

POSSÍVEL APRENDIZADO EM NINHADAS SUCESSIVAS E
INFLUÊNCIA DE VARIAÇÕES AMBIENTAIS NA DINÂMICA
POPULACIONAL DE UMA AVE DE BREJOS SALINOS DO
BIOMA FLORESTA ATLÂNTICA

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“So nature does indeed need protection from man; but man, too, needs protection from his own acts, for he is part of the living world. His war against nature is inevitably a war against himself. His heedless and destructive acts enter into the vast cycles of the earth, and in time return to him”

— Rachel Carson

RESUMO

A compreensão das estratégias adaptativas e dos fatores ambientais que afetam a produtividade e a sobrevivência de aves é crucial para a conservação das espécies. Nos brejos salinos, fatores adicionais, como fragilidade da vegetação e alagamentos periódicos, podem tornar a adaptação mais complexa, bem como influenciar diretamente a dinâmica populacional. O principal objetivo desta pesquisa é abordar as estratégias adaptativas e dinâmica demográfica em brejos salinos por aves, utilizando *Formicivora acutirostris*, endêmica de brejos salinos subtropicais no Brasil, como espécie modelo. Coletamos dados em campo, realizados no estuário da Baía de Guaratuba, Paraná, Brasil durante quase duas décadas. No Capítulo 1, avaliamos a adoção da estratégia “win-stay, lose-switch” para a nidificação de *F. acutirostris*. Investigamos se altura, altitude, espessura, posição e tipo ambiente variam entre ninhos subsequentes em resposta aos destinos dos ninhos prévios, e exploramos, também, o significado adaptativo das eventuais mudanças. Nossos resultados revelaram que os atributos dos ninhos variam pelos diferentes destinos. Ainda observamos que a espécie ajusta a altura do ninho, atributos-chave no sucesso, após alagamento do ninho prévio. No entanto, nenhuma alteração realizada aumenta a chance de sucesso reprodutivo do ninho subsequente. Verificamos que alagamento, predação e tombamento de ninhos são fatores sinérgicos que afetam a viabilidade de longo prazo de *F. acutirostris*. Discutimos a necessidade de ações de conservação que diminuam a pressão sobre ela, como manejo de populações de predadores. No Capítulo 2, investigamos o impacto de fatores ambientais e climáticos na produtividade de filhotes, mortalidade de adultos e desempenho demográfico de territórios de *F. acutirostris* em duas áreas do gradiente altitudinal do estuário. Nossos resultados demonstraram que a produtividade de filhotes varia conforme o tipo, quantidade, densidade e características da vegetação, número de vizinhos e condições climáticas. A mortalidade de adultos varia conforme a densidade de vegetação, altura de maré e precipitação. Aspectos da vegetação foram os mais importantes contribuintes para a dinâmica populacional final. Condições climáticas, vulnerabilizam os indivíduos e podem expô-los a predadores. Destacamos a importância do Cladietum como um ambiente-chave para a manutenção da espécie. Esta pesquisa oferece uma visão detalhada sobre pressões, estratégias adaptativas e fatores ambientais correlatos à dinâmica populacional de *F. acutirostris*, além de ações prioritárias para a sua conservação.

Palavras-chave: alagamento, *Cladium jamaicense*, conservação, dinâmica fonte-ralo, *Formicivora acutirostris*, microclima, mortalidade, predação, produtividade.

ABSTRACT

Understanding the adaptive strategies and environmental factors affecting bird productivity and survival is crucial for species conservation. In salt marshes, additional factors such as vegetation fragility and periodic flooding may make adaptation more necessary and complex, directly influencing population dynamics. The main objective of this research is to address the adaptive strategies and demographic dynamics of birds in salt marshes, using *Formicivora acutirostris*, a bird endemic to subtropical salt marshes in Brazil, as a model species. We collected longitudinal field data from the Guaratuba Bay estuary, Paraná, Brazil, over almost two decades. In Chapter 1, we evaluated the adoption of the “win-stay, lose-switch” strategy for the nesting behavior of *F. acutirostris*. We investigated whether height, altitude, thickness, position, and environment type vary between successive nests in response to the fate of previous nests and also explored the adaptive significance of potential changes. Our results revealed that nest attributes vary according to different fates. We also observed that the species adjusts nest height, a key attribute for success, after flooding. However, the changes did not increase the chances of success in subsequent nests. We found that flooding, predation, and nest collapse are synergistic factors affecting the long-term viability of *F. acutirostris*. We discussed the need for conservation actions that reduce pressure on the species, such as predator population management. In Chapter 2, we investigated the impact of environmental and climatic factors on juvenile productivity, adult mortality, and demographic performance in *F. acutirostris* territories in two areas of the estuarine altitudinal gradient. Our results showed that juvenile productivity varies according to the type, quantity, density, and characteristics of vegetation, number of neighbors, and climatic conditions. Adult mortality varies according to vegetation density, tidal characteristics, and precipitation. Vegetation aspects were the most important contributors to overall population dynamics. Climatic conditions increased vulnerability and exposed individuals to predators. We highlighted the importance of *Cladietum* as a key habitat for species maintenance. This research provides a detailed view of pressures, adaptive strategies, and environmental factors related to the population dynamics of *F. acutirostris*, along with priority conservation actions.

Keywords: conservation, *Cladium jamaicense*, flooding, *Formicivora acutirostris*, micro-climate, mortality, predation, productivity, source-sink dynamics.

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INTRODUÇÃO

A dinâmica populacional é um aspecto fundamental da ecologia e da conservação das espécies que, em populações fechadas, depende das taxas de produtividade e de mortalidade (Gotelli 2009; Ricklefs 2010). Esses parâmetros demográficos podem ser influenciados por características individuais, padrões comportamentais de adaptabilidade e diversos fatores externos (Pulliam e Danielson 1991; Pulliam et al. 1992; Franklin et al. 2000; Saether et al. 2004; Low et al. 2009). Compreender os padrões demográficos é essencial para identificar as fragilidades das espécies e priorizar ações de conservação eficazes (Budnik et al. 2000; Breininger and Oddy 2004; Cowley e Siriwardena 2005; Sergio et al. 2009; Heinrichs et al. 2010; Brambila and Bionda 2013; McGinn et al. 2022).

A seleção do local de nidificação e das características do ninho é um aspecto comportamental das espécies particularmente importante para a reprodução das aves (Marzluff 1988; Benvenuti et al. 2018), e, conseqüentemente, para a dinâmica populacional. Elas podem usar diferentes estratégias para enfrentar os desafios comportamentais (MaBoudi et al., 2020), como a escolha das melhores características de nidificação. Uma das maneiras de escolher envolve adotar plasticidade para ajustar ou manter os atributos do ninho subsequente com base nas informações do ninho prévio (Refsnider e Janzen, 2012; Benvenuti et al., 2018; Bressler et al., 2020). Essa estratégia, conhecida como “*win-stay, lose-switch*” (WSLS; Freund [2017]), envolve associar as características do ninho aos riscos e benefícios percebidos, por meio de um mecanismo de feedback que recompensa as escolhas feitas (Marzluff, 1988; Freund et al., 2017).

Em outra abordagem relativa à dinâmica populacional das espécies, tem-se os principais fatores externos, habitat e condições climáticas (Saether et al., 2004; Low et al. 2009). O ambiente influencia diretamente na oferta de alimento, adequação dos locais de nidificação e presença de predadores (Franklin et al., 2000; Calf et al., 2003; Low et al., 2009; Narango et al., 2018; Hart et al., 2021). Além disso, ambientes desfavoráveis impõem altos custos energéticos para a reprodução, o que pode comprometer a sobrevivência das aves (Martin, 1995). A precipitação e a temperatura do ambiente podem ter efeitos fisiológicos diretos nas aves, afetando a sobrevivência de adultos e filhotes (Skangen e Adams, 2012; Conrey et al., 2016; Bourne et al., 2020). Ainda, condições climáticas podem afetar indiretamente as taxas demográficas das aves ao alterar a disponibilidade de recursos, dificultar o acesso aos alimentos, limitar oportunidades de forrageamento e afetar a capacidade de regulação da

temperatura corporal (Cowley e Siriwardena, 2005; Skangen e Adams, 2012; Oberg et al., 2015; Aranzamendi et al., 2019).

Complementado os desafios à reprodução, a predação é a principal causa de insucesso reprodutivo em aves tropicais (Oniki 1979; Winkler 2016). Em brejos salinos de regiões temperadas, a predação também é alta (Ricklefs 1969) e ainda facilitada pela simplicidade da vegetação e pela grande quantidade de predadores visuais de ninhos (Greenberg et al. 2006). Porém, nesses ambientes, ventos fortes e frequentes alagamentos pela maré representam desafios adicionais às aves (Reinert 2006; Reinert 2008). A fragilidade da vegetação quando exposta a fortes ventos pode causar tombamento das plantas utilizadas como apoio de ninhos ou deles próprios (Burger, 1985; Reinert, 2008). Os alagamentos, por sua vez, diminuem as opções de forrageamento (Reinert 2008) e podem afogar filhotes, inviabilizar ovos e dispersar ovos carregados pela água (Reinert 2006; Greenberg et al. 2006; Reinert 2008; Reinert et al. 2012). Dessa forma, em brejos salinos há um desafio para as aves potencializado pelo *trade-off* entre alocar o ninho em maior altura para evitar marés altas, mas sem expô-lo a predadores visuais e ao tombamento pelo vento (Greenberg et al. 2006; Hunter et al. 2016; Benvenuti et al. 2018).

Com o objetivo de investigar a dinâmica populacional das aves em brejos salinos, incluindo o uso de estratégias de plasticidade comportamental na nidificação e a influência de variações ambientais nas taxas demográficas, selecionou-se como modelo de estudo *Formicivora acutirostris*, uma pequena ave endêmica de brejos salinos subtropicais (Bornschein et al. 1995, 2024). A espécie é ameaçada de extinção no Brasil, principalmente devido à perda de habitat (Portaria MMA 148, de 7 de junho de 2022; Silva et al. [2018]). Além disso, *Formicivora acutirostris* enfrenta ameaças adicionais associadas à mudança climática, que incluem o aumento da intensidade e frequência dos alagamentos, devido à elevação do nível do mar, alterações na precipitação e vazão fluvial, e aumento dos ventos fortes (Marengo 2006; Jong 2019).

Utilizando dados longitudinais coletados por quase duas décadas, esse trabalho aborda estratégias de plasticidade adaptativa de nidificação e fatores relacionados à dinâmica demográfica de *F. acutirostris*. O Capítulo 1 é dedicado a testar a existência de adoção da estratégia WSLs pela espécie, analisando se já comportamento de mudança na altura, altitude, espessura, posição e/ou tipo de ambiente entre ninhos sucessivos em resposta ao destino do ninho anterior, explorando-se, ainda, o significado adaptativo dessas mudanças. No Capítulo 2, por sua vez, explora-se a importância de fatores ambientais na produtividade de filhotes,

mortalidade de adultos e desempenho demográfico em territórios de *F. acutirostris* de duas áreas diferentes do gradiente atitudinal estuarino.

CAPÍTULO 1

The win-stay, lose-switch renesting strategy of a territorial bird endemic to subtropical salt marshes

Research Article – submitted to “Frontiers in Ecology and Evolution”

Original Research

The win-stay, lose-switch reneating strategy of a territorial bird endemic to subtropical salt marshes

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Keywords: conservation, flooding, *Formicivora acutirostris*, marsh stratification, predation, reproductive success.

Abstract

The “win-stay, lose-switch” (WSLS) strategy used by birds involves decisions to maintain or alter the characteristics of the subsequent nest according to the outcome of the previous one. In salt marshes, nest failure occurs due to flooding, predation, or tipping, creating a trade-off for nest placement: it should be low enough to avoid predators from above and tipping by the wind, and high enough to avoid flooding. In salt marshes of Southern Brazil, predation from above is carried out by rails that also prey on nests from below, promoting non-directional pressure capable of neutralizing bird responses. We aim to test the WSLS strategy and to assess its adaptive significance for *Formicivora acutirostris*, the only thamnophilid endemic to salt marshes. Our general premise is that the adoption of the WSLS strategy would vary in response to the fate of the previous nest, considering also the environment type. We evaluated fate, environment type, height, altitude, and thickness of nests of *F. acutirostris* in southern

Brazil, between 2006–2023. We assessed the effects of the nest attributes, tested the adoption of WSLS strategy, and explored its adaptative significance using generalized linear mixed models. We also examined the influence of factors such as nest environment, nesting timing and pair age on nest fate and parental behavior. We studied 98 renesting cases. Flooded nests were at a lower height than predated, tipped, and successful nests, and tipped nests were thicker than flooded and successful nests. Nest heights differed among environment types. The species adopted the WSLS strategy by increasing nest height after flooding, but we do not support its adaptive significance. No additional factors influenced the behavior of the species. We emphasize the threat of the high reproductive failure for the conservation of *F. acutirostris*.

1. Introduction

Birds' breeding decisions and the reasons behind them are directly related to their success (Martin and Roper, 1988; Filliater et al., 1994; Chalfoun and Martin, 2009; Parejo and Avilés, 2010; Benvenuti et al., 2018), so understanding it is crucial for conservation (Campomizzi et al., 2012). Essentially, bird parents have the challenge of selecting nest characteristics that minimize risks and increase their reproductive success (Forstmeier and Weiss, 2004; Jiang et al., 2017). Animals can address behavioral tasks in several forms (MaBoudi et al., 2020), and one simple strategy involves adopting behavioral plasticity to maintain or change the characteristics of the current nest using information from the previous one (Refsnider and Janzen, 2012; Benvenuti et al., 2018; Bressler et al., 2020). This behavior requires the association of nest characteristics with the risks and advantages of those characteristics through a mechanism of reward or disappointment (Marluff, 1988; Freund et al., 2017). Such plasticity characterizes a strategy known as “win-stay, lose-switch” (WSLS; following Freund et al. [2017]) and has been detected in several bird species (Marzluff, 1988; Chalfoun and Martin, 2010; Beckmann and McDonald, 2016; Hunter et al., 2016; Benvenuti et al., 2018; Ma et al., 2019). However, this nesting behavior is not universal in birds and some studies have shown that there are species with unconditional strategies (Hendricks, 1991; Grand and Flint, 1996; Howlett and Stutchbury, 1996; Kershner et al., 2004).

In salt marshes, habitats dominated by herbaceous plants adapted to the salinity and tidal flooding (Tiner, 2013), breeding challenges for birds are particularly complex due to several environmental factors and conflicting pressures. The sparse and simple vegetation can make nests more vulnerable to being tipped by the wind (Burger, 1985; Reinert, 2008) and more

exposed to abundant predators from above (Greenberg et al., 2006). In these environments, the regular tidal effect also increases reproductive failure by flooding the nests (Reinert, 2006; Reinert, 2008). Thus, in salt marshes, there is a trade-off for birds between placing the nest low enough in the dense vegetation to avoid aerial predation and tipping by the wind, but also high enough to avoid flooding (Greenberg et al., 2006). This height trade-off presents an ideal opportunity to evaluate the WSLs strategy, and the two studies that evaluated it in salt marsh-dwelling birds from temperate regions have found that they do indeed adopt the strategy for flooding and predation (Hunter et al., 2016; Benvenuti et al., 2018).

