



# Appearance of a population of the mangrove rail *Rallus longirostris* (Rallidae) in salt marshes invaded by the exotic tanner grass *Urochloa arrecta* (Poaceae) and its disappearance after plant management

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## Abstract

Biological invasions cause species extinction but can also provide benefits. Wetlands, such as salt marshes, include little-known but important ecosystems that are sometimes severely invaded by exotic plants. Salt marshes in eastern South America are increasingly impacted by invasions of the African grass *Urochloa arrecta*. This study investigated the appearance of a population of the mangrove rail *Rallus longirostris* in areas dominated by *U. arrecta* and its disappearance with the eradication of this plant. We monitored four areas (54.47 ha) in the Guaratuba Bay estuary in southern Brazil, from 2006 to 2022, two of which contained four patches of *U. arrecta* as the dominant species. In 2012, we started to eradicate *U. arrecta* with mechanical management, and in 2020, it was eradicated locally. We recorded *R. longirostris* for the first time within a patch of *U. arrecta* in 2007. In subsequent years we saw the species in two other patches of the exotic plant. *Rallus longirostris* was no longer observed once *U. arrecta* was eradicated. Differences in patch occupancy between invaded and uninvaded habitats observed for *R. longirostris* and *Pardirallus nigricans*, and the disappearance of *R. longirostris* following the exotic plant management suggest competitive advantage and/or differential habitat preference and population density as hypotheses to explain observed patterns. The invasion of *U. arrecta* can increase the local populations of *R. longirostris*. Since this bird is not endangered, we encourage the management of *U. arrecta* because of its impact on salt marshes, including an endemic endangered bird.

**Keywords** Competition · Ecological trap · Estuary · Nesting site · *Pardirallus nigricans* · Restoration

## Introduction

The introduction of alien species has intensified with globalization in recent decades (Meyerson and Mooney 2007). Exotic species are defined as species that are not native to

an ecosystem and that cause or are likely to cause economic, environmental, and/or human health damage (Catling 2005). They can change the composition of ecosystems rapidly and profoundly (Hobbs et al. 2009) and, through their direct and indirect effects, contribute substantially to species extinction (Vitousek et al. 1997; Bellard et al. 2016). Consequently, biological invasions are considered the second most common cause of biodiversity loss (Simberloff 2007). However, the effects of invasive species are not all negative, and the “native good/alien bad” dichotomy has been questioned (Goodenough 2010). Exotic species can benefit native species through habitat modification, trophic subsidy, pollination, competitive release, and predator release mechanisms (Lees and Bell 2008; Overton et al. 2014), besides having educational potential (Battisti 2016; Battisti et al. 2018). Comprehending and studying the responses of native species to invasive alien species and their management is

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essential for understanding impacts and deciding conservation actions (Schlaepfer et al. 2002; Lees and Bell 2008).

Wetland ecosystems can be greatly disturbed by biological invasions (Levin et al. 2006; Reinert et al. 2007; Norbdy et al. 2009; Cuassolo et al. 2012). These environments are vital, and despite covering only 6% of the Earth's surface, they host 24% of the most invasive species on the planet (Zedler and Kercher 2004). Salt marshes, as a type of wetland, are possibly the most important and least understood of the world's major ecosystems (Gedan et al. 2011). They are dynamic coastal areas (Watson and Byrne 2009; Gedan et al. 2011) that host salt-tolerant plant species (Doody 2001). They are regularly flooded by tides, have rapid sediment accumulation, and include transitions to non-tidal vegetation in the absence of human interference (Doody 2001). They occur in temperate areas across the globe, are more extensive in the northern hemisphere, and support seagrass *Spartina* spp. as the most common plant species (Doody 2001). Recently, some marshes on the South American Atlantic coast have been recognized as salt marshes—specifically subtropical salt marshes (Bornschein et al. 2017). They are characterized by the dominance of the crinum lily *Crinum americanum* L. and the California bulrush *Schoenoplectus californicus* (C. A. Mey.) Soják; therefore, the presence of smooth cordgrass *Spartina alterniflora* Loisel is rare (Bornschein et al. 2017). Subtropical salt marshes are associated with mangroves, distributed thinly in Brazil from the estuaries of the central-south coast of São Paulo to the north coast of Santa Catarina (Bornschein et al. 2017).

Currently, South American salt marshes are being invaded and dominated by tanner grass *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga, which causes major problems for the region (Reinert et al. 2007). This species, when established, profoundly alters the communities in the environment (Casatti et al. 2009; Michelan et al. 2010; Carniatto et al. 2013). This poses a great threat to the conservation of endemic birds in southern Brazil, such as the marsh antwren *Formicivora acutirostris* (Bornschein, Reinert & Teixeira, 1995), which was first described in 1995 (Bornschein et al. 1995; Reinert et al. 2007). Environments completely invaded by this exotic grass are no longer occupied by the bird, which is why the impact is considered an area suppressor (Reinert et al. 2007). In contrast, marshes in California, in the United States, were invaded by a hybrid species of *Spartina* that benefited populations of the threatened Ridgway's rail *Rallus obsoletus* Ridgway 1874 (taxonomy according to Maley and Brumfield [2013]). The hybrid increased the survival of this bird by providing refuge against predators during extreme tides that inundated native vegetation, particularly during winter, when native vegetation entered senescence (Overton et al. 2014). Hybrid plant management programs have reduced the survival rate

of *R. obsoletus* and plans for its conservation suggest offering refuge against the high tides caused by rising sea levels (Overton et al. 2014).

In 2006–2022, salt marshes in southern Brazil were studied as part of a long-term project aiming to monitor and conserve *F. acutirostris*—a vulnerable (VU) species at risk of extinction in Brazil (Ordinance 148 of the Brazilian Ministério do Meio Ambiente [MMA], June 7, 2022). This bird is included in the Brazilian National Action Plan for the conservation of Atlantic Forest Birds, one of the specific objectives of which is to deter and control alien species in the bird's natural habitat (Ordinance 208 of the Brazilian MMA and Instituto Chico Mendes de Conservação da Biodiversidade [ICMBio], March 3, 2018). In 2012 conservation efforts to protect *F. acutirostris* involved a challenging program that aimed to eradicate *U. arrecta* (Bornschein 2013), which impacted a local population of the mangrove rail *Rallus longirostris* Boddaert 1783. *Rallus longirostris* is generally restricted to mangroves (Vieira 2015) and is distributed across small portions of the Pacific coastal region, Central America, northern South America, and vast stretches of the Atlantic coast in South America (Maley et al. 2016). The species' geographic distribution primarily occurs along the Atlantic coast of Brazil—a country in which its conservation status was officially considered to be of least concern (LC; ICMBio 2018), although it may be threatened with extinction (Vieira 2015). In this article, we report on the appearance and distributional expansion of *R. longirostris* in subtropical salt marshes invaded by *U. arrecta* and its disappearance after the plant was eradicated. We also discuss the possible causes of this event.

