejandro D. Canepuccia is an ecologist interested in the community ecology of tidal marshes and the factors that shape biodiversity patterns across different spatial scales. He also works on the interface between tidal marshes and inland habitats. Webpage: www.iimyc.gob.ar/iimyc/es/grupos-de-investigacion/grupo-ecologia/.

María Sol Fanjul is an ecologist interested in small mammals' ecological behaviour and physiology. Webpage: https://www.iimyc.gob.ar/iimyc/es/grupos-de-investigacion/grupo-efyc/.

Oscar O. Iribarne is an ecologist interested in issues that span marshes functioning and their interaction with marine ecosystems. Webpage: www.iimyc.gob.ar/iimyc/es/grupos-de-investigacion/grupo-ecologia/.

Author contributions: ADC, MSF and OOI conceived the ideas and designed the methodology; ADC conducted statistical analyses and drafted the manuscript. All authors contributed to the literature revision, data interpretation and edited the manuscript and also gave final approval for publication.

SUPPORTING INFORMATION

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

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