Thamnophilids are generally found in forest and avoid open areas (Zimmer and Isler, 2003), such as marshes. In southern Brazil, however, there is a particular salt marsh habitat called “subtropical salt marsh” (Bornschein et al., 2017), to which the threatened Parana Antwren (*Formicivora acutirostris*) is endemic (Bornschein et al., 2024; Ordinance MMA 148, of June 7, 2022). That species and the Marsh Antwren *F. paludicola* (Buzzetti et al., 2013), from southeastern Brazil, are the only members of the species-rich thamnophilid family (c. 240 species; Winkler et al. [2020]) that exclusively inhabit marshes (Buzzetti et al., 2013; Winkler et al., 2020).

Our objective is to test the WSLs strategy in *F. acutirostris*. Nest flooding, predation, and tipping are the main causes of nest failure for this species (Reinert, 2008). However, in the subtropical salt marshes that *F. acutirostris* occurs, predation pressure comes less from visual aerial predators like raptors, which are rare in the area (Guerra, 2023), and more from the Blackish Rail *Pardirallus nigricans* and the Black Rat *Rattus rattus* (GS-S and MRB, personal observation), which can access the nest from above or below, depending on its height and the environment type. Therefore, the non-directional predator pressure could increase complexity or eventually neutralize possible bird reward or disappointment responses following predation. Based on previous field knowledge regarding environment types of salt marshes and their available strata for nest placement and local pressures on them (Figure 1), our general premise is that the species adopts the strategy by changing or maintaining the attributes based on previous nest fate. This adoption would involve bird responses in relation to nest height after losses due to flooding and tipping, nest position after losses to predation, and nest thickness after tipping. Also, it would vary according to the type of the nest environment, with birds preferring to remain in the same type when nesting in favorable environments, regardless of the fate of the previous nest (Figure 2).

2. Methods

2.1 Target species

Formicivora acutirostris, a threatened species in Brazil (Ordinance MMA 148, of June 7, 2022), is a territorial and socially monogamous bird that forms long-term pairs, sharing reproductive and defensive activities throughout the year (Sobotka, 2011; Reinert et al., 2012; Bornschein et al., 2015). The breeding season extends from August to February (Reinert et al., 2012); the species builds cup-shaped nests attached to vegetation, at a height between 30–220 cm above the ground (Reinert et al., 2012), and may renest up to eight times during a breeding season (Reinert, 2008). *Formicivora acutirostris* lays two eggs (Reinert et al., 2012), incubates them for approximately 16 days (Reinert, 2008), and the nestling stage extends for approximately 10 days (Reinert, 2008).

2.2 Study area

The study was conducted in the Guaratuba Bay, Guaratuba Ramsar Site (see <https://rsis Ramsar.org/ris/2317>), municipality of Guaratuba, on the southern coast of Paraná, southern Brazil (Figure 3). We worked at the confluence of the Claro and São João rivers (“Continente”; c. 25.873° S, 48.761° W; 8.7 ha) and on Jundiaquara Island (“Jundiaquara”; c. 25.873° S, 48.759° W; 11.5 ha), located upstream on the São João river, and in part of the Folharada Island (“Folharada”; c. 25.866° S, 48.723° W; 16.3 ha), located downstream on this river. The studied areas contain “estuarine marshes” (*sensu* Doody, 2001), or “tidal marshes” (Reinert et al., 2007), or “subtropical salt marshes” (Bornschein et al., 2017), or pioneer formation of fluvio-marine influence (*sensu* Veloso et al., 1991; IBGE, 1992). The environment experiences two daily floodings according to a mixed semi-diurnal tide (Lee and Chang, 2019).

The dominant plant species are crinum lily (*Crinum americanum*) and California bulrush (*Schoenoplectus californicus*). Locally, can be abundant the herbaceous southern cattail (*Typha domingensis*), swamp sawgrass (*Cladium mariscus*), and giant leather fern (*Acrostichum danaeifolium*), the bush (*Talipariti pernambucensis*), and the trees pond apple (*Annona glabra*), Brazil beauty-leaf (*Calophyllum brasiliense*), and white mangrove (*Laguncularia racemosa*) (Reinert et al., 2007; Bornschein et al., 2017; Favretto et al., 2022).

2.3 Nest search and monitoring

Fieldwork was conducted between January 2006 and March 2023. Until May 2008, it was conducted daily during the breeding season and for 10 days per month outside of it. From June 2008 to March 2023, fieldwork was conducted for 3–8 days per month throughout the year. We worked in the field as a group of two to five people, usually three, from dawn to about 1 p.m. and for a further two to three-and-a-half hours in the afternoon, before dusk.

All territorial birds were banded (with a metal numbered band and three colored plastic bands) in unique color codes for individual's recognition with binoculars in order to determine the owners of the nests and the nest sequences. During banding, each individual was assigned with an identity code (referred to as "ID number") and its minimum age was estimated based on the plumage (for details on juvenile and adult plumage patterns, see Reinert [2008]). To reduce data variability, we estimated the birth date as either October 1st (a period with many early breeding season births) or February 1st (a period with the latest births in the season), in accordance with Bornschein et al. (2015). We assigned the closest birth date that best matched the observed plumage pattern at the time of the banding (Bornschein et al., 2015). Every year, we calculated the resulting age of the individuals by summing a year.

Target nests were systematically searched in 14–41 territories per year during the breeding seasons (August to February), making a total of 521 monitored territories. The nests were located mainly by observing the behavior of individual birds (e.g., carrying plant material or food and alarm vocalizations), that we followed up to discover nests. When finding nests at different stages, we calculated their initiation, as the date of nest construction completion and the start of egg laying, based on mean reproductive times studied by Reinert (2008). The nests were numbered and marked with a ribbon tied on the vegetation to facilitate the correct identification in the returns. We took the geographic coordinates of each nest and information on its height (as lip to the ground), thickness, and environment type. The thickness, that represent the robustness of the nest, may be a factor related to losses due to rips and holes (Palomino et al., 1998; Suárez et al., 2005) and was estimated as the average of the differences between 1) internal and external diameters and 2) nest height and depth of the incubation chamber.

We classified the environment type in which the nest was constructed, based on the dominant plant species. We named them by adding the suffix "etum" to the genus of the dominant species, following Braun-Blanquet (1979), as follow: 1) "Crinetum" (for the domain of the herbaceous *C. americanum*), 2) "Schoenoplectetum" (for the domain of the herbaceous *S. californicus*), 3) "Cladietum" (for the domain of the herbaceous *C. mariscus*),

4) “Acrostichetum” (for the domain of the herbaceous *A. danaeifolium*), 5) “Typhetum” (for the domain of the herbaceous *T. domingensis*), 6) “Taliparitetum” (for the domain of the bush *T. pernambucensis*), and 7) “Laguncularietum” (for the domain of the tree *L. racemosa*).

We calculated nest altitude based on an altimetric mapping, made with the Real Time Kinematic (RTK) technique in 2014 (when more than four thousand altitude points were taken with 1 mm precision). The altitude points were distributed in grids of 20 m x 20 m or 5 m x 5 m, the latter for regions with terrain slope. A map was generated with contour lines for every 10 cm of altitude. The altitude of each nest was taken to be that of the altitude of the point that were closest to the nest, but within the same contour line as the nest.

Monitored nests were considered as having success or failure (= nest fate), and failure was attributed to predation, flooding or tipping. We consider the nest to be successful if at least one fledgling left it. We attributed failure to predation when observed or inferred attacks on nests that led to loss of eggs, hatchlings or entire nest. We inferred predation if observed evidences in the nests such as bottom or side holes, eggshell bottoms, or completely ripped nest material, with no signs of friction in the plant fibers. We attributed nest failure to flooding when observed flooded nests, floating eggs around the nests, drowned chicks inside the nests, wet nests (on non-rainy days), and presence of debris inside the nests. Finally, we attributed nest failure to tipping when observed or inferred fallen nests due to the observation of friction in the plant support. We observed many empty nests that should have been active, but it was not possible to attribute the cause of the loss, such as nests that may have been lost due to strong winds or the approach of a predator. In these cases, we attributed the cause of failure as undetermined and removed these data from the analyses.

After determining success or failure, we only counted subsequent nest attempts by the same pair (re-nesting case) that were carried out to completion (i.e. a complete cup), since there are changes in the height and thickness of nests during construction. We concluded that we were dealing with a case of re-nesting only when we were certain that no third nest had been built between the previous and subsequent nests.

2.4 Statistical analysis

We compared the characteristics of the previous and the subsequent nests (re-nesting) to evaluate the changes adopted by the individuals. We calculated the differences in nest attributes by subtracting the height (change in nest height), altitude (change in nest altitude), and thickness (change in nest thickness) of the nests (*change in nest attribute = second nest*

attribute – previous nest attribute). Additionally, considering the position and environment of the nests, we calculated the distance between subsequent nests and assessed whether there was change in environment type.

We conducted three different analyses to assess the adoption of the WSLs strategy by *F. acutirostris*, as well as its adaptive significance. Initially, we tested the relationship between the nest attributes and their fates (analysis 1). Next, we evaluated the relationship between changes in nest characteristics in re-nesting cases and the fate of the previous nest (analysis 2), to determine whether the species makes systematic changes (Figure 2). Finally, we tested the relationship between the changes in nest characteristics and the success or failure of the second nest (analysis 3) to assess the adaptive significance of these changes. In addition to the previously mentioned nest attributes (analysis 1) and changes in these attributes (analyses 2 and 3) to test our main hypotheses, we also included potential factors associated with nest fate or nesting behavior, such as seasonality (indicated by month of nesting initiation), environment type (simplified according to the sample size and objective), and parental age (Table 1) in the models. We did not include these potential factors in analysis 3 due to the low sample size resulting from the model's specificity (see below). For the same reason of sample size, thickness and altitude were not included in the models of this analysis. We used generalized linear mixed models (GLMMs) with different functions (see below) from the *lme4* 1.1-35.1 package (Bates et al., 2024) in R (version 4.3.3; R Core Team, 2024).

For analysis 1, we constructed three models, one for each nest attribute (height, altitude, and thickness), analyzing each one for the different nest fates (Table 1). For analysis 2, we constructed 15 models, one model for each of the five changes in nest attributes (nest height, altitude, thickness, distance between nests, and environment type) across the three comparisons between success ("win") or failure ("lose" = flooded, predated or tipped) of the previous nest (Table 1). For analysis 3, we built four models, one for each fate of the first nest (flooded, predated, tipped, and successful nests), comparing what led to the success or failure of the subsequent nest (Table 1).

We included random variables in all models. Territory and year were treated as structural random predictors, meaning they were retained in all models (i.e., not removed during model selection; see below) to account for the identifier and time of repeated measures or longitudinal samples. Additionally, in all models, female ID number and male ID number were also included as random predictors, but they could be removed during model selection

(see below) if this improved the model fit. The complete model structure can be found in Table 1.

We disregarded the models with a sample size smaller than twice the number of predictor variables included. To avoid over-testing due to multiple parallel analyses, we adjusted the *p*-values for each of the three analyses separately. For this, we used the *p.adjust* function from the *stats* 4.3.3 R package (R Core Team, 2024), applying the Bonferroni method.

After selecting the best complete model distribution based on AIC values and convergence success, we proceeded with variable selection. We evaluated the importance ranking of the predictors using the *MERF* function from the *LongituRF* 0.9 package (Capitaine, 2020). We designated territory as the identifier and year as the time trajectory – for this reason, they are treated as structural variables in our GLMMs, as they contributed to the longitudinal structure of the models and didn't have their importance obtained. The model was configured without any stochastic process, two predictor variables per split, and with other default settings. For random effect predictors, importance was measured by summing their estimates, and for fixed effect predictors, we assessed importance based on the percent increase in mean squared error (%IncMSE; Supplementary Tables 1–3). We sequentially removed the least significant random effect predictors until identifying their best combination based on AIC. Next, we applied the same method of removing the least important fixed predictors to obtaining the best model.

Model validation was conducted by verifying normality and homoscedasticity of residuals using *residual*, *fitted*, *bptest*, and *shapiro.test* functions of the *stats* (R Core Team, 2024) and *lmtest* 0.9-40 (Hothorn et al., 2022) R packages for normal and log-normal models. For binomial models, we validated the results by analyzing the receiver operating characteristic (ROC) curve and calculating the area under the curve (AUC) using the *predict* and *roc* functions of the *stats* (R Core Team, 2024) and *pROC* 1.18.5 (Robin et al., 2023) R packages. If our best models did not validate, we removed outliers, tested alternative distributions, or selected more complete models of the best distribution. In order to verify the differences in nest fate for analysis 1, we applied pairwise comparison tests using the *emmeans* and *pairs* function from the *emmeans* 1.10.4 (Lenth, 2024) and *multcomp* 1.4.26 (Hothorn et al., 2024) R packages.

3. Results

We located 963 nests, of which 785 were build up to completion (the rest had been abandoned during the construction phase). We monitored 98 renesting cases involving a total of 166 nests, of which 150 proceeded to the egg-laying stage, and the remaining 16 we could not monitor after became a cup. In half of the cases, we studied only one annual renesting by each pair ($n = 49$ cases), but the pairs carried out up to six successive renestings tracked by us ($\bar{x} = 1.46$). The renesting cases included a total of 90 individuals in 50 pair combinations. The nests were built by females with 0.5 to 14.5 years ($\bar{x} = 3.88$ years; DP = 2.93) and by males with 0.5 to 13.5 years ($\bar{x} = 4.24$ years; DP = 3.42). The largest number of renesting events occurred after the predation of the previous nest ($n = 42$), followed by renesting after flooding ($n = 22$), after tipping ($n = 15$), and after the success of the previous nest ($n = 19$). The main cause of nest failure was predation ($n = 66$), followed by flooding ($n = 34$) and tipping ($n = 27$). The overall nest success rate was 23.49%. The renesting attempts occurred at 3.4 m to 116.3 m from the first nest ($\bar{x} = 33.38$ m, $n = 93$).