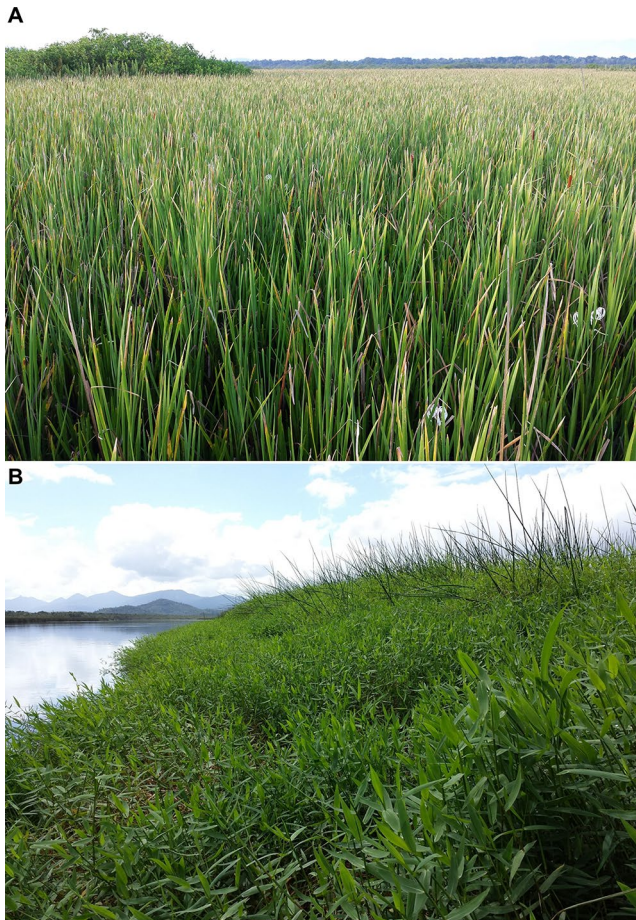
## Methods

### Study species

The target species was the mangrove rail *Rallus longirostris*, which is considered a separate species from the North American *R. obsoletus* and the clapper rail *R. crepitans* Gmelin 1789 (Maley and Brumfield 2013; Chesser et al. 2014).

### Study areas and field time

We worked at the Ramsar Site Guaratuba in the Guaratuba Bay estuary in Guaratuba Municipality, which is on the southern coast of Paraná in southern Brazil. Specifically, we studied four areas: Jundiaquara Island (c. 25°52'25"S, 48°45'32"W; 11.30 ha), the confluence of the Claro and São João Rivers ("Continente"; c. 25°52'28"S, 48°45'44"W; 8.47 ha), Folharada Island and its surroundings (c.



**Fig. 1** (A) Subtropical salt marsh dominated by the crinum lily *Crinum americanum* L. and the southern cattail *Typha domingensis* Pers. (Crinum-Typhetum), with mangroves of *Laguncularia racemosa* (L.) C.F. Gaertn in the background on the left of the image (Laguncularietum; Folharada Island). (B) A subtropical salt marsh invaded by the alien *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga (Urochloetum; Patch 1, Riozinho). Guaratuba Bay, Guaratuba Municipality, Paraná, southern Brazil. Photograph: Marcos R. Bornschein

25°51'58"S, 48°43'23"W; 30.72 ha), and the Riozinho River mouth ("Riozinho"; c. 25° 52'00"S, 48°45'05"W; 3.98 ha; see Favretto et al. 2022). Folharada Island and its surroundings are located downstream, and the remaining areas are further upstream, in the São João river.

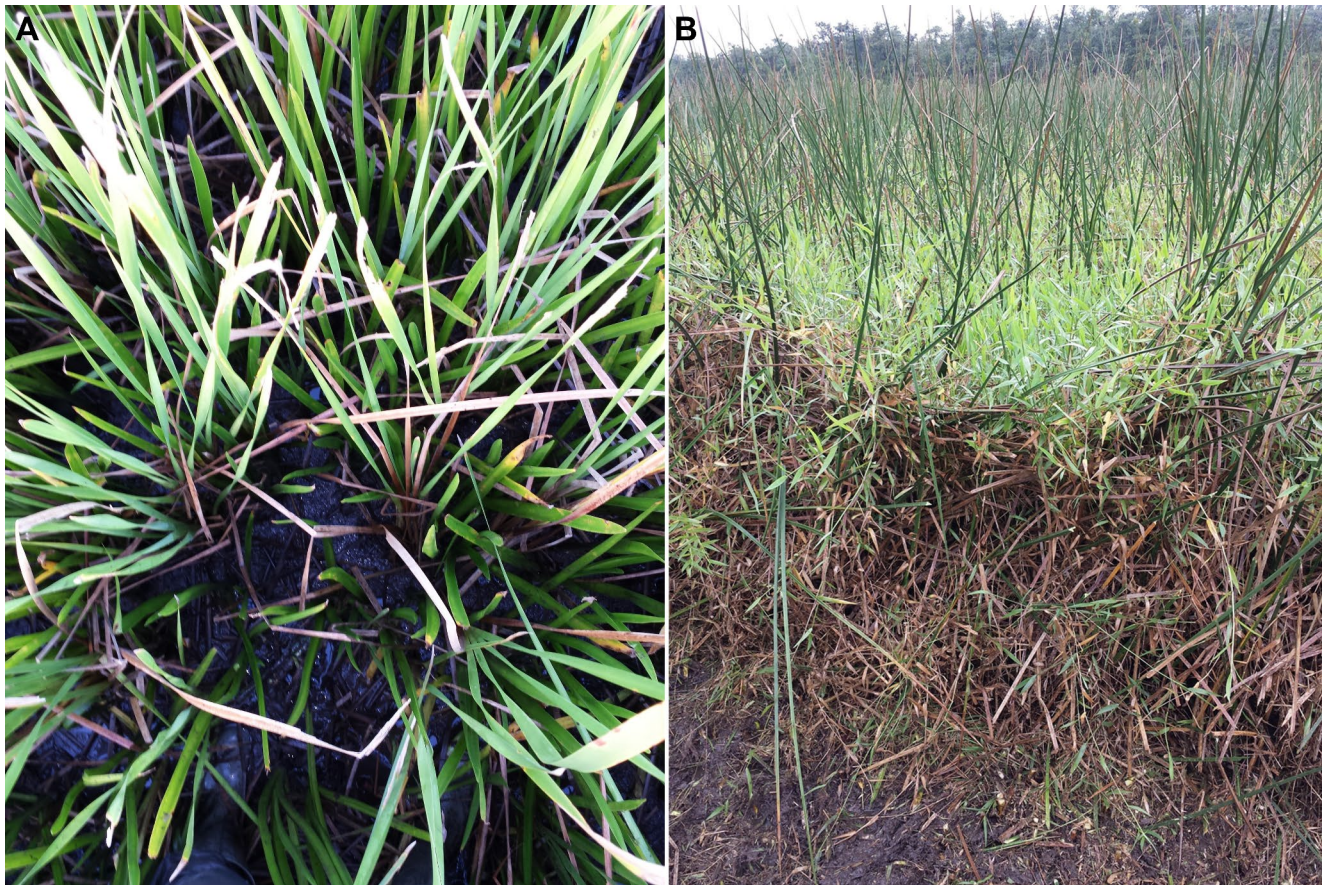
The study areas are estuarine marshes (Doody 2001: 65), tidal marshes (Reinert et al. 2007), or subtropical salt marshes (Bornschein et al. 2017). According to the criteria for the classification of Brazilian vegetation proposed by the RADAMBRASIL Project (Veloso et al. 1991), marshes are pioneer formations with fluvio-marine influences. The following herbaceous species dominate: *C. americanum* (Amaryllidaceae), *S. californicus*, *Fuirena robusta* Kunth, *Cladium mariscus* (L.) Pohl (Cyperaceae), *Acrostichum danaeifolium* Langsd. and Fisch. (Pteridaceae), and *Stephostachys mertensii* (Roth) Zuloaga and Morrone (Poaceae) (Reinert et al.