3.1 The relationship between nest attributes and fates (analysis 1)

The attributes of the nests of *F. acutirostris* were related to their fate (Figure 4; Table 2). The height of the nests varied according to nest fate (Figure 4A), with flooded nests being at lower heights than predated (pairwise, $p < 0.001$), tipped (pairwise, $p < 0.001$), and successful nests (pairwise, $p < 0.001$). However, there was no difference in the height of successful nests versus predated (pairwise, $p = 0.986$) and tipped nests (pairwise, $p = 1.000$), and in the height of predated versus tipped nests (pairwise, $p = 0.996$). Nest height also varied between environments, with nests in Cladietum being at higher heights than those in Crinetum (pairwise, $p = 0.001$), Taliparitetum, Typhetum, and Schoenoplectetum (“other”; pairwise, $p < 0.001$), at lower heights than nests in Acrostichetum (pairwise, $p = 0.002$), and at similar heights of nests in Laguncularietum (pairwise, $p = 0.195$). Nests in Acrostichetum were at higher heights than those nests in Crinetum (pairwise, $p < 0.001$), in Laguncularietum (pairwise, $p < 0.001$), and in Taliparitetum, Typhetum, and Schoenoplectetum (“other”; pairwise, $p < 0.001$). There was no difference in the height of nests in Crinetum versus nests in Laguncularietum (pairwise, $p = 0.560$), nests in Crinetum versus nests in Taliparitetum, Typhetum, and Schoenoplectetum (“other”; pairwise, $p = 0.856$), or nests in Laguncularietum versus nests in Taliparitetum, Typhetum, and Schoenoplectetum (“other”; pairwise, $p = 0.116$).

Nest thickness was related to nest fate (Figure 4C; Table 3), with predated and tipped being thicker than flooded (pairwise, $p = 0.046$ and $p = 0.012$), and tipped nests being thicker than successful nests (pairwise, $p = 0.043$). Predated nests were equally thicker than tipped (pairwise, $p = 0.664$) and successful nests (pairwise, $p = 0.274$), and flooded nests were also equally thicker than successful nests (pairwise, $z = 0.251$; $p = 0.774$). We did not observe a relationship between nest altitude and fate (Figure 4B; Table 3).

3.2 Testing the WSLS strategy (analysis 2)

Changes in subsequent nest characteristics were related to the fate of the first nest (Figure 5; Table 3). After losing the nests due to flooding, the species constructed the second nest higher, making significant changes in nest height compared to changes in height after experiencing success (GLMM, $p = 0.020$; Figure 5A). The changes in nest height following a successful nest were similar to those after predation and tipping (Figures 5B–C; Table 3). Similarly, the changes in nest altitude after experiencing success were similar to those after experiencing flooding and predation of the nest (Figures 5D–E; Table 3), and changes in nest thickness after a successful nest was similar to those after a predated nest (Figure 5H; Table 3). The distances between nests after experiencing success were similar to those after experiencing flooding, predation, and tipping (Figures 5J–L; Table 3), as well as the changes in nest environment (Figures 5M–O; Table 3). No other factors significantly influenced the changes in nests' attributes adopted by the species (Table 3). Due to small sample sizes, it was not possible to analyze changes in nest altitude after tipping ($N = 16$), and nest thickness after flooding ($N = 14$) and tipping ($N = 13$).

3.3 Testing the adaptative significance of the changes (analysis 3)

Changes in nest height, distance between nests, and changes in the environment type did not influence the success rate of subsequent nests following flooding, predation, or success of the previous nest (Figure 6; Table 4). The analysis 3 could not be conducted following previous nest tipping due to the small sample size ($N = 11$).

4. Discussion

We found that *F. acutirostris* shows some behavioral plasticity according to previous nesting experience. Compared to after success, the species makes greater changes in nest height, a key attribute for nesting in salt marshes (Figure 4; Table 2), to avoid flooding,

(Figure 5; Table 3). However, the species does not make greater changes in nest attributes after predation and tipping. This result partially support the adoption of the WSLs strategy by the species and our general premise. However, this strategy does not influence the success rate of the subsequent nest (Figure 6; Table 4).

Tidal flooding is an important factor for the dynamics of salt marshes birds because it constantly threatens their productivity by drowning chicks and eggs, and by displacing eggs, which are carried away by the water (Reinert, 2006; Greenberg et al., 2006; Reinert, 2008; Reinert et al., 2012; this study). Marsh-dwelling bird species have thus evolved some ways to respond to flooding (Reinert, 2006; Shriver et al., 2007; Hunter et al., 2016; Benvenuti et al., 2018). The increase in nest height after nest flooding detected for *F. acutirostris* in the present study corroborates the results found for other species (Hunter, 2016; Benvenuti, 2018) and highlights the importance of nest height for estuarine birds (Greenberg et al., 2006; Hunter et al., 2016; Benvenuti et al., 2018). However, the adjustment in nest height in response to flooding did not increase the reproductive success of the subsequent nest of *F. acutirostris*, probably because of its exposure to other pressures, such as predation and tipping.

In general, predation is the main reason for nest failure and an important driver of evolution in birds (Oniki, 1979; Winkler, 2016). Therefore, many species adopt the WSLs strategy against this threat by systematically building nests at higher, or lower, heights (Marzluff, 1988; Chalfoun et al., 2010; Hunter et al., 2016; Benvenuti et al., 2018; Ma et al., 2019). For *F. acutirostris*, the nest height was not a significant attribute associated with predation, as it was similar between predated, tipped, and successful nests (Figure 4A). This might be due to a balanced effect of predators from above and below that results in non-directional predation pressure. Rallids forage for food all the time (Taylor, 1996), and *P. nigricans* could predate the nest from below, when moving in the lower strata of the vegetation, or from above, when moving in the intermediate strata of the vegetation (*sensu* Bornschein et al., 2022). *Rattus rattus*, more abundant downstream on Folharada, also could access the nests through the mangrove branches, both from above and below (GS-S and MRB, personal observation). In fact, we detected nests with small holes in the bottom of the nest cup, nests with nesting material pulled upwards, and also observed an eight-day-old nestling stuck alive pinned by wing feathers on leaves beside the nest with a curved tarsus and some removed remiges, indicating predation from above and below.

The thickness of the nests proved to be an important factor influencing their fate, with thicker nests being more frequently tipped (Figure 4C; Table 2). Despite the suggestion that

more nest material improves nest stability (Collias and Collias, 1984), this may be the opposite in the vegetation of salt marshes, where more nesting material could imply in heavier nests and the need for attachment to a greater number of plant stems, favoring the tipping of the nest as a result of the movement of these stems due to the action of the wind. This fate will probably become more frequent due to increased wind speed caused by the climate change (Jong et al., 2019), so would be valuable to the species adopts the strategy to reduce thickness after tipping, tendency already observed (Figure 5I). Although we could not statistically assess the adaptive significance of the changes in nest thickness, the graphic suggests that they do not impact the reproductive success (Figure 6).

We expected to observe the adoption of greater distances between nests after predation by *F. acutirostris*, as observed in other studies (Chalfoun and Martin, 2010; Benvenuti et al., 2018). This could benefit the species by helping it to find environments with different predator compositions, vegetation susceptibility, and nest site concealment (Chalfoun and Martin, 2010; Benvenuti et al., 2018). The absence adoption of a distance strategy by *F. acutirostris* could be related to the active foraging behavior (see Taylor, 1996) and abundance (Guerra, 2023) of its main predator, that is likely present throughout the territory of *F. acutirostris*, regardless of position, interfering with the reward system of the adopted changes. Furthermore, the absence of adoption of a strategy for distance may occur due to an eventual choice of micro-habitat characteristics that were not explored in the present study and that are independent of nest position, since the influence of micro-habitat appears to be quite significant for the reproduction of the species (Sandretti-Silva, 2024). In opposition, large distances in renesting are not expected after success, as well as after flooding, as the species aims to maintain favorable characteristics and minimize the time spent making new choices to ensure a rapid nesting attempt since tidal conditions is also a temporal threat (Chalfoun and Martin, 2010; Benvenuti et al., 2018).

Although the environment types exhibit different rates of nesting success for *F. acutirostris* (Figure 1), the species does not systematically choose distinct environments following failures, nor does it consistently remain in the same environments after success (Figure 5). This may be related to the quantity (ha) and quality (vegetation density) of each environment type for each pair at the time of the change, which was not accounted in our models. Vegetation characteristics in the species' territories are important factors influencing the production of independent juveniles by due to the safety of the nesting site and exposure to predators and bad weather (Sandretti-Silva, 2024).

5. Conclusion

The biotic (environment) and abiotic (high tides and altitudes) heterogeneity of *F. acutirostris* habitats are propitious to the occurrence of behavioral plasticity in nest construction by the species, which is crucial for marsh-dwelling species to deal with the strong pressures in dynamic environments (Benvenuti et al., 2018). Simultaneously, the interplay of nest flooding, predation, and tipping creates a complex challenge for the reproductive success of *F. acutirostris*. Our results highlight that the WSLs strategy is adopted by this species in relation to flooding but is insufficient for increasing its reproductive success, likely because it exposes the nests to other pressures, leading to uncertain long-term viability (Sandretti-Silva et al., 2024).

This adaptability of *F. acutirostris* is particularly important in response to flooding, and could also be important in response to tipping events, which are becoming more frequent due to climate change, potentially affecting the reproductive success of birds in salt marshes (Jong et al., 2019; Ma et al., 2019, this study). The timing of this adaptation is also crucial, as climatic events tend to vary fastest than species' responses (Meyer and Pie, 2022), making the adoption of conservation measures essential. Given that direct mitigation of flooding and tipping due to high tides and strong winds is not feasible, conservation strategies must focus on reducing predation pressure. Managing predator populations could improve reproductive success not only by directly reducing nest predation but also by enhancing the effectiveness of the already adopted WSLs strategy. We recommend management aimed at reducing populations of *R. rattus* and *P. nigricans*. Since this bird is native to Brazilian fauna, though not endangered, obtaining permits from the relevant environmental agencies may be challenging. Therefore, a pilot project in the studied areas could yield consistent short-term results, leading to approval and implementation of long-term predator management.

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Tables

Table 1 – Structure of the generalized linear mixed models for testing the adoption of the “win-stay, lose-switch” strategy by *Formicivora acutirostris* and its potential adaptative significance. The levels of categorical variables are presented in italics in parentheses. Abbreviations: ID = identity; PN = previous nest; SN = subsequent nest.

Model		Response variable	Fixed-effect predictors	Random-effect predictors	Structural random-effect predictors	
					Time	Identifier
Analysis 1						
1	Height	Nest fate, nest environment	Female ID	Year	Territory	
2	Altitude	type (<i>Acrostichetum</i> , <i>Cladietum</i> , <i>Crinetum</i> , <i>Laguncularietum</i> , <i>other</i>),	number, male ID number			
3	Thickness	month of nesting initiation (<i>Aug</i> , <i>Sep</i> , <i>Oct</i> , <i>Nov</i> , <i>Dec</i> , <i>Jan</i> ; <i>ordered</i>), female age, male age				
Analysis 2						
1	Change in nest height after flooding or success	PN fate, PN environment type	Female ID	Year	Territory	
2	Change in nest altitude after flooding or success	(<i>Cladietum</i> , <i>other</i>), month of	number, male			
3	Change in nest thickness after flooding or success	nesting initiation (<i>Aug</i> , <i>Sep</i> ,	ID number			
4	Distance between nests after flooding or success	<i>Oct</i> , <i>Nov</i> , <i>Dec</i> , <i>Jan</i> ; <i>ordered</i>),				
5	Change environment type after flooding or success	female age, male age				

6	Change in nest height after predation or success				
7	Change in nest altitude after predation or success				
8	Change in nest thickness after predation or success				
9	Distance between nests after predation or success				
10	Change environment type after predation or success				
11	Change in nest height after tipping or success				
12	Change in nest altitude after tipping or success				
13	Change in nest thickness after tipping or success				
14	Distance between nests after tipping or success				
15	Change environment type after tipping or success				
Analysis 3					
1	Success or failure of the SN after flooded PN	Change in nest height, change	Female ID	Year	Territory
2	Success or failure of the SN after predated PN	in environment type and	number, male		
3	Success or failure of the SN after tipped PN	distance between nests	ID number		
4	Success or failure of the SN after successful PN				

Table 2 – Generalized linear mixed models for testing relationship between the nest fates and nest attributes (analysis 1) of *Formicivora acutirostris*. Significant p-values are shown in bold. Abbreviations: AIC = Akaike information criterion; df = degrees of freedom; N = sample size; SE = standard error.

Variables	Estimate	SE	df	t-value	p-value (corrected)
Nest height (N = 143, AIC = -36.22)					
Intercept	-0.075	0.061	64.981	-1.234	1.000
Nest fate – predated	0.270	0.045	118.069	6.046	>0.001
Nest fate – tipped	0.261	0.052	119.871	5.010	>0.001
Nest fate - success	0.256	0.050	124.270	5.151	>0.001
Environment type - Acrostichetum	0.232	0.056	44.595	4.119	0.004
Environment type - Crinetum	-0.268	0.060	63.489	-4.442	0.001
Environment type - Laguncularietum	-0.165	0.072	49.060	-2.285	0.587
Environment type - Other	-0.339	0.075	83.080	-4.526	>0.001
Nest altitude (N = 98, AIC = -412.61)					
Intercept	0.923	0.005	9.310	176.2	>0.001
Nest thickness (N = 78, AIC = 532.04)					
Intercept	15.036	4.497	30.153	3.344	0.049
Nest fate – predated	9.118	3.324	62.369	2.743	0.174
Nest fate – tipped	12.782	3.887	62.926	3.288	0.036
Nest fate - success	3.639	3.677	62.867	0.990	1.000
Environment type - Acrostichetum	-0.295	2.468	62.546	-0.119	1.000
Environment type - Crinetum	1.229	3.110	62.156	0.395	1.000
Environment type - Laguncularietum	3.237	4.845	64.290	0.668	1.000
Environment type - Other	5.941	5.565	62.493	1.068	1.000

Month	-6.336	2.712	62.7800	-2.337	0.499
Male age	0.209	0.486	61.605	0.430	1.000

Table 3 – Generalized linear mixed models for testing the relationship between previous nest fates and changes in characteristics of the nests in renesting cases (analysis 2) of *Formicivora acutirostris*. Significant p-values are shown in bold. Abbreviations: AIC = Akaike information criterion; df = degrees of freedom; L = linear; N = sample size; PN = previous nest; Q = quadratic; SE = standard error.

Variable	Estimate	SE	df	t-value z-value	p-value (corrected)
Flooded versus successful PN nests					
Change in nest height (N = 34, AIC = 39.93)					
Intercept	0.416	0.094	14.896	4.424	0.026
PN – success	-0.495	0.124	31.924	-3.975	0.020
Change in nest altitude (N = 26, AIC = -28.78)					
Intercept	0.011	0.018	16.699	0.616	1.000
Month (L)	0.045	0.047	17.876	0.946	1.000
Distance between nests (N = 34, AIC = 263.86)					
Intercept	34.269	14.232	24.874	2.408	1.000
Nest fate - success	-13.010	7.706	16.506	-1.688	1.000
Environment type - Other	12.355	11.522	21.956	1.072	1.000
Month (L)	36.158	11.345	11.865	3.187	0.412
Female age	-1.054	2.111	24.478	-0.499	1.000
Male age	-1.083	1.944	17.253	-0.557	1.000
Change in environment type (N = 36, AIC = 53.07)					
Intercept	1.361	1586.771		0.001	1.000
Environment type - Other	2.152	1.073		2.006	1.000
Month (L)	-12.842	5017.810		-0.003	1.000
Predated versus successful PN nests					
Change in nest height (N = 47, AIC = 82.16)					
Intercept	-0.093	0.091	10.117	-1.026	1.000
Month (Q)	-0.375	0.170	42.941	-2.210	1.000
Change in nest altitude (N = 29, AIC = -8.31)					

Intercept	0.007	0.036	19.322	0.201	1.000
Nest fate - success	0.075	0.033	5.641	2.235	1.000
Environment type - Other	0.025	0.042	19.726	0.594	1.000
Month (Q)	0.103	0.018	5.643	5.749	0.077
Female age	0.006	0.004	15.342	1.541	1.000
Male age	-0.006	0.004	15.342	-1.489	1.000
Change in nest thickness (N = 24, AIC = 163.41)					
Intercept	-15.289	7.467	16.000	-2.047	1.000
Nest fate - success	11.058	6.023	16.000	1.836	1.000
Environment type - Other	1.414	5.374	16.000	0.263	1.000
Month (L)	-12.651	6.973	16.000	-1.814	1.000
Female age	1.233	1.260	16.000	0.979	1.000
Male age	2.636	1.466	16.000	1.798	1.000
Distance between nests (N = 52, AIC = 429.80)					
Intercept	51.901	10.937	31.500	4.745	0.002
Nest fate - success	-11.122	6.537	26.341	-1.701	1.000
Environment type - Other	3.781	9.823	26.472	0.385	1.000
Month (Q)	27.148	10.462	13.762	2.595	1.000
Female age	-2.845	1.384	31.741	-2.056	1.000
Male age	0.613	1.369	25.972	0.448	1.000
Change in environment type (N = 52, AIC = 65.79)					
Intercept	-0.942	0.613		-1.536	1.000
Tipped versus successful PN nests					
Change in nest height (N = 28, AIC = 30.22)					
Intercept	-0.112	0.097	10.724	-1.156	1.000
Distance between nests (N = 28, AIC = 74.96)					
Intercept	3.015	0.164	14.585	18.42	<0.001
Change in environment type (N = 30, AIC = 39.35)					
Intercept	-7.200	208.474		-0.035	1.000

Environment type -	2.269	1.054	2.152	1.000
Other				
Month (L)	12.908	559.391	0.023	1.000

Table 4 – Generalized linear mixed models for testing the relationship between changes in characteristics of the nests in renesting cases and the success of the subsequent nest attempt (analysis 3) of the *Formicivora acutirostris*. Significant p-values are shown in bold.

Abbreviations: AIC = Akaike information criterion; df = degrees of freedom; N = sample size; PN = previous nest; SE = standard error.

Variable	Estimate	SE	z-value	p-value (corrected)
PN flooded nests (N = 17, AIC = 19.16)				
Intercept	-14.946	10.457	-1.429	0.918
Change in nest height	11.704	15.062	0.777	1.000
Distance between nests	-0.187	0.1567	-1.194	1.000
Change in environment type	-21.658	3.936	-1.554	0.721
PN predated nests (N = 32, AIC = 21.48)				
Intercept	-12.001	4.175	-2.874	0.024
PN successful nests (N = 14, AIC = 21.04)				
Intercept	-10.099	4.317	-2.340	0.116