2007). The herbaceous southern cattail *Typha domingensis* Pers. also occurs locally (Typhaceae; Fig. 1 A) together with trees such as *Calophyllum brasiliense* Cambess. (Clusiaceae), *Annona glabra* L. (Annonaceae), and *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae) (Reinert et al. 2007). The areas are characterized by mixed semi-diurnal tides (Lee and Chang 2019), with two high tides and two low tides of different amplitudes on all lunar days.

We characterized the vegetation (phytophysiognomy) according to one or two dominant plant species. We consider as becoming a phytophysiognomy the vegetation with at least three plant species, but two of them in dominance, with the living aerial parts of each covering at least 20% of the soil surface. For this evaluation, we defined more than 1,000 phytosociological description plots of 1 m<sup>2</sup> (Braun-Blanquet 1979; see Favretto et al. 2022). We also estimated the soil coverage by the living aerial parts of the plants systematically, according to Bolòs et al. (1991). We refer to each phytophysiognomy using the suffix "etum", according to Braun-Blanquet (1979).

The studies began in January 2006 on Jundiaquara Island and at Riozinho, in 2007 at Continente, in 2009 on Folharada Island, and in 2011 in the surroundings of Folharada Island. In all areas, we carried out the work until August 2022. Between January 2006 and May 2008, we worked in the areas daily from September to February and for 6–8 days per month for the rest of the year. From 2009 onward, we worked in the areas for 3–8 days per month, every month. We did not work in the areas for six straight months (March–August) in 2020 due to the COVID-19 pandemic. Fieldwork was carried out by 2–7 people (usually three) accessing the areas by boat. On each fieldwork day, we worked from dawn until 12 p.m. or 1 p.m., and for a further 2–3.5 h in the afternoon, before dusk.

This work occurred in concert with research focused on *F. acutirostris* (see Reinert et al. 2012; Bornschein et al. 2015), the wren-like rushbird *Phleocryptes melanops* (Vieillot 1817), and the many-colored rush tyrant *Tachuris rubrigastra* (Vieillot 1817) (see Favretto et al. 2022). Our quantitative sampling consisted of point counts of all species of birds seen or heard within a 50 m radius of the observer (Bibby et al. 1998; see also Bornschein et al. 2017), for 15 min at each point. We established two bird censuses, each with six-point counts in subtropical salt marshes. Six points were allocated to Jundiaquara Island and Continente and six to Folharada Island and its surroundings. The edge of each point was at least 45 m from the edge of the closest point. The census was conducted on consecutive days each month, with sessions starting at sunrise and interrupted only by rain. Rainy days or extremely low tides downstream prevented us from conducting many censuses or completing bird counts at all six points of each census. The census



**Fig. 2** Comparison of the vertical structure of a subtropical salt marsh (A) dominated by the crinum lily *Crinum americanum* L. and the southern cattail *Typha domingensis* Pers. (Crinum-Typhetum) with a place (B) dominated by the alien *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga (Urochloetum; Patch 1) and hosting the

California bulrush *Schoenoplectus californicus* (C.A. Mey) Soják. In B, the edge of the vegetation was resulted from partial cutting, due to management intervention. Guaratuba Bay, Guaratuba Municipality, Paraná, southern Brazil. Photographs: Marcos R. Bornschein

results were recorded as punctual abundance index (PAI) values, which were obtained by summing all recorded individuals per species and dividing the number by the number of points in each census (Uezu et al. 2005).

### Local impact of *Urochloa arrecta*

In patches in the studied areas, the alien African grass *Urochloa arrecta* (or *Brachiaria subquadripara*) was the dominant species (Urochloetum; Fig. 1B). In these patches, native species co-occurred with this alien species but at low frequencies, because *U. arrecta* had become a dominant species due to the accumulation of stolons that shade and crush native vegetation, killing native plants (Fig. 2B; Reinert et al. [2007]). This process replaces the normal salt marsh vegetative structure and impairs bird displacement in the vegetation understory by obstructing ground space with intermixed stems that prevent movement through the marsh. (Fig. 2 A; Reinert et al. [2007]). *Urochloa arrecta* also advances on the water as floating banks of vegetation

that are sometimes ripped out by floods and transferred to other areas previously free of their presence (Reinert et al. 2007).

### Management of *Urochloa arrecta*

*Urochloa arrecta* was mechanically managed to ensure its complete local eradication, with permissions from the Instituto Ambiental do Paraná (357/11) and Instituto Água e Terra (12.20). The eradication was achieved by clear-cutting vegetation with brush cutters and stacking plant biomass without using herbicides (Bornschein 2013). The stacked biomass was contained with stakes to prevent movement by high tides (Fig. 3).