Figures

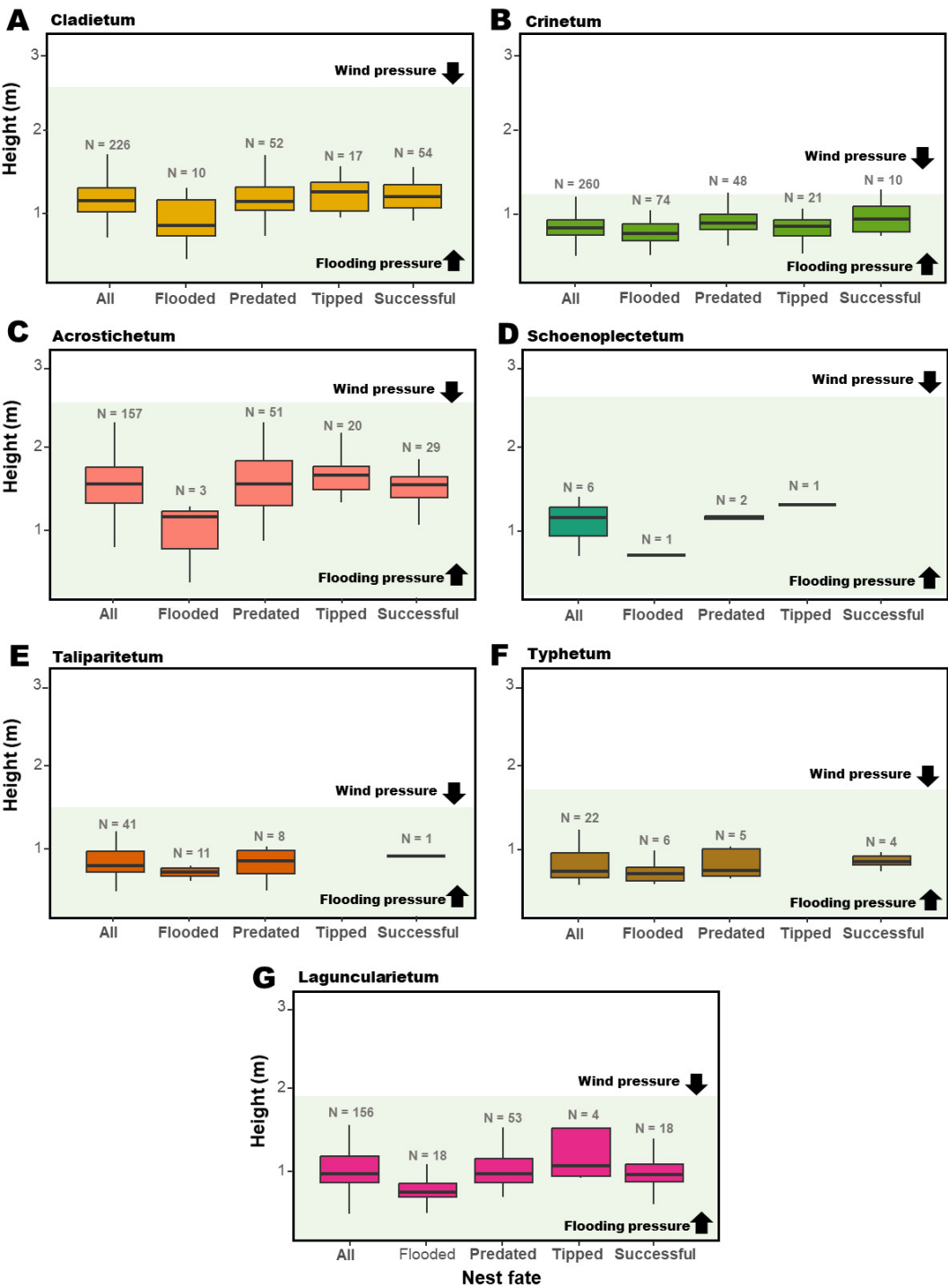


Figure 1

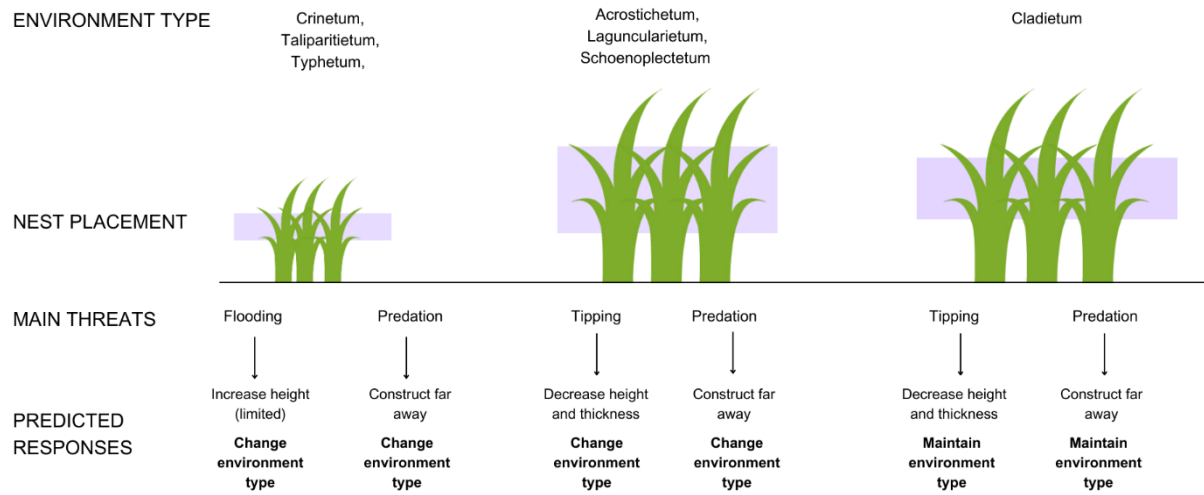


Figure 2

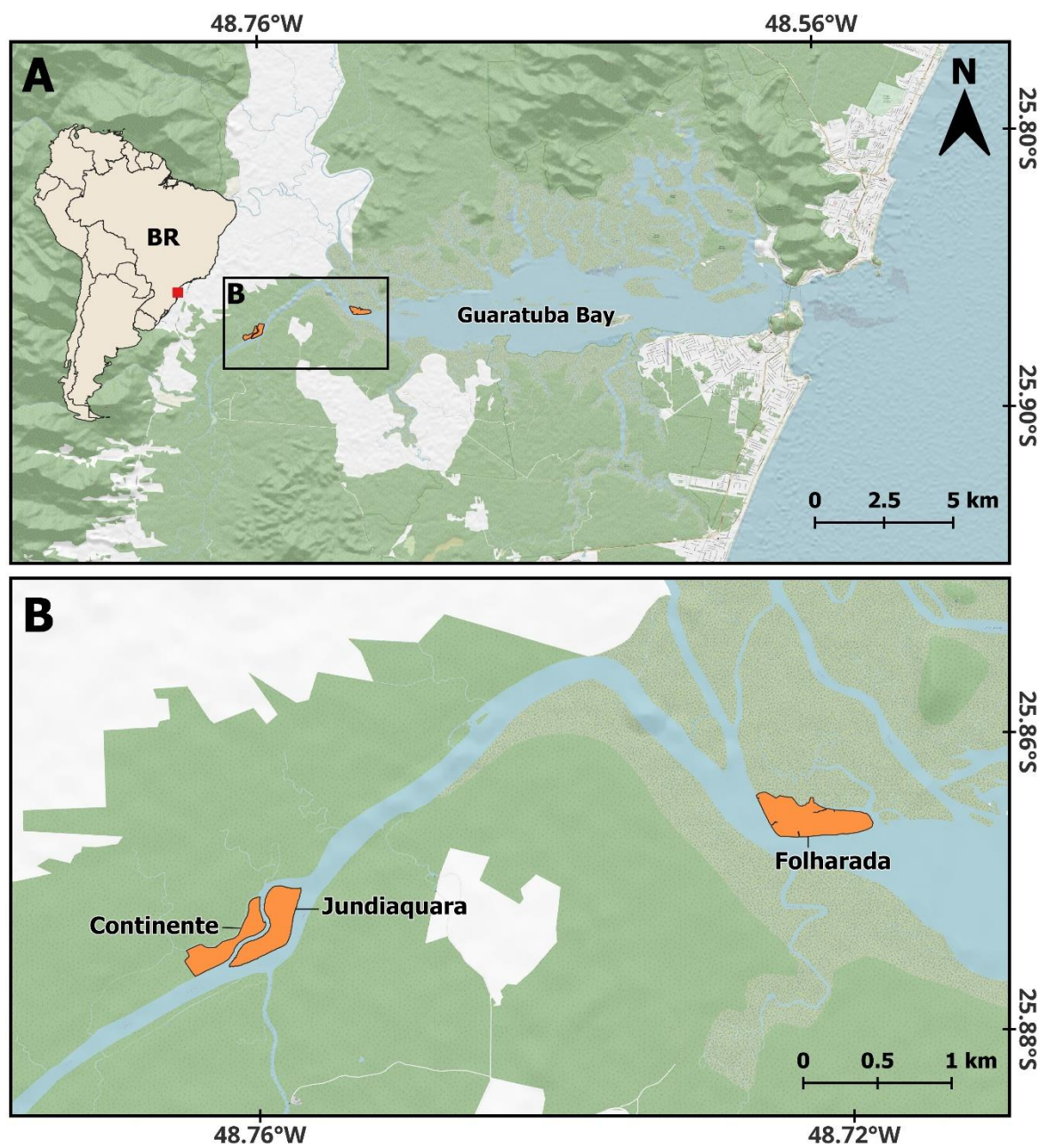


Figure 3

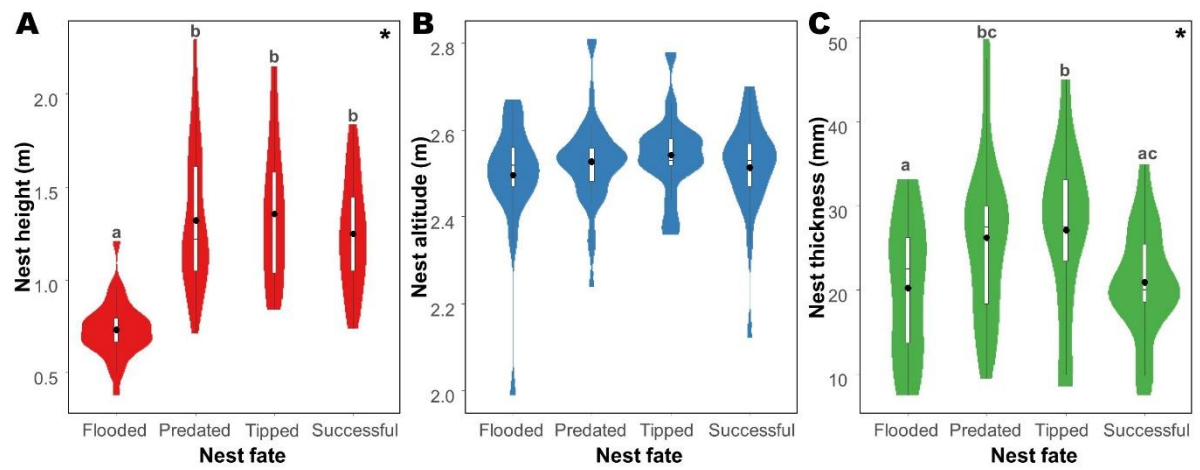


Figure 4

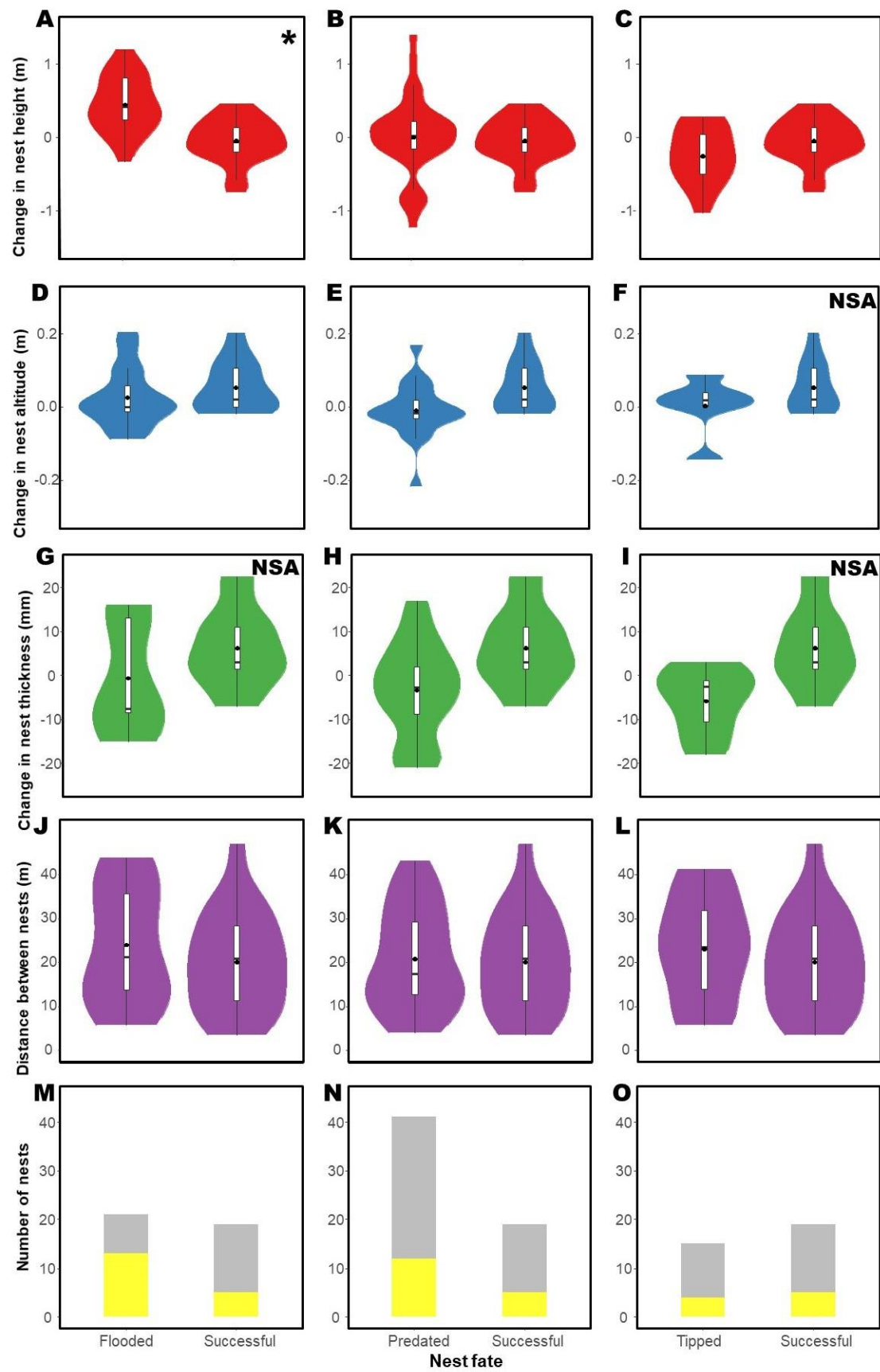


Figure 5

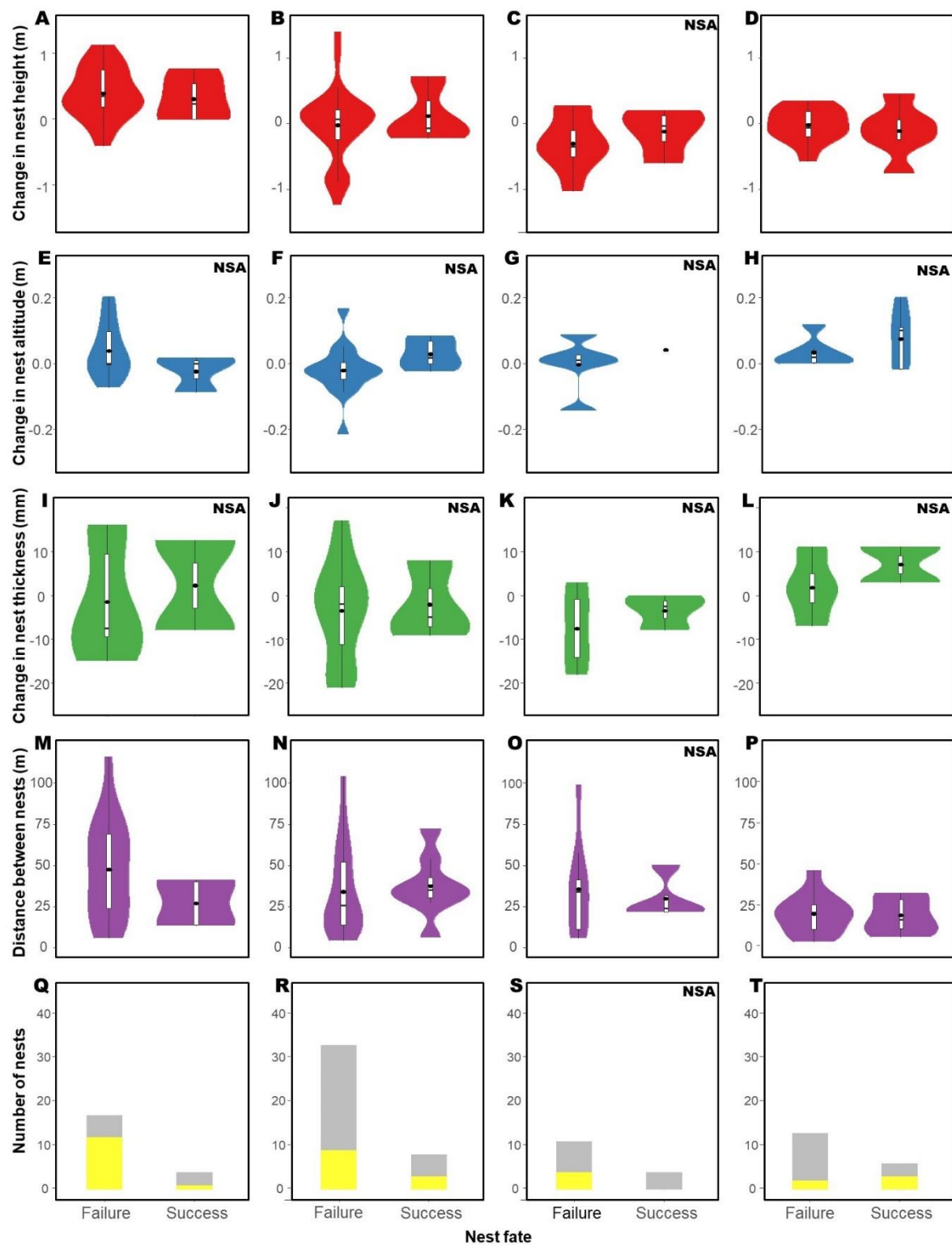


Figure 6

Figure legends

Figure 1 – Nest height and fate of *Formicivora acutirostris* in different environments in Guaratuba Bay, Paraná, southern Brazil, from 2006-2024. The light background indicates the height of the environment, based on the mean of the height of the dominant plant species. The boxplot represents the interquartile range (IQR) of nest heights, the line inside the box indicates the median, and the whiskers show the range of heights within 1.5 times the IQR from the quartiles.

Figure 2 – Predicted responses for the premise regarding the adoption of the “win-stay, lose-switch” strategy by *Formicivora acutirostris* (analysis 2), for all nest fates and environments, based on Reinert 2008 and Sandretti-Silva et al. (2024). The best response for each environment and nest fate is in bold. Designed by Freepik.

Figure 3 – Study areas for *Formicivora acutirostris* at the Guaratuba Bay, Paraná, southern Brazil. Background images: Geomorphometric Database of Brazil (TOPODATA), National Water and Sanitation Agency (ANA), OpenStreetMap contributors

Figure 4 – Attributes of *Formicivora acutirostris* nest in Guaratuba Bay, Paraná, southern Brazil for all nest fates. (A) Nest height, (B) altitude, and (C) thickness. The violin plots provide a visual representation of the data distribution (width of the violin) and the box-plot provides the following summary statistics: mean value (blackpoints), interquartile range (IQR) of data (boxplot), median (line inside the box), and the range of heights within 1.5 times the IQR from the quartiles (whiskers). Asterisks (*) indicate significance, and the lowercase letters (“a”, “b”, and “c”) show significant differences between groups.

Figure 5 – Changes in characteristics of the nests in renesting cases of *Formicivora acutirostris* in Guaratuba Bay, Paraná, southern Brazil, after failure or success of the previous nest, independent of the fate of the subsequent nest. Changes in nest height after (A) flooding *versus* success, (B) predation *versus* success, and (C) tipping *versus* success. Changes in nest altitude after (D) flooding *versus* success, (E) predation *versus* success, and (F) tipping *versus* success. Changes in nest thickness after (G) flooding *versus* success, (H) predation *versus* success, and (I) tipping *versus* success. Changes in distance between posterior nests after (J) flooding *versus* success, (K) predation *versus* success, and (L) tipping *versus* success.

Changes in nest environment selected after (M) flooding *versus* success, (N) predation *versus* success, and (O) tipping *versus* success. The cases highlighted in yellow indicate changes in the environment, while those in grey represent environmental maintenance. The violin plots provide a visual representation of the data distribution (width of the violin) and the box-plot provides the following summary statistics: mean value (blackpoints), interquartile range (IQR) of data (boxplot), median (line inside the box), and the range of heights within 1.5 times the IQR from the quartiles (whiskers). Asterisks (*) indicate significance. Abbreviation: NSA = Not statistically assessed

Figure 6 – Changes in characteristics of the nests in renesting cases of *Formicivora acutirostris* in Guaratuba Bay, Paraná, southern Brazil, after all previous nest fates, presented for success and success of the subsequent nest separately. Changes in nest height after (A) flooding, (B) predation, (C) tipping, and (D) success. Changes in nest altitude after (E) flooding, (F) predation, (G) tipping, and (H) success. Changes in nest thickness after (I) flooding, (J) predation, (K) tipping, and (L) success. Changes in distance between nests after (M) flooding, (N) predation, (O) tipping, and (P) success. Changes in nest environment after (Q) flooding, (R) predation, (S) tipping, and (T) success. The cases highlighted in yellow indicate changes in the environment, while those in grey represent environmental type maintenance. The violin plots provide a visual representation of the data distribution (width of the violin) and the box-plot provides the following summary statistics: mean value (blackpoints), interquartile range (IQR) of data (boxplot), median (line inside the box), and the range of heights within 1.5 times the IQR from the quartiles (whiskers). Asterisks (*) indicate significance. NSA = Not statistically assessed

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CAPÍTULO 2

Effects of environmental heterogeneity on the population dynamics of a threatened bird
endemic to subtropical salt marshes

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Research Article – submitted to “Ecology and Evolution”

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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[†] *In memoriam*

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Abstract

Understanding how environmental factors affect population dynamics is crucial for conservation. In this study, we examine the importance of habitat and climate factors on juvenile productivity, adult mortality, and demographic performance (DP) of *Formicivora acutirostris* in a floristic gradient (upstream and downstream) in the Guaratuba Bay estuary, Brazil. We monitored 14–41 territories annually during 18 years, which totaled 214 adult territorial individuals and 297 independent juveniles. Data imputation, generalized linear mixed models, and random forest models were used in the analysis. The average annual juvenile productivity per territory was 0.64 upstream and 0.56 downstream. Juvenile productivity upstream was positively associated with the number of neighbors, *Cladietum* area, and vegetation density in *Crinetum*, and showed a quadratic relationship with *Acrostichetum* density. Downstream, productivity increased with precipitation and rainy days but decreased with maximum temperature; and was higher in areas with forks in *Acrostichetum*. Adult mortality averaged 0.32 upstream and 0.25 downstream. Upstream, mortality decreased with maximal tidal height, increased with the number of rainy days, and showed a quadratic relationship with vegetation density in *Crinetum*. The overall DP upstream was 0, and downstream was 1.5. DP was positively influenced by *Cladietum* area upstream and by the presence of forks in *Acrostichetum* downstream. The study highlights *Cladietum*'s critical role in productivity, offering safe nesting sites. *Acrostichetum*, beneficial when forks are present, also provides predator refuge, impacting productivity. *Crinetum* contributes minimally due to predation and flooding. Climatic and tidal factors further

influence vulnerability. We discuss population dynamics and the importance of conservation prioritization.

Keywords: *Formicivora acutirostris*, micro-climate, mortality, productivity, source-sink dynamics

STATEMENTS & DECLARATIONS

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Author contributions: MRB conceived the idea. GS-S, BLR and MRB collected the data. GS-S, MRP and MRB analyzed and interpreted the data. GS-S and MRB led the writing of the manuscript. All authors, except BLR, contributed critically to the drafts and gave final approval for publication.

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1. Introduction

Population dynamics is an essential topic in ecology and depends intrinsically on the birth (or productivity) and mortality rates (Gotelli 2009; Ricklefs 2010). The importance and the ways in which these rates contribute to the regulation of population dynamics vary according to the species' life history (Pulliam and Danielson 1991; Saether et al. 1996; Saether et al. 2004). Together with individual characteristics, extrinsic spatial and temporal factors, such as habitat and climate factors can influence birds' reproduction and death (Pulliam and Danielson 1991; Pulliam et al. 1992; Franklin et al. 2000; Saether et al. 2004; Low et al. 2009). Identifying these factors and understanding patterns of environmental variation are crucial for determine and guide priority conservation actions (Cowley and Siriwardena 2005).

The habitat can interfere in population dynamics, although most studies to date only focused on its influence on productivity, ignoring mortality (Low et al. 2009). The structure, composition, and availability of habitat can affect reproduction and mortality rates of the birds through factors such as food availability, quantity and safety of breeding sites, and predator abundance (Franklin et al. 2000; Calf et al. 2003; Low et al. 2009; Narango et al. 2018; Hart et al. 2021). Additionally, the high energy cost of maintaining one of the rates in certain unfavorable habitats can negatively influence the other one (Martin 1995).

The timing and magnitude of climatic conditions influence the patterns of bird response to them (Saether et al. 2004). Precipitation may indirectly influence bird reproduction and mortality rates by affecting their access to resources through regulation of food availability and foraging opportunities, consequently impacting their health and parental care (Cowley and Siriwardena 2005; Skagen and Adams 2012; Oberg et al. 2015; Aranzamendi et al. 2019). Similarly, temperature impacts birds by regulating foraging conditions and their capacity to maintain body temperature (Skagen and Adams 2012). Under extreme conditions, precipitation and temperature can also directly affect the survival of adults and offspring (Skagen and Adams 2012; Conrey et al. 2016; Bourne et al. 2020).

For territorial birds, the territory is the spatial unit that encompasses a significant portion of the extrinsic characteristics that may influence demographic performance (Goodburn 1991; Brambilla and Bionda 2013; Zabala and Zuberogitia 2014; Sergio 2009; Reynolds et al. 2019). These variations are most notable when studied in highly distinct territories from each other (Zabala and Zuberogitia 2014). It is possible to verify the source-sink dynamics, a model widely applied to populations, at a fine scale, allowing the characterization of demographic dynamic patterns in territories (Breininger and Oddy 2004; Nystrand et al.

2010). In a source territory, the production of juveniles exceeds the mortality of territorial individuals in the absence of migration, whereas in a sink, the mortality of territorial individuals exceeds the production of juveniles (Breininger and Carter 2003; Nystrand et al. 2010).

Similar to tropical bird species (Oniki 1979; Winkler 2016), predation is high for birds in subtropical and temperate salt marshes (Greenberg et al. 2006). However, these environments also experience periodic flooding, which can affect the birth rate of birds through the drowning of nestlings, egg unviability, and dispersal of eggs (Reinert 2006, 2008; Greenberg et al. 2006; Reinert et al. 2012), as well as reducing foraging conditions (Reinert 2008), thus impacting both birth and mortality rates. Therefore, the tidal height, as well as the elevation of the territory over the sea level, could be important demographic-related factors, in conjunction with habitat structure, in salt marshes.

To assess the importance of different extrinsic factors in juvenile productivity, adult mortality, and demographic performance of marsh-dwelling birds, we studied the Parana Antwren (*Formicivora acutirostris*) as a model. This is a small (9–10 g) territorial bird endemic to the Brazilian salt marshes (Bornschein et al. 1995; Bornschein et al. 2024). It serves as a model for these studies due to long-term population monitoring conducted by the Parana Antwren Project (*Projeto Bicudinho-do-brejo*; 2006 onwards), which provides longitudinal data that reduces the risk of bias caused by temporary conditions (Nystrand et al. 2010). We predict that environmental heterogeneity, including both climate and habitat factors, plays a crucial role in the population dynamics of this species. Specifically, we hypothesized that a better perimeter-to-area ratio of territory, large areas of important vegetation types for species nesting, and moderate climate conditions are key variables for increasing productivity and decreasing mortality. A better perimeter-to-area ratio of territory reduces the energy expenditure involved in interspecific territory defense and increases foraging opportunities and resource availability. Larger areas of important vegetation types for *F. acutirostris* provide more nesting sites, can reduce the effects of wind and waves, and can reduce the likelihood of nests being encountered by predators. Intense rainfall conditions can decrease foraging opportunities, alter vegetation structure (e.g., reducing the height of the plants), interrupt nest construction, destroy nests, and directly affect individuals, while low rainfall conditions can reduce the availability of insects for feeding. Intense rainfall also can contribute to incorporating more water in the system, increasing high tides and nest flooding rates. Finally, high temperatures could increase juvenile and adult mortality due to heat.

2. Methods

2.1 Target species

Formicivora acutirostris is a recently described bird (Bornschein et al. 1995). The species presents long-term monogamy, with pairs occupying fixed territories ranging from 0.25 to 3.23 ha, depending on location and habitat type (Reinert et al. 2007; Bornschein et al. 2015; Sandretti-Silva et al. 2024). Both males and females participate in territory defense throughout the year and in all reproductive activities, except incubation at night, exclusively done by females (Reinert et al. 2012). During the breeding season, from August to February, the species attaches its nests to herbaceous and arboreal vegetation and lays two eggs per clutch (Reinert et al. 2012). Nests, which can be lost primarily due to predation, flooding, and tipping (Reinert 2008), are typically replaced through multiple successive attempts (Reinert 2008). As a result, up to four independent juveniles can be produced in a season (Sandretti-Silva et al. 2024). The species has a long life-span, with females living up to 15 years (Sandretti-Silva et al. 2024) and males up to 16.8 years (a male that is still alive in August 2024; MRB, personal observation). However, the average age of monitored individuals is 3.72 to 6.91 years (Sandretti-Silva et al. 2024).

Formicivora acutirostris occupies marshes in Southern Brazil, covering an estimated 41 km², which could support 6,285 territorial individuals (Bornschein et al. 2024). However, due to threats that affects its population dynamics, such as high nest predation, low juvenile success, and declines in habitat quality and availability, the current population is estimated at only 918 territorial mature individuals, with drastic projected declines and short-term predicted extinction (Sandretti-Silva et al. 2024). In Brazil, it is considered threatened with extinction under the Vulnerable category (VU; Portaria MMA No. 148, June 7, 2022), and globally, it is classified as Near Threatened (NT; BirdLife International 2019), but proposed as Endangered (EN; Sandretti-Silva et al. [2024]).

2.2 Study areas

We worked in three areas in the Guaratuba Bay, Ramsar Site Guaratuba, municipality of Guaratuba, situated on the southern coast of Paraná State, southern Brazil: on Jundiaquara Island (c. 25°52'25"S, 48°45'32"W; 11.50 ha) and at the Confluence of Claro and São João Rivers (hereinafter referred to as "Continente"; c. 25°52'28"S, 48°45'44"W; 8.73 ha), located upstream in the Guaratuba Bay estuary (hereinafter referred to "upstream"), and on part of the Folharada Island (c. 25°51'58"S, 48°43'23"W; 16.30 ha), located downstream in the estuary

(hereinafter referred to “downstream”; Figure 1). These study sites are flooded daily by mixed semi-diurnal tides (Lee and Chang 2019).

The vegetation is classified as Pioneer Formation with Fluviomarine Influence (according to criteria of Veloso et al. [1991] and IBGE [1992]). The herbaceous vegetation of the area was referred as tidal marshes (*brejo de maré*; Reinert et al. [2007]), and, later, classified as a specific type of salt marsh, known as subtropical salt marshes (Bornschein et al. 2017). Alongside this herbaceous marsh vegetation, there are patches of arboreal vegetation, with *Calophyllum brasiliense* dominating upstream (“tree formation dominated by *C. brasiliense* with herbaceous plants” or *guanandizal com herbáceas*, according to Reinert et al. [2007] and Bornschein et al. [2024]) and *Laguncularia racemosa* dominating downstream (“tree formation dominated by *L. racemosa* with herbaceous plants” or *manguezal com herbáceas*, according to Reinert et al. [2007] and Bornschein et al. [2024]). The subtropical salt marshes upstream have 1–8 species recorded per square meter, totaling 12 plant species in 50 m² of an evaluation (Reinert et al. 2007; Bornschein 2013), and the subtropical salt marshes downstream have a low floristic richness, with 1–4 plant species recorded per square meter, totaling five species in 50 m² of an evaluation (Reinert et al. 2007; Bornschein 2013). According to the Köppen classification (Alvares et al. 2014), the region falls under the Humid Subtropical Zone with oceanic climate, no dry season, and hot summer (Cfa).

2.3 Field surveys and sampling design

From January 2006 to May 2008, we conducted fieldwork every day from September to February and for 10 days per month from March to August. After this period, we conducted fieldwork for 3–8 days every month. We worked on Jundiaquara Island from 2006 to 2024, at Continente from 2009 to 2024, and on Folharada Island from 2009 to 2024. We worked in teams of two to five ornithologists, from dawn until 1 p.m. and again from 4 p.m. until dusk.

In the field, we studied the population of *F. acutirostris*, focusing in the reproduction from nest construction to juvenile independence, composition of territorial pairs, survival of individuals, territory characteristics, and some habitat features (see below). We were unable to accurately monitor reproduction until juvenile independence (see below) at Continente in 2011 and 2017 and on Folharada Island in 2017. To maintain consistency in our sample, these years were excluded from analyses for these two areas. Annually, we studied 14 to 41 territories (see Online Resource 1).

We excluded all samples from territories that existed for less than three years. For non-permanent territories that existed for at least three years, but not in all 19 years of monitoring,

we started to consider the data from the third year onward (Online Resource 1). This is justified by the biases during the establishment of these territories, including intense disputes, frequent turnover of the occupants, occasional abandonment of females, with loss of territorial defense by the remaining male, and variable territory areas (MRB, personal observation). This fluctuating conditions in the firsts years of newly established territories make challenging to accurately assess the factors affecting the dynamics during them.

To monitor the pairs and collect data, all territorial individuals were periodically ringed. We used 12-meter-wide mist nets with a 28-mm mesh and attracted the birds by playing playback of different songs. The birds were ringed with a metal band and a unique combination of colored plastic bands. Each bird was assigned with an individual code number used to refer to it (hereafter referred to as “male ID number” or “female ID number”). We were unable to ring one or both members of a pair during part or all of one breeding season (23 individuals of 16 territories involved, totaling 22 annual territory samples) primarily to avoid disrupting ongoing reproductive activities, so we excluded these samples from all analyses until specimens became ringed again, as individual identity was a predictor in our study.

During banding, we estimated the minimum age for individuals with unknown birth dates based on their plumage pattern, assigning the birth date as occurring in 1st October (time with many early breeding season births) or 1st February (time with last births in the season), to reduce data variability, according to Bornschein et al. (2015). For unbanded juveniles during the capture of both sexes, we attributed the birth date that provide the youngest age considering that female juveniles acquire adult plumage at six months of age and male juveniles acquire adult plumage at nine months of age (Reinert 2008; Bornschein et al. 2015). For adult unbanded individuals, we also assigned the earliest date of birth (one of the two options cited above) considering the months needed to acquire adult plumage.

Annually, we assessed the identity (ID number) and age of all territorial individuals within our study areas. We considered an individual to be the territory owner if it occupied the territory for at least six months. In eight cases, there were multiple pair changes during the breeding season, and no pair occupied it for at least six months, so we also excluded them from our analyses (Online Resource 1).

2.4 Variables

2.4.1 Juvenile productivity

The annual juvenile productivity of a territory was considered as the number of independent juveniles produced there during a breeding season (*sensu* Streby et al. 2014). The independence occurs between the seventh and ninth week of life (Reinert 2008). A juvenile seen at least until the sixth week of life was considered as produced. We summed all the annual juvenile productivity to obtain the total for each territory. The contribution of the 30% and 50% most productive territories to juvenile productivity was assessed to evaluate the disproportional population contribution among territories (Brambilla and Bionda 2013).

2.4.2 Adult mortality

The annual adult mortality of a territory was considered as the number of territorial owners that disappeared in the year cycle counted from April and March (individuals changes of territory were not considered). We routinely surveyed surrounding areas (up to 1 km from the borders of monitored areas) from 2007 to 2011, as well as during specific campaigns in 2012, 2014, and 2022, using playback calls and visual sightings, to search for missing monitored individuals (Sandretti-Silva et al. 2024). We summed all the adult missing to obtain the total mortality for each territory.

2.4.3 Demographic performance

The annual demographic performance (DP; *sensu* Breininger and Oddy [2004]) of a territory was assessed as the number yearlings (see below) produced minus the annual number of dead individuals in that year cycle (see above), allowing us to determine whether the territory produced enough offspring to compensate for the losses during the period. The yearlings were chosen over fledglings or independent juveniles due to the recognized high mortality during the first year (Sandretti-Silva et al. 2024). The number of yearlings produced was estimated as half of the independent juvenile productivity (see above), as an approximation of 45.6%, the survival rate during the first year, as reported by Sandretti-Silva et al. (2024). We summed all the demographic performances of each territory to classify it as a sink ($DP < 0$), source ($DP > 0$), or stable ($DP = 0$) territory. Based on these total DP, we created a map of territory dynamic (DP) of our study areas using QGIS 3.28.0.

2.4.4 Habitat features

The area (m²), perimeter (m), perimeter-to-area ratio, and number of neighboring territories for each territory were assessed annually from each year cycle (April to March) since 2006 using Google Earth Pro 7.3.4. Territories were considered neighbors if their

boundaries were 1–12 meters apart. Territory delineation during fieldwork followed the methodology of Bornschein (2013).

In 2014, we collected altitude data for all our study areas. Data from 4,000 altitude points (20 x 20 m grid in flat areas and 5 x 5 m grid on slopes) were obtained with millimeter precision using the Real Time Kinematic (RTK) technique and transferred to Google Earth Pro. Using this altitude mapping, we evaluated the median altitude of each territory, as delimited annually, by considering all altitude points collected within the territory boundaries.

We assessed the area (m²) and proportion of vegetation types dominated by *Crinum americanum*, *Acrostichum danaeifolium*, *Cladium jamaicense*, and *Laguncularia racemosa*. These habitats were classified, according to Braun-Blanquet (1979), as Crinetum, Acrostichetum, Cladietum, and Laguncularietum, respectively. This assessment was made, after previous mapping in the field, on satellite images from Google Earth Pro. After this, we made field verifications of the mapping and returned to Google Earth for rectifications.

Some vegetation features were characterized qualitatively, always *in loco* assessing all patches of the habitats, based on their expected influence on species dynamics (Table 1). We examined vegetation density (VD) in Crinetum upstream, noting a temporary increase in density and height with an increased presence of *Panicum mertensii* following a landslide in the mountains near the estuary in 2008, which was accompanied by a change in nest allocation (MRB, personal observation). We observed that the vegetation density in Crinetum became moderately increased from mid-2009 until later 2010, and highly increased from early 2011 to later 2014. Following this density peak, it began to decrease, returning to moderately increased from early 2015 to later 2017 to, finally, return to normal density after 2018, as Crinetum was originally, in 2006 to early 2009. During these periods of moderately and highly increased density of Crinetum, the gain in vegetation height was constant. Additionally, we characterized qualitatively the vegetation in Cladietum and Acrostichetum, based on density. We evaluated the presence of forks made of shrubs, vines, and small trees. These features were considered relevant because some nests were built in such structures and reached success. Finally, we characterized qualitatively the presence of trees shading Acrostichetum and Cladietum upstream, for the effect of reducing the density of herbaceous vegetation. We used simplified classes that indicated only whether trees covering herbaceous vegetation were present or absent and complete classes that indicate the extent of their presence in each environment (Table 1).