Cut and stacked piles of biomass were mixed up to six times to isolate living material by pulling dead vegetation from the interior of the pile to the edge and removing and reburying rooted and sprouted fragments (Bornschein 2013). *Urochloa arrecta* does not form seed banks locally, which facilitated successful management techniques. As a

**Fig. 3** Management of *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga that invaded the subtropical salt marsh in southern Brazil. Management consisted of clear-cutting the vegetation with brush cutters and piling up the biomass, which was stacked with bamboo supports to prevent it from being carried away by high tides (since the water usually almost reached the tops of the highest piles). The managed area was inspected to manually remove of sprouts of exotic grass up to six times, and the biomass piles were turned over regularly up to six times to ensure the death of sprouts. Photographs: Marcos R. Bornschein



**Table 1** Sizes of *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga patches (Urochloetum) on subtropical salt marshes before and after management in Guaratuba Bay, Paraná, southern Brazil. We present only the years with the availability of images from the Google Earth program (7.3.3.7786), used to measure the area of the patches. The years in which *Rallus longirostris* Boddaert, 1783 was recorded by patch are highlighted in bold. We also indicate the sizes of the patches of *U. arrecta* in 2003 as a reference value prior to the beginning of the fieldwork (in 2006)

Year	Patches dominated by <i>Urochloa arrecta</i> (in bold the ones with records of <i>Rallus longirostris</i> )			
	#1 <sup>a</sup>	#2 <sup>a</sup>	#3 <sup>a</sup>	#4 <sup>b</sup>
2003	0.38 ha	0.00 ha	0.11 ha	0.01 ha
2010	<b>1.23 ha</b>	0.22 ha	0.17 ha	<b>0.1 ha</b>
2012	<b>1.00 ha</b>	0.32 ha	0.18 ha	<b>0.13 ha</b>
2014	<b>0.59 ha</b>	0.45 ha	0.23 ha	<b>0.15 ha</b>
2016	0.01 ha	<b>0.57 ha</b>	0.00 ha	<b>0.16 ha</b>
2017	0.00 ha	<b>0.40 ha</b>	0.00 ha	0.01 ha
2018	0.01 ha	<b>0.28 ha</b>	0.00 ha	0.01 ha
2019	0.02 ha	<b>0.30 ha</b>	0.00 ha	0.00 ha
2020	0.25 ha	<b>0.46 ha</b>	0.00 ha	0.00 ha
2021	0.00 ha	0.00 ha	0.00 ha	0.00 ha

<sup>a</sup> Riozinho

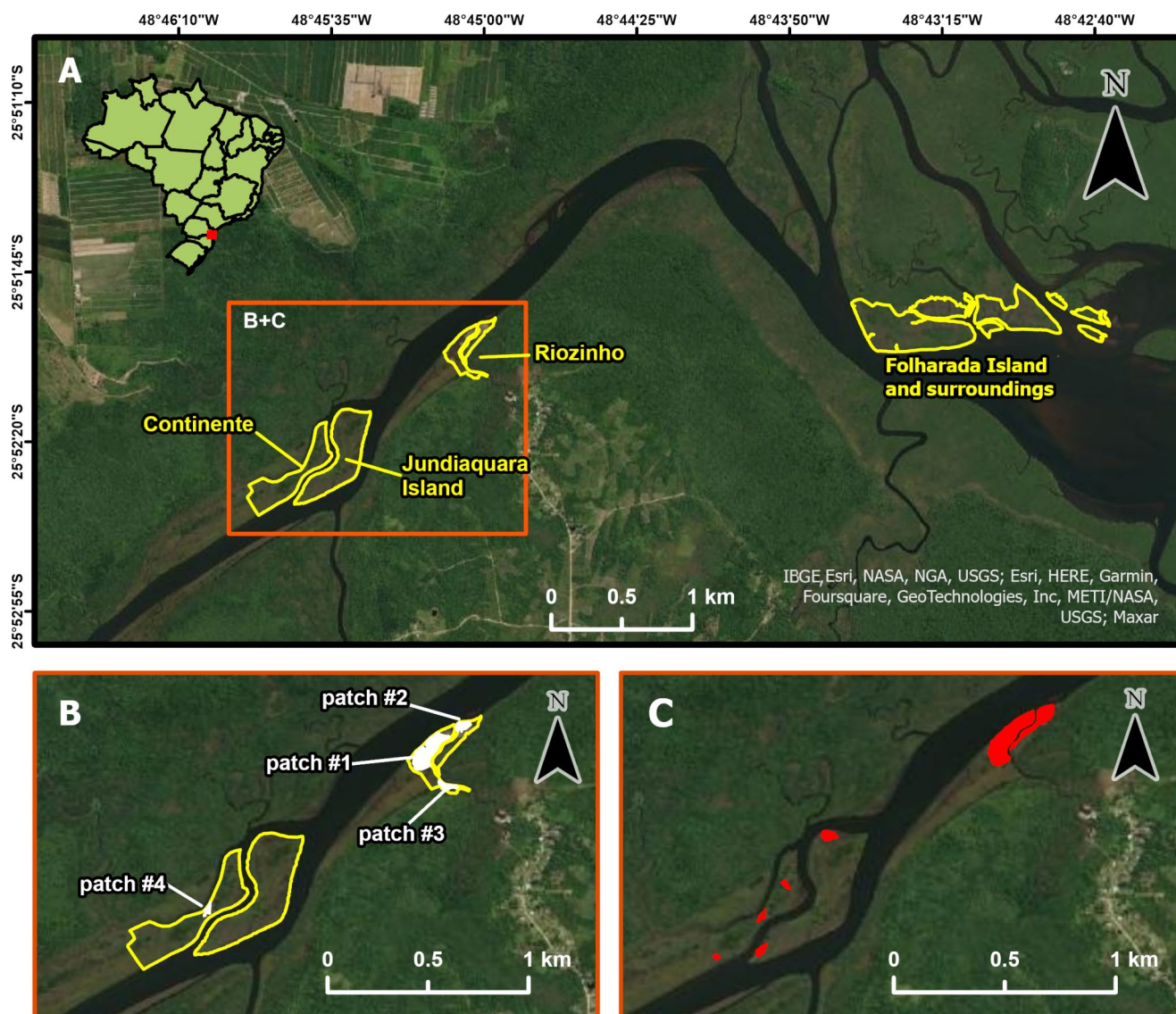
<sup>b</sup> Continente

fast-growing pioneer formation, with the sprouting of plants or germination of seeds, natural regeneration fully developed within about six months of management commencing. In 7 months, the landscape was completely changed, and in 10 months, the native vegetation covered the land again, free of alien species (Bornschein 2013). The resulting environment following the intervention was dominated by *S. californicus*. This is common in tidal marsh environments, especially along riverbanks (Bornschein 2001; Reinert et al. 2007). We delimited and measured polygons of areas invaded by *U. arrecta* and monitored them with the Google Earth Pro program (7.3.3.7786) for each year (2003–2006) for which images were available (Table 1).

## Results

### Records of *Rallus longirostris* and nesting points

We recorded *Rallus longirostris* for the first time in the study region in 2007, one year after the beginning of our studies in Guaratuba Bay. We observed two individuals vocalizing in duet in a patch dominated by *U. arrecta* (Urochloetum) in Riozinho (Patch 1; Fig. 4). In 2010 this patch of Urochloetum covered 1.23 ha (Table 1). This bird was always observed in Patch 1, where it also nested, and in the surrounding salt marshes free of *U. arrecta* (Fig. 4 C). Two photographs on the WikiAves website (<https://www.>



**Fig. 4** The area studied in 2006–2022 in Guaratuba Bay, Guaratuba Municipality, Paraná, southern Brazil (polygons with yellow limits; A–B), B) Indications of patches dominated by the alien *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga (at their 2010 size; white polygons) C) Maximum area with the occurrence of *Rallus longirostris* Boddaert, 1783 (red polygons). Map generated

[wikiaves.com.br/](http://wikiaves.com.br/)), one from 2007 and another from 2012 (WA280252 and WA832943)—document the presence of the bird in the surroundings of Patch 1.

In 2010, we recorded *R. longirostris* at the Continente in a 0.10-ha patch of *Urochloetum* (Patch 4; Table 1; Fig. 4), three years after the beginning of the studies in this area. We observed three nests containing eggs in subsequent years on a mass of *U. arrecta* stolons. We also observed lone individuals or pairs of *R. longirostris* in surrounding salt marshes free of *U. arrecta* up to 400 m away from Patch 4 (Fig. 4 C).

In 2016, we recorded *R. longirostris* for the first time in a 0.57-ha patch of *Urochloetum* (Patch 2; Table 1; Figs. 4),

with ArcGIS Pro. Imagery source: Instituto Brasileiro de Geografia e Estatística (IBGE), National Aeronautics and Space Administration (NASA), National Geospatial-Intelligence Agency (NGA), United States Geological Survey (USGS), Esri, HERE, Garmin, Foursquare, GeoTechnologies, Inc, Maxar, Ministry of Economy, Trade, and Industry (METI)/NASA

10 years after the beginning of our studies in this area. On Patch 3, with up to 0.23 ha of *Urochloetum* (Table 1; Fig. 4), we recorded no *R. longirostris*.

In 2012, we started managing *U. arrecta* in Patch 1 (see Table 1). In 2015, we continued to record *R. longirostris* in this patch (Table 1), and on one occasion, we observed *R. longirostris* feeding on *Uca mordax* on the mudflat, but chased away by management brush cutters. The bird was nesting on top of a biomass pile of managed vegetation (but the eggs were preyed upon). In 2016, Patch 1 of *Urochloetum* was practically eliminated, and since then, *R. longirostris* has not been recorded at this location. At the end of

**Table 2** Average of Rallidae punctual abundance index (PAI) recorded in censuses in subtropical salt marshes in Guaratuba Bay, Paraná, southern Brazil. There was N = 12 points of 50 m radius, with N = 6 points per census in Continente and Jundiaquara Island (upstream region) and N = 6 per census in Folharada Island and surroundings (downstream region). PAI = sum of individuals of each species recorded by census divided by the number of count point (N = 6). We indicated the N of censuses made by region per year

Year / region	N	Mangrove rail <i>Rallus longirostris</i> (Boddaert, 1783)	Blackish rail <i>Pardirallus nigricans</i> (Vieillot, 1819)	Gray-necked wood-rail <i>Aramides cajaneus</i> (Statius Muller, 1776)	Rufous-sided crane <i>Laterallus melanophaius</i> (Vieillot, 1819)	Common gallinule <i>Gallinula galeata</i> (Lichtenstein, 1818)
<b>Upstream</b>						
2011	3	0.00	1.11	0.00	0.00	0.00
2012	9	0.00	2.18	0.00	0.00	0.00
2013	12	0.01	2.72	0.00	0.00	0.01
2014	12	0.08	2.75	0.00	0.00	0.00
2015	12	0.04	2.86	0.00	0.00	0.04
2016	12	0.00	2.25	0.00	0.00	0.01
2017	10	0.00	1.85	0.00	0.00	0.00
2018	5	0.00	2.83	0.00	0.00	0.03
2022	2	0.00	2.83	0.00	0.00	0.00
<b>Downstream</b>						
2011	3	0.00	2.00	0.11	0.00	0.00
2012	10	0.00	1.97	0.12	0.02	0.00
2013	12	0.00	0.92	0.03	0.00	0.00
2014	12	0.00	1.07	0.08	0.01	0.04
2015	11	0.00	0.95	0.05	0.00	0.06
2016	10	0.00	1.03	0.07	0.00	0.05
2017	9	0.00	0.93	0.04	0.00	0.02
2018	5	0.00	0.57	0.10	0.00	0.03
2022	2	0.00	0.92	0.00	0.00	0.17

2016, we started managing *U. arrecta* in Patch 4, practically eliminating this grass in 2017, after which we no longer recorded *R. longirostris* there (Table 1). During 2017 and 2018, we managed *U. arrecta* on Patch 2, but we were unable to eliminate it before financial resources expired. When management ended, the *Urochloetum* patch started to expand again (Table 1). Finally, we resumed management in 2020, eliminating *U. arrecta* in the same year, and recording our last observation of *R. longirostris* in the study region (Table 1).