2.4.5 Climate factors

Mean, maximum, and minimum average temperature per month (°C), accumulated precipitation (mm), number of heavy or violent rain events (precipitation ≥ 10 mm/h, according to World Meteorological Organization [2008]), and number of rainy days (precipitation > 0 mm in 24 h) were obtained for each annual cycle, from March to April, since 2006. The number of heavy or violent rain events was only obtained until 2018 due to data sharing guidelines that reduced the resolution available. The climatic data were sourced from the meteorological station of the Paraná Environmental Technology and Monitoring System (SIMEPAR; ticket numbers #12068, #24833, #28597, and #29622). This climate station is located in Guaratuba municipality, 44 km away from the nearest study site.

We identified periods without climatic variables measurements from SIMEPAR for 2008 (15 consecutively days) and 2012 (25 consecutively days). To complete the data and avoid data gaps, precipitation and temperature were also obtained from the historical monthly weather raster database of WorldClim with 2.5 minutes of resolution to assist an imputation. We verified the correlation between the databases and identified only two outliers per variable (2006 and 2019 for precipitation; 2013 and 2014 for maximum average temperature; 2007 and 2019 for minimum average temperature). After excluding these outliers from the WorldClim data, all the correlation coefficients were high ($r > 0.7$). We then used the *impute* function from the *funspace* 0.2.1 package (Carmona et al. 2024) in R (version 4.3.3; R Core Team 2024) and completed the data from SIMEPAR.

2.4.6 Tidal heights

Maximum tidal heights (m) were obtained from each annual cycle (March to April), from 2006 to 2021. The information was obtained from the Brazilian Navy Hydrographic Center. The station is located at the Ponta do Félix harbor (25°27'18"S, 48°40'42"W), in Antonina Bay, Paraná. We performed data imputation for the maximum tidal heights of 2022 to 2024 by combining this data with the imputation of climatic data, as described above.

2.5 Statistical analyses

2.5.1 Variable filtering

Due to the large number of predictor variables, we performed a filtering of the variables before constructing our models (see below) to avoid including those highly correlated. The variables from upstream and downstream areas were treated separately. We calculated and plotted (Online Resource 2) correlation matrices using the standard *cor* function and the *corrplot* function from the *corrplot* 0.92 package (Wei and Simko 2024) in R. The variance

inflation was assessed using the *vif* function from the *car* 3.1-2 package (Fox et al. 2023), and those with the highest total correlation coefficients were removed until there were no more issues with inflation.

2.5.2 Models

We constructed models for the upstream and downstream areas separately. A complete generalized linear mixed model (GLMM) was built for each response variable (juvenile productivity, adult mortality, and DP) with some functions of the *lme4* 1.1-35.1 package (Bates et al. 2024). We included the name of the territory and the year as structural random effect variables, as they configure the model as longitudinal, i.e., accounting for the repeated measures across years for the same territories. As structural variables, they remained in all models and were not removed (see below) to avoid compromising the inherent characteristics of the data. Additionally, we included female and ID number and age as other (non-structural) random effect variables.

The fixed effect variables considered in each of the full models can be found in Table 2, and include territory, habitat, climate, and tidal. All qualitative variables were considered as factors, ordered or non-ordered (Table 1). All the quantitative variables were log-transformed ($\log[x+1]$) and scaled to stabilize variance. To optimize the models and address convergence issues, we used the bobyqa optimizer with a maximum of 100,000 function evaluations. We tested multiple distributions and compared the best fit based on AIC, considering models within two units of difference as equally adjusted (Bolker 2008). The families and functions of each model can also be found in Table 2.

After identifying the best complete model, we proceeded with variable selection. We evaluated the importance of both fixed and random effect variables using the *MERF* function from the *LongituRF* 0.9 package (Capitaine 2020). It was configured with the Ornstein-Uhlenbeck as the stochastic process, five predictor variables considered at each split, 1000 trees, a stopping criterion of 0.001, and a maximum of 100 iterations. For random effect variables, importance was determined by summing their estimates (Online Resource 3). For fixed effect variables, we assessed it based on the percent increase in mean squared error (%IncMSE; Tables S3 and S4). The least important random effect variables (Online Resource 3) were sequentially removed until obtain their best combination based on AIC, but the structural variables (see above) were always maintained. Subsequently, we removed the least important fixed effect variables with the same approach. Model results (intercept, SE, z-value, and p-value) were then obtained using the standard summary function for non-categorical and

ordered variables, and using the *Anova* function from the *car* package for non-ordered categorical variables. We also obtained the results of each variable of the model using the *effect* function of the *effects* 4.2-2 package (Fox et al. 2022) and plotted them using the *ggplot* function from the *ggplot2* 3.5.0 package (Wickham et al. 2024), using the variables in their original scale. For significative categorical variables, we performed post hoc comparisons between groups, using the *glht* function of the *multcomp* 1.4-26 package (Hothorn et al. 2024) with the Tukey method.

3. Results

We monitored 297 juveniles reaching independence, with 230 of them upstream (172 on Jundiaquara Island and 58 at Continente) and 67 downstream (Online Resource 1). The average annual juvenile productivity per territory was 0.64 upstream and 0.56 downstream. The most productive 30% of territories accounted for 69.6% of the juvenile productivity upstream and 61.2% downstream; the most productive 50% of the territories accounted for 89.7% and 94.0% of the juvenile productivity upstream and downstream, respectively (Online Resource 1; Figure 2). Juvenile productivity varied significantly between years, peaking in 2019 when more than 60% of the territories produced at least one juvenile, and reaching a minimum in 2008, when no juvenile was produced, and in 2020, when only one juvenile was produced (Online Resource 1).

We monitored 214 adult territorial individuals, of which 146 died in the accounted years (other individuals died in excluded years; Online Resource 1). The average annual adult mortality in the territories was 0.32 individuals upstream (0.27 for Jundiaquara Island and 0.42 for Continente) and 0.25 downstream. Adult mortality varied significantly between territories (Figure 2). In two cases, more than two individuals of a territory died during an annual cycle.

The DP varied significantly among the territories. Upstream, the overall DP was 0 (23 for Jundiaquara Island and -24 for Continente), while downstream, the overall DP was 1.5, resulting in a total performance of 1.5 for our study areas (Online Resource 1). The resulting dynamic pattern was 13 source territories (9 upstream and 4 downstream), 4 stable territories (all upstream), and 23 sinks territories (16 upstream and 7 downstream; Figure 2). Among the territories with considerable area of *Cladietum* ($> 25 \text{ m}^2$), 75% was classified as source territories (Figure 2).

3.1 Juvenile productivity

Juvenile productivity was influenced by several environmental factors. Upstream, productivity increased by the following variables: 1) number of neighbors, 2) area of Cladietum, and 3) vegetation density in Crinetum (Table 3). Juvenile productivity upstream also showed a quadratic relationship with Acrostichetum density, being 4) higher in those territory with moderate density of this type of habitat (Table 3). Downstream, productivity increased with 1) accumulated precipitation and 2) number of rainy days, but decreased with 3) average maximum temperature (Table 4). Additionally, productivity downstream was higher when forks were present in Acrostichetum compared to when forks were present in Crinetum ($p = 0.022$; Table 4). None of the individual factors influenced juvenile productivity in the areas because they were all excluded during the model selection process.

3.2 Adult mortality

Adult mortality was also influenced by several environmental factors, but only upstream. In this area, adult mortality decreased with maximal tidal height but increased with the number of rainy days. Upstream, mortality also showed a quadratic relationship with vegetation density in Crinetum, being lower in moderately increased conditions (Table 5). No environmental factors influenced adult mortality downstream (Table 6).

3.3 Demographic performance

The annual DP was influenced by environmental factors in both areas. Upstream, annual DP increased with the increase in area of Cladietum (Table 7). Downstream, annual DP increased when forks were present in Acrostichetum, compared to when forks were present only in Crinetum ($p = 0.007$; Table 8).

4. Discussion

In this study, we explored the effects of environmental factors on the population dynamics of *F. acutirostris*. Using extensive sample series of the species from three areas in Guaratuba Bay and equally long term 1:1 environment evaluation, we identified notable spatial variations in juvenile productivity and adult mortality, as well as a source-sink pattern at a territorial scale. Consistent with our general hypothesis and to previous studies (e.g., Franklin et al. 2000; Breininger and Carter 2003; Breininger and Oddy 2004; Förschler et al. 2005; Nystrand et al. 2010; Brambilla and Ficetola 2012; Brambilla and Bionda 2013; Zuckerberg et al. 2018; Rosamond et al. 2020; McCloy and Grace 2023; Whitenack et al. 2023), the results indicate that several environmental factors influence population dynamics,

with habitat characteristics and climatic conditions playing the most significant role in determining productivity and mortality rates. Contrary to our previous expectation and to results from other studies (e.g., Brambilla and Ficetola 2012), territory area or perimeter characteristics did not affect species dynamics, indicating that the composition of vegetation in the territory is more important than its size or shape. Additionally, factors not initially hypothesized by us as significant, such as the number of neighbors, vegetation density, and presence of forks, were confirmed as playing also crucial role for the species.

Habitat characteristics within the territories were very important for all demographic rates, as observed in some other studies (Franklin et al. 2000; Breininger and Oddy 2004; Folschler et al. 2005; Nystrand et al. 2009; Brambilla and Ficetola 2012). Cladietum is a very favorable nesting environment due to its height and density, that avoids nest flooding and limits the locomotion of the Blackish Rail *Pardirallus nigricans* (Bornschein et al. 2022). This medium-sized species, the most abundant resident bird in the study areas (Guerra 2023), prefers the lower, less dense layer of the vegetation (Bornschein et al. 2022), where it moves quickly and silently. So, high amounts of Cladietum provide better-quality breeding sites, facilitating the production and survival of juveniles, improving the demographic performance.

It is important to note that Cladietum at the upper limit of the flood plain, in the border of forests (Angulo 1992), situation in which it was called as *zonas de Cladium* or *brejos de capim-serra* (Angulo 1990, 1992; Angulo and Müller 1990; Reinert et al. 2007), have the lowest density for *F. acutirostris* (Bornschein et al. 2024). The Cladietum of this location are flooded only during spring tides and storms (Angulo 1990; 1992). This characteristic of occasional and ephemeral flooding might be the key explanation for the low density of *F. acutirostris*. Water may play an important and essential role for the species, as evidenced in the Lagoa do Parado in 2013, where the species began building nests only when the rains filled the river, forming a constant layer of water. This start of reproduction occurred over a month later than in the study areas during the same period (MRB, personal observation).

Vegetation density in Crinetum was also an important factor for upstream productivity and mortality. In a linear relationship with juvenile productivity, high vegetation density (and height; see Methods) in this environment provides 1) a greater abundance of invertebrates (Favretto et al. 2022) for juvenile nutrition, 2) higher nesting sites that protect against tidal flooding, 3) more concealed nesting sites that protect against predators, and 4) a limitation on the movement of predators in the nesting vegetation layer, such as *P. nigricans* (see above and Bornschein et al. [2022]). However, the quadratic relationship with mortality requires an intricate and particular explanation. Higher densities of Crinetum may provide worse

nighttime sleeping locations, probably due to the movement of the long and vertical stolons of *P. mertensii*, perhaps forcing *F. acutirostris* to sleep for example in *Acrostichetum*, which is also the preferred resting site of *P. nigricans* (GS-S and MRB, personal observation), leaving the bird exposed to predation. This dichotomy between the effects of habitat characteristics on productivity and mortality has been recorded for other species (Franklin et al. 2000; Mumme et al. 2001). The density of *Acrostichetum* was also important for juvenile production upstream in a quadratic relationship. *Formicivora acutirostris* avoid nest in low density *Acrostichetum* due to the low density of the vegetation, making the nests quite exposed, while moderate density provides good nesting sites. However, high density *Acrostichetum* also serves as a nesting site for native rat species and *P. nigricans*, with the former potentially preying on the nests of *F. acutirostris* and, the latter, effectively preying on them (GS-S and MRB, personal observation).

The presence of forks was significant for juvenile productivity and population dynamics downstream. In this area, forks in *Crinetum*, made by *Talipariti pernambucense*, might be less effective due to low vegetation height, which allows predators to access nests more easily and also permits nest flooding by high tides, potentially creating an ecological trap for territories with this type of feature. Conversely, in this area, forks in *Acrostichetum*, also made by *T. pernambucense*, offer better nest protection from predators due to the challenge of accessing fragile distal branches. In addition, the layer with appropriate density for nests construction in *Acrostichetum* is normally above high tide levels, unlike what often occurs with forks in *Crinetum* (Reinert 2008).

Surprisingly, the number of neighboring territories positively contributed to juvenile production upstream. *Formicivora acutirostris* emits an alarm call when nest or juveniles are in danger that quickly attract the territorial partner, a behavior that we frequently observe/heard (see more details in Reinert [2008]). Sometimes, brood defense escalates to physical attacks against the predator (see <https://youtu.be/watch?v=gSDrEGbo9Rk>). The existence of this alarm call may represent a strategic advantage for nesting close to neighboring territories, as some individuals may approach and help in the attack on the predator or the alarm of an individual. Also, pairs may alert neighbors about the approaching of a predator. If confirmed, the first behavior could be interpreted as altruistic and the second as a form of cooperative strategy, well-developed traits for a suboscine bird and with no reports for thamnophilids. This effect was not observed downstream, likely due to the larger size of the territories in that region (Bornschein et al. 2024; Sandretti-Silva et al. 2024) and the existence of unoccupied environmental edges often separating nearby territories.

Climate factors had a significant impact on productivity and mortality rates but did not affect overall population performance. Upstream, we found that increased number of rainy days correlated with higher mortality. This is likely due to reduced foraging during rain and increased energy demands (Oberg et al. 2015), as well as the indirect effect in interspecific relationships (Stenseth et al. 2002; Rosamond et al. 2020). In this area, the dominant tree is *C. brasiliense*, which provides little to no protection against rain, so the rain could directly affect the individuals. The most suitable environment for serving as refuge during the rain is *Acrostichetum*, where *P. nigricans* also shelters (see above; MRB, personal observation), so the rain could indirectly affect the individuals by leaving them more vulnerable to predation. Downstream, the results were very different. In this area, we found that accumulated precipitation and an increased number of rainy days correlated with increased productivity. This could be explained by the fact that, downstream in the *Laguncularietum*, where *P. nigricans* density is low, the trees are like low shrubs, offering better protection from rain. This characteristic likely reduces the direct and indirect effects of rain on the reproductive fitness of *F. acutirostris*. Additionally, in *Laguncularietum*, *Rattus rattus* is an important nest predator (see above). Rats depends on chemical cues (Johnston 2003), which could be washed by the rain, reducing predation pressure over nests.