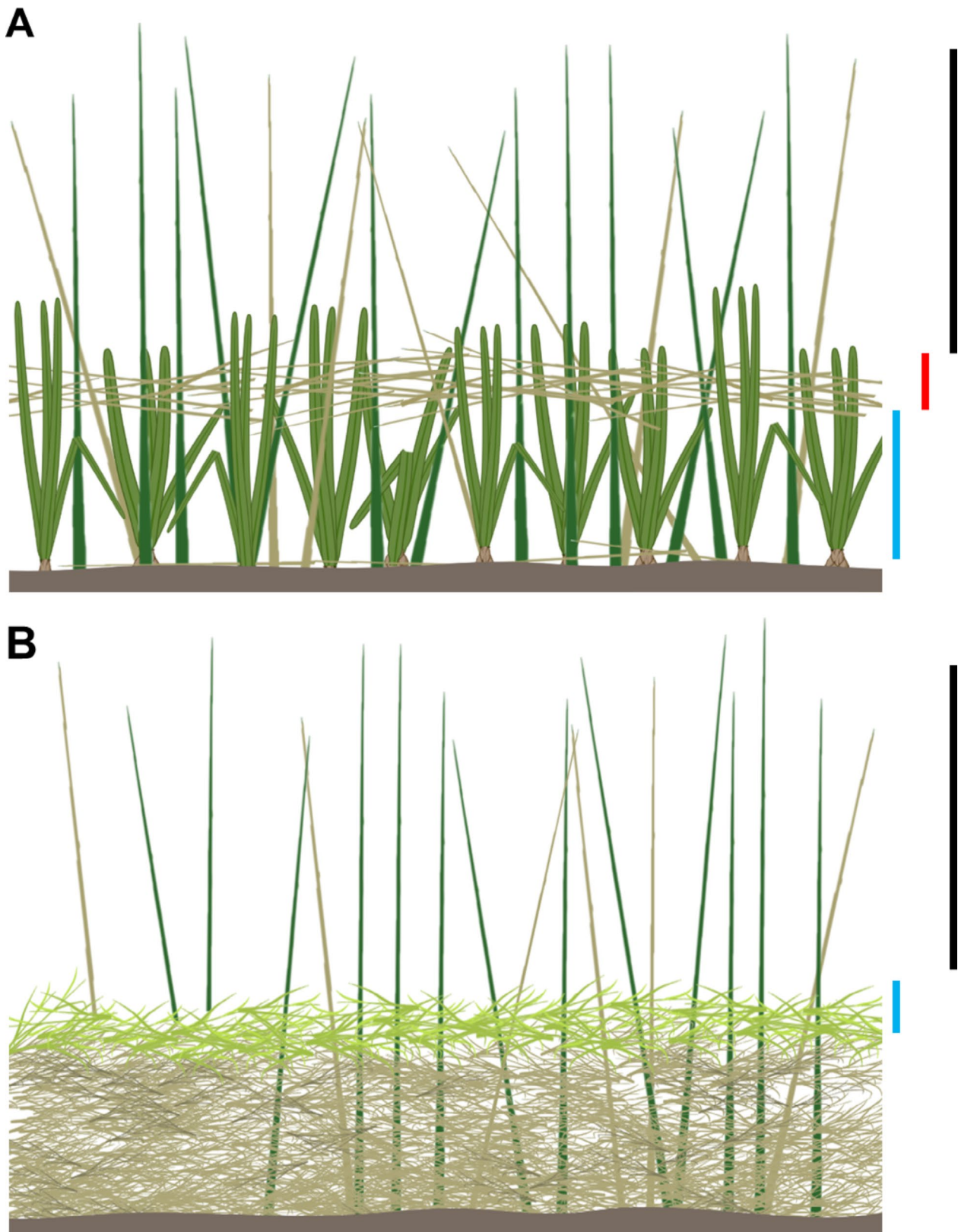
During the censuses (N = 151; Table S1), we recorded *R. longirostris* occasionally in 2013–2015, in small numbers in subtropical salt marshes, but only in censuses conducted near patches of *Urochloetum* (Table 2). On Folharada Island and in the surrounding area, where *U. arrecta* was absent, we recorded no *R. longirostris* (Table 2; Fig. 4). In this area, we started our studies in 2009 and the censuses in 2011.

### Use of the environment by *Rallus longirostris* and its relationship with other Rallidae

We observed *R. longirostris* occupying mudflats where the management had removed *U. arrecta* from patches of *Urochloetum*, and in native subtropical salt marsh vegetation. The subtropical salt marshes phytophysionomies used by *R. longirostris* were the ones dominated by *S. californicus*

(*Schoenoplectetum*), *C. americanum* and *S. californicus* (*Crinum-Schoenoplectetum*), *C. americanum* and *F. robusta* (*Crinum-Fuirenetum*), *C. americanum* and *T. domingensis* (*Crinum-Typhetum*), *C. americanum* and *C. mariscus* (*Crinum-Cladietum*), and, finally, by *A. danaeifolium* (*Acrostichetum*). Regarding these phytophysionomies, we observed *R. longirostris* in the lower layer of the vegetation (Fig. 5 A), occupying the sediment between the plants and accumulated dead leaves, and in the intermediate layer, which contained a high density of live and dead leaves (Fig. 5 A). We did not observe *R. longirostris* in the upper layer of vegetation, where the plants were vertical and less dense than in the lower layers. In *Urochloetum*, we observed *R. longirostris* only on top of the plant mass. Because this bird does not occupy areas with dense stolons of *U. arrecta* (Fig. 5B), the *Urochloetum* surface functions as the lower layer of vegetation, which is quite open and exposed. It was in this layer that we observed the *R. longirostris* nests (see above). The remaining native vegetation in *Urochloetum* constitutes the upper layer, with no intermediate layer.

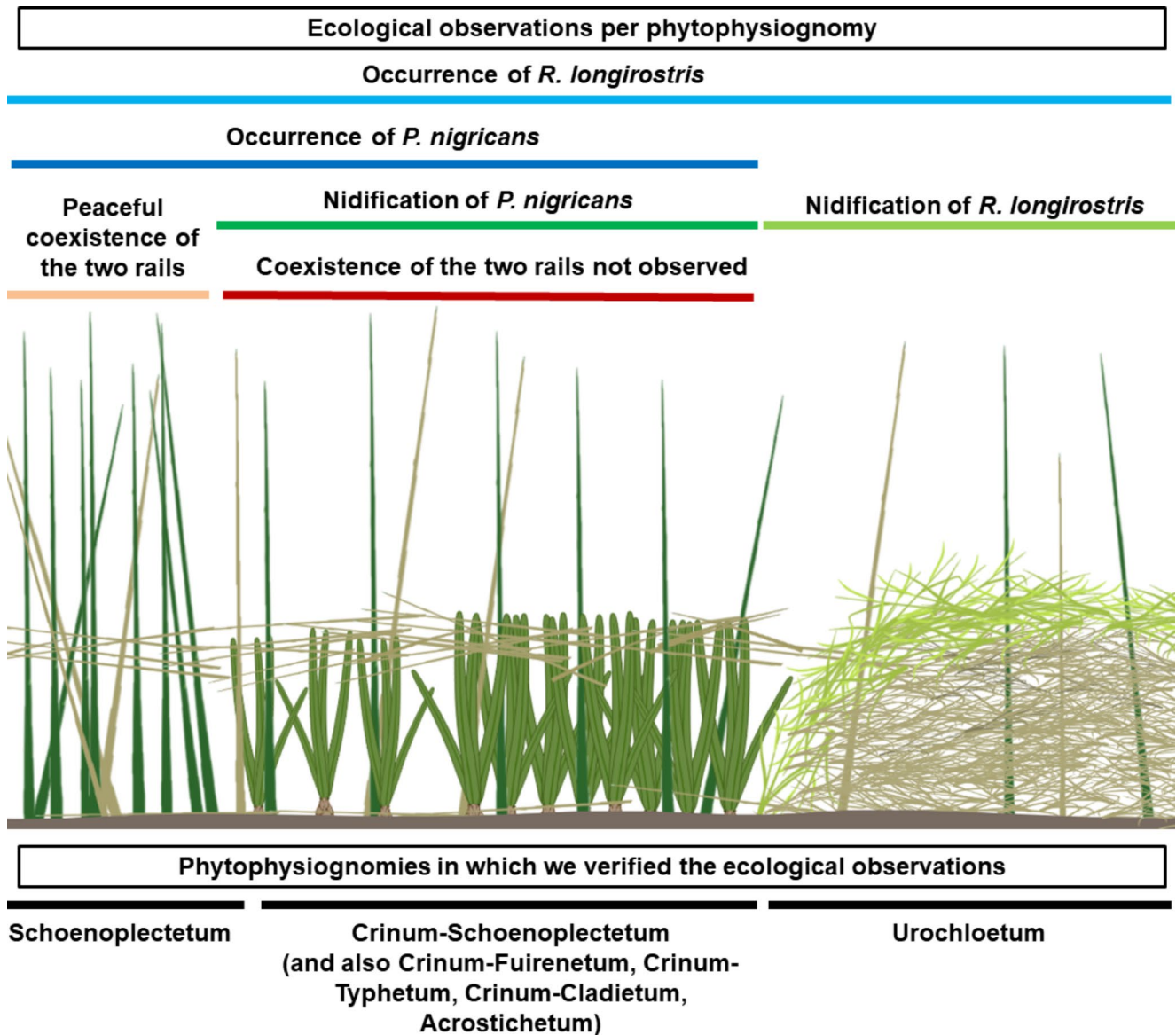
We also observed blackish rail *Pardirallus nigricans* (Vieillot 1819), associated with the same phytophysionomies and vegetation layers as *R. longirostris*, except on *Urochloetum* and mudflats (Fig. 6). We observed that coexisted only in *Schoenoplectetum*, with no evidence of aggression between them (Fig. 6). *Pardirallus nigricans* is



**Fig. 5** Schematic representation of subtropical salt marsh vegetation layers (A) and an area invaded and dominated by the alien *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga (B), according to its use by the mangrove rail *Rallus longirostris*. Blue ver-

tical bars indicate the lower layer, red vertical bars indicate the intermediate layer, and black vertical bars indicate the upper layer. Created with [BioRender.com](https://www.biorender.com)





**Fig. 6** Schematic representation of subtropical salt marshes invaded and not invaded by the alien *Urochloa arrecta* (Hack. ex T. Durand and Schinz) Morrone and Zuloaga (right third) relative to the occurrence

and nidification of *Rallus longirostris* Boddaert, 1783 and *Pardirallus nigricans* (Vieillot, 1819). Created with [BioRender.com](https://www.biorender.com)

the most abundant non-migratory species in the subtropical salt marshes (Table S2), and we saw this bird nesting in the intermediate layers of vegetation in all phytophysiognomies, except Schoenoplectetum and, obviously, Urochloetum. Other Rallidae are exceptional in subtropical salt marshes (Table 2) and we never observed them coexisting with *R. longirostris*.

## Discussion

This long-term study allowed us to verify (1) the appearance of a population of *R. longirostris* occupying and nesting in patches dominated by the exotic grass *U. arrecta*; (2) an increase in the population's local distribution, occupying of other patches dominated by this plant and surrounding salt marshes free from the alien species; and (3) its local disappearance after the eradication of the plant, in salt marshes free from the alien plant. This constitutes a further case of a native species benefiting from an alien species invasion (Overton et al. 2014; Casazza et al. 2014) and provides evidence of a preference for an altered environment over

a natural environment for nesting. This suggests that the subtropical salt marsh structurally impedes the nesting of *R. longirostris* (Hypothesis 1) or there is an ecological impediment to nesting in an environment not invaded by *U. arrecta* (Hypothesis 2).

Regarding Hypothesis 1, the most abundant resident bird at the study sites was *P. nigricans* (Table S2), which is similar in size to *R. longirostris* (Dunning 2008) and nests in subtropical salt marshes (Fig. 6). Locally, these two birds build nests as baskets constructed from fragments of native herbaceous plants of similar size, supported above the herbaceous vegetation (4 nests of *R. longirostris*; c. 150 nests of *P. nigricans* [unpublished data]). Thus, subtropical salt marshes are environments in which herbaceous plants support the construction of relatively large birds nests. However, it is known that due to rising tides, tidal marshes have far fewer nesting sites than foraging areas, and this characteristic shape the social organization of the environment (Post 1974). So, there is a high likelihood of disputes over reproductive sites between these birds in subtropical salt marshes (Hypothesis 2), with *P. nigricans* dominating *R. longirostris*. We suggest that *R. longirostris* could have occupied patches of Urochloetum as vacant nesting niches to avoid disputes with *P. nigricans*. There were other rail species in the subtropical salt marshes of the study region, but they occur in low numbers and only occasionally (Table 2); therefore, we did not expect that any ecological interaction with *R. longirostris* that influence its local ecology and preferences.

*Rallus longirostris* and *P. nigricans* do not seem to use the interiors of areas dominated by *U. arrecta*, possibly due to the high density of stolons (Fig. 2B) limiting their movements and access to food (MRB per. obs.). The non-use of this part of the very dense vegetation means that the invaded environment, regarding to its use by the rails, has only two layers—not three, as in non-invaded environments (Fig. 5). Hence, the invaded areas have vegetation with reduced structural complexity. Likewise, the lower and upper layers of areas invaded by *U. arrecta* are quite open (Fig. 5), which seems to be why *P. nigricans* do not occur or nest there. *Rallus longirostris*, in turn, seems to prefer less dense vegetation, since it breeds in the lower layer of invaded areas, and occurs in mangroves and even on mudflats.

The layers of native vegetation in the phytophysiognomies in which *R. longirostris* occurs comprise: a lower layer with low to moderate vegetation density, an intermediate layer with moderate to high vegetation density, and an upper layer with low vegetation density (Fig. 6). As a consequence of the rosette shape of this species, the phytophysiognomies where *C. americanum* is dominant are characterized by increments of leaves overlap in the intermediate layer of the vegetation, forming several “Ys” side by side. The top of

each “Y” supports the dead leaves of other plant species, contributing to the high density of vegetation in the intermediate layer. The erect plants *T. domingensis* and *C. mariscus* develop leaves from their stems, which touch at mid-height of the vegetation and support dead leaves, contributing to increased vegetation density in the intermediate layer of phytophysiognomies where these species are the dominant plant species. In Schoenoplectetum, although *S. californicus* has smooth leaves without ramification, the three layers still have different vegetation densities because the leaves of intersect, forming multiple intersecting “Xs”. Additionally, the points of intersection of *S. californicus* leaves also accumulate dead leaves, contributing to increased density in the intermediate layer. However, this density tends to be much lower than that associated with other phytophysiognomies (Teixeira and Bornschein unpublished data).

Birds such as *R. obsoletus* generally prefer more complex environments for nest building (Rush et al. 2010). The apparent advantages of nesting in the lower layer in Urochloetum are the support for the nests and the buoyancy of the biomass under high-tide conditions, which could potentially reduce reproductive losses from flooding—an impact that is quite significant for wetland birds (Marshall and Reinert 1990; Shriver 2002; Greenberg et al. 2006; Reinert 2006; Norbdy et al. 2009). In the study region, high tides flood the nests of *F. acutirostris* (Reinert et al. 2012), the least bittern *Ixobrychus exilis* (Gmelin, 1789), *P. nigricans*, *Phleocryptes melanops*, the yellow-chinned spintail *Certhiaxis cinnamomeus* (Gmelin, 1788), *Tachuris rubrigastra*, and the Brazilian tanager *Ramphocelus bresilia* (Linnaeus, 1766; MRB per. obs.).

The principle of equal opportunity (MacArthur 2002) predicts that the occupation of environments by species depends on the relationship between the resources in those habitats and the pressure to use them, meaning that individuals to a certain extent prefer less competitive environments, could be a factor in the choice of the environment by *R. longirostris* and *P. nigricans* and their consequent nesting in patches of *U. arrecta* by the former. The occupation of environments depends on competition (Cody 1985), and few species can occupy resource-poor habitats, such as patches of Urochloetum with impoverished flora and a simple vegetation structure, which leads to reduced competition (Cody 1985). *Rallus longirostris* could have benefited from the occupation of patches containing exotic plants. Although *R. longirostris* and *P. nigricans* coexist in vegetation free of exotic plants without apparent mutual aggression, even when they are side by side, the similarity between these species suggests that they compete silently without obvious aggression (MacArthur 2002).

Benefits were verified for the congeneric *R. obsoletus* following the invasion of a hybrid form of *Spartina* grass,

which increased the survival rate of individuals by offering refuge against predators (Overton et al. 2014). Following the introduction of an exotic-plant eradication program, the bird population declined (McBroom 2013), as observed in the present study of *R. longirostris*. Conversely, biological invasions of clonal grass *Phragmites australis* (Cav.) Trin. ex Steud. in Canada had long-term negative impacts on birds, decreasing species richness and changing community compositions (Robichaud and Rooney 2017).

*Rallus longirostris* is not threatened with extinction either globally (BirdLife International 2016) or in Brazil (Ordinance 148 of the Brazilian MMA, June 7 2022), but it has been deemed VU in that country (Vieira 2015). Regionally, *R. longirostris* is considered VU in the state of Paraná (Decree 1.797/2018 of the State of Paraná, November 22, 2018), where the present research was carried out. The fact that *R. longirostris* has benefited from areas dominated by an exotic plant, allowing it to colonize a previously uncolonized environment (Vieira 2015), does not seem to justify interrupting or preventing the management of *U. arrecta*. It is a distinctly aggressive species (Kissman 1997; Thomaz et al. 2009) that reduces the functional diversity of native species due to the presence of allelopathic compounds and its high energy efficiency, resistance to drought periods, and high rates of germination, growth, regrowth, and regeneration (Freitas and Pivello 2005; Bianchini Jr. et al. 2010). The impacts of this grass on native macrophyte (Michelan et al. 2010) and fish (Casatti et al. 2009; Carniatio et al. 2013) communities have been reported, as well as the impact of habitat suppression on *F. acutirostris* (Reinert et al. 2007)—a species at risk of extinction in Brazil (Ordinance 148 of the Brazilian MMA, June 7, 2022). Moreover, the high cost of management and the difficulty of raising funds for this activity make it impossible to implement a program with the objective of eradicating some areas invaded by *U. arrecta*, but not all of them to sustain a population of *R. longirostris*. Permanent management of the Urochloetum to keep them with the same extension would make the program very expensive and unrealistic. The cost of restoring 1 ha dominated by the alien *U. arrecta* varies from 13,404 to 29,356 USD, depending particularly on the traveling distance by boat to access the areas requiring management (Teixeira and Bornschein unpublished data).

The use of subtropical salt marshes and areas dominated by exotic grasses by *R. longirostris* demonstrates ecological plasticity. With the advancing invasion of *U. arrecta* in estuaries, this new nesting niche of *R. longirostris* may increase its population and warrant reversion to its previously endangered status (Vieira 2015). Conversely, invasive plants can be ecological traps, attracting species but not sustaining them in the long term (Norbdy et al. 2009; Kloskowski 2012; Stinson and Pejchar 2018). Long-term monitoring of

different estuaries is encouraged because it may reveal this or other population trends of *R. longirostris*, as confirmed by those presented here, in addition to allowing a deeper assessment of the impacts of *U. arrecta* invasions.

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**Data availability** The raw data in this article are included in the tables and figures.

## Statements & declarations

**Competing interests** The authors have no relevant competing interests to disclose.

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