We found that high temperatures negatively affected juvenile production downstream. Effects of climatic factors on birds are complex and depend on variables such as microhabitat refugia (McCloy and Grace 2023), which is likely the case for *F. acutirostris*. Downstream, a large part of the nests (approximately 50%; MRB and GS-S, personal observation) are built at the edge of mangrove, potentially leading to greater solar exposure and unfavorable microclimate conditions for nestling production. In an ongoing study, we verified microclimate reaching higher temperatures in a study area (Jundiaquara Island) than reported for the same period in the closest meteorological station of SIMEPAR (see Methods). During autumn, microclimate temperatures was 1.25 degree hotter than that recorded by the meteorological station, with differences reaching up to 3.70 degrees (MRB, personal observation). Microclimate challenges for *F. acutirostris* reproduction is also supported by a few observations of nestlings that died due to excessive heat or sun exposure (B.L.R. and MRB, personal observation). In addition to the direct effects on nests downstream, high temperatures have been associated with reduced insect availability, as well as mismatches between prey peaks and bird reproduction (Visser and Gienapp 2019; Neate-Clegg et al. 2021), indirectly affecting reproduction by decreasing food availability for parents and nestlings.

Surprisingly, the maximum tidal height was associated with a decrease in *F. acutirostris* mortality, and it was equally surprising that this was only the case in one area, upstream. Although height tide provided less space available for foraging and refuge for *F. acutirostris*, it can also alter the predation pressure. Like other situations discussed above, this explanation may lie in a level of detail not explored by the study. It is possible that the association of the vegetation structure upstream with high tides limits the movements of *P. nigricans* and restrict it to sites above the tides with low vegetation density, which would be avoided by *F. acutirostris*, positively impacting the reduction of its mortality. Downstream, *R. rattus* is an important predator that uses branches of the abundant *L. racemosa* tree for locomotion and is also capable of swimming, therefore, the tide height would not affect predation pressure.

5. Conservation

We observed considerable variations in population dynamics across the territories in our study area. A small number of territories produced the majority of independent juveniles, and mortality rates varied up to sixfold between territories (Figure 2). This pattern of disproportional populational trends between territories indicates a vulnerability to local disturbances (Brambilla and Bionda 2013) and must be considered in conservation actions (Sergio et al. 2009). For instance, one of the territories that contributed more to juvenile production (*Azulzinho* on Jundiaquara Island; N = 10) experienced an invasion by exotic tanner grass *Urochloa arrecta*, which, if unmanaged, could severely affect upstream overall population performance. For the study areas, protecting the half territories with better demographic performance could lead to an overall DP of 56, compared to a DP of 11.5 when conservation actions are randomly applied (data not shown). This is even more crucial considering that good-quality habitats make individuals less vulnerable to external stressors, such as changes in climatic conditions (Franklin et al. 2000; Zuckerberg et al. 2018).

The occupancy rate (e.g., Brambilla and Bionda 2013), often used to assess territory quality, proved unreliable for *F. acutirostris* because some source territories were extinct over time (e.g., *Ypsilone*; DP = 1), while sink territories remained throughout the historical series (e.g., *Vitório Pai*; DP = -11.5). Therefore, areas with Cladietum, that provided the higher DP, are key conservation priority for the species. This approach does not oppose the proposal of minimum areas for the conservation of the species based on the cost-benefit perspective of managing environments invaded by the exotic African grasses *U. arrecta* and/or *U. mutica* (exotic-free zones; Bornschein et al. [2024]). On the contrary, it complements it, highlighting

an even more critical conservation scenario, in which only some environments are a source of individuals within the scarce minimum areas.

The effects of changes in climatic variables are more pronounced in specialized species with a narrow niche breadth (Lucio-Puig et al. 2023), and *F. acutirostris* is in its restrict fundamental niche (Sandretti-Silva et al. 2024). In this context, climate change and rising global temperatures (IPCC 2021) can represent a significant threat to the species due to its very specialized microclimates. Mitigating the effects of climate and high tides on the productivity and survival of species in the environment, reversing the extinction trajectory (Sandretti-Silva et al. 2024), is not possible. However, managing predator populations is a possible strategy, which we suggest be implemented.

6. Conclusion

Like a long-lived species, the demographic performance of *F. acutirostris* was more sensitive to factors that influence juvenile productivity (Noon and Biles 1990). Rigorous longitudinal analyses, although rare, are crucial for understanding the population dynamics (McGinn et al. 2022). Some studies assume a constant mortality rate when assessing demographic performance (e.g., Brambilla and Bionda 2013), but this metric was very distinct between the territories of our study species and vital to our findings and complete conclusions (McGinn et al. 2022). We consider that the lack of data for some years in some of the study areas, which is frequent in similar field studies, and the filtering of samples from non-permanent territories and years when we did not band individuals, did not affect our conclusions due to the long-term sample and extreme values of parameters (e.g., Nystrand et al. 2009; Brambilla and Bionda 2013).

The capacity of *F. acutirostris* to nest is key to defining territory boundaries rather than its own food supply, which are the two primary reasons explaining this spatial ecological attribute in many species (Ricklefs 2010). This is supported by the numerous years in which the species used environmental patches not included in territories that provided food and refuge to pairs during the winter period, but did not sustain it during the breeding period after successive attempts to build nests which were periodically flooded by high tides (MRB, personal observation). The altitudinal and salinity gradients in salt marshes create a gradient of floristic richness (Schaeffer-Novelli and Cintrón-Molero 2016), with great influence on demographic performance and establishment of territories. The dominance of species characterizes types of environments with significant influence on juvenile productivity. *Cladietum*, almost exclusively restricted to upstream areas in the studied gradient, has the

highest juvenile productivity because it is high enough to allow density for nest placement above the tides, and is dense enough to limit the movement of the most frequent bird predator from nest in the area, *P. nigricans*. *Acrostichetum*, dispersed throughout the study areas, is also high enough to allow density for nest placement above the tides, but serves as an obligatory refuge for *P. nigricans* during flooding, providing a good offspring productivity when associated with plants that form forks, which are excellent for supporting nests and limiting the movement of the rail. *Crinetum* is the most abundant type of environment in the study areas and, sometimes, is the only nesting option in some territories, but is also occupied by *P. nigricans*. Its medium stratum, which is the one that provide density for nest placement, has a height equivalent to high tides, contributing little to productivity. When an extreme climatic event, in 2008, caused sediment transport, *P. mertensii* dominated or co-dominated with *C. americanum* in *Crinetum*, elevating total height of the environment, as well the dense intermediate layer used for nest build. Nests became less exposed to high tides, resulting in the higher productivity (Figure 3). This change in vegetation density also affected adult mortality, as the abundance of *P. mertensii*, a plant with long stolons that swing significantly in the wind, likely limited its use as a sleeping site, causing the individuals to return to sleeping in *Acrostichetum*, where they were exposed to *P. nigricans*.

Climatic variables, along with the refuge structure provided by the habitat, directly influence the survival of the individuals and can also expose them to predators. Climate can influence species' reproduction even on very small spatial scales (Shutt et al. 2022). In our results, hot temperatures reduced the number of juveniles where the nests are exposed. Microclimatic assessments are desirable for each environment occupied by *F. acutirostris*, both downstream and upstream. In this sense, the measurement of tides is an additional key factor due to its influence in productivity and mortality of *F. acutirostris* individuals. However, obtaining this data is challenging due to the lack of tide measurement instruments near the study area. Expanding the network of tide gauge stations in Brazil, as well as initiating studies on sedimentation in estuarine environments in the country, is essential for conducting more accurate assessments of the effect of rising tides on environments and populations.

The results reveal significant spatial variation in population performance, highlighting that considering this variation when designing conservation actions could improve the potential outcomes and optimize limited resource allocation (Budnik et al. 2000; Breininger and Oddy 2004; Sergio et al. 2009; Heinrichs et al. 2010; Brambilla and Bionda 2013; McGinn et al. 2022). Our findings indicate that prioritizing the protection of territories with

good area and quality of important nesting vegetation types can substantially enhance overall conservation efficiency. The vulnerability of species to certain climate factors, such as high temperatures, serves as a warning for potential threats to the species' viability in the face of global climate change and rising temperatures (IPCC 2021). Continuing the long-term monitoring is recommended to further understand population dynamics, specially to enhance knowledge relative to the emergence treats (e.g., tide level rise, heat, tropicalization of flora communities, and biological contamination) and ballast effective conservation strategies.

7. References

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8. Tables

Table 1. Qualitative vegetation features classes included in the Generalized Linear Mixed Models (GLMMs) of population dynamics of *Formicivora acutirostris*. The symbol “---” indicates that the feature was not considered in that area. Abbreviations: Acr = Acrostichetum; Clad = Cladietum; comp = complete; Crin = Crinetum; simp = simplified; VD = vegetation density.

Habitat feature	Upstream classes	Downstream classes
VD of Crin	Normal, moderately increased, highly increased (ordered)	---
Clad density	Absent/low density, moderate density, or high density (ordered)	---
Acr density	Absent/low density, moderate density, or high density (ordered)	
Forks	Absent, present in Crin, present in Clad, present in Acr, present in both Crin and Acr (non-ordered)	Absent, present in Crin, present in Acr, present in both Crin and Acr (non-ordered)
Trees (simp)	Present in Clad, present in Acr, present in both Clad and Acr (non-ordered)	---
Trees (comp)	Absent, partially present in Clad, partially present in Acr, partially present in both Clad and Acr, entirely present in Clad, entirely present in Acr, entirely present in both Clad and Acr, entirely present in Clad and partially present in Acr, entirely present in Acr and partially present in Clad (non-ordered)	---

Table 2. Characteristics of the best complete Generalized Linear Mixed Model (GLMM) of population dynamics of *Formicivora acutirostris* for each area and response variable. The table presents the selected fixed effect variables after correlation and variance inflation analysis, the family that provided the best adjust, and the function used for model construction. Abbreviations: Acr = Acrostichetum; Clad = Cladietum; comp = complete; Crin = Crinetum; DP = annual demographic performance; JP = annual juvenile productivity; Lag = Laguncularietum; M = annual adult mortality; VD = vegetation density.

Response	Fixed effect	Family	R function
Upstream			
JP	Perimeter, perimeter-area ratio, neighbors,	Poisson	glmer
M	median altitude, Crin area, VD of Crin, Acr area,	Poisson	glmer
DP	Acr density, Clad area, Clad density, trees in Acr and Clad (comp), forks, accumulated precipitation, rainy days, maximum average, temperature, average minimum temperature, maximum tidal height	Gaussian	lmer
Downstream			
JP	Area, neighbors, median altitude, Crin	Poisson	glmer
M	proportion, Acr proportion, Lag proportion, forks, accumulated precipitation, rainy days, average	Poisson	glmer
DP	maximum temperature, average minimum temperature, maximum tidal height	Gaussian	lmer

Table 3. Generalized Linear Mixed Model (GLMM) of juvenile productivity of *Formicivora acutirostris* in areas located upstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviations: Acr = Acrostichetum; Clad = Cladietum; Crin = Crinetum; L = linear effect; Q = quadratic effect; SE = standard error; VD = vegetation density.

Variable	Estimate	SE	z-value	p-value
Intercept	-0.599	0.348	-1.722	0.085
Perimeter	0.042	0.119	0.351	0.725
Perimeter-area ratio	-0.0950	0.115	-0.831	0.406
Neighbours	0.246	0.092	2.675	0.007
Crin area	-0.070	0.186	-0.378	0.706
VD of Crin (L)	0.568	0.268	2.122	0.034
Acr area	-0.014	0.120	-0.115	0.909
Acr density (Q)	-0.512	0.178	-2.878	0.004
Clad area	0.701	0.230	3.043	0.002
Clad density (L)	-0.079	0.225	-0.353	0.724
Trees in Clad and Acr entirely	0.900	0.725	1.240	0.215
Trees in Clad entirely	0.472	0.930	0.508	0.612
Trees in Clad entirely, partially in Acr	-1.294	0.782	-1.655	0.098
Trees in Acr entirely	0.541	0.505	1.072	0.284
Trees in Acr entirely, partially in Clad	-0.298	0.491	-0.608	0.543
Trees in Clad and Acr partially	0.401	0.443	0.906	0.365
Trees in Clad partially	-1.409	1.103	-1.277	0.202
Trees in Acr partially	-0.075	0.451	-0.167	0.867
Forks in Clad	-0.791	0.426	-1.857	0.063
Forks in Crin	-0.126	0.278	-0.455	0.649

Forks in Acro	-1.110	0.763	-1.455	0.146
Forks in Acro and Crin	-0.269	0.406	-0.663	0.507
Accumulated precipitation	0.201	0.216	0.931	0.352
Rainy days	0.318	0.227	1.402	0.161
Average maximum temperature	-0.003	0.195	-0.015	0.988
Average minimum temperature	-0.219	0.194	-1.129	0.259
Maximum tidal height	-0.024	0.178	-0.133	0.894

Table 4. Generalized Linear Mixed Model (GLMM) of juvenile productivity of *Formicivora acutirostris* in areas located downstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviations: Crin = Crinetum; L = Lagularietum; SE = standard error.

Variable	Estimate	SE	z-value	p-value
Intercept	-0.870	0.189	-4.597	<0.001
Area	-0.010	0.138	-0.076	0.940
Neighbours	-0.117	0.149	-0.784	0.433
Median altitude	0.347	0.239	1.454	0.146
Crin proportion	0.343	0.248	1.386	0.166
Lag proportion	0.235	0.177	1.330	0.183
Forks in Crin	-0.653	0.422	-1.546	0.122
Forks in Acro	0.871	0.401	2.170	0.030
Forks in Crin and Acro	0.223	1.053	-0.212	0.832
Accumulated precipitation	0.487	0.245	1.989	0.047
Rainy days	0.580	0.264	2.196	0.028
Average maximum temperature	-1.247	0.366	-3.405	0.001
Average minimum temperature	0.078	0.209	0.373	0.709
Maximum tidal height	0.218	0.182	1.194	0.232

Table 5. Generalized Linear Mixed Model (GLMM) of adult mortality of *Formicivora acutirostris* in areas located upstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviations: Acr = Acrostichetum; Clad = Cladietum; Crin = Crinetum; L = linear effect; Q = quadratic effect; SE = standard error; VD = vegetation density.

Variable	Estimate	SE	z-value	p-value
Intercept	-1.958	0.514	-3.810	<0.001
Perimeter	0.082	0.151	0.542	0.588
Perimeter-area ratio	-0.281	0.156	-1.799	0.072
Neighbours	-0.033	0.109	-0.300	0.765
Median altitude	-0.062	0.161	-0.387	0.699
Crin area	-0.389	0.238	-1.637	0.102
VD of Crin (Q)	0.771	0.296	2.603	0.009
Acr area	-0.086	0.170	-0.508	0.611
Acr density (L)	-0.008	0.306	-0.025	0.980
Clad area	-0.078	0.308	-0.253	0.800
Clad density (L)	-0.314	0.329	-0.955	0.340
Trees in Clad and Acr entirely	-0.768	1.196	-0.642	0.521
Trees in Clad entirely	-1.213	1.236	-0.982	0.326
Trees in Clad entirely, partially in Acr	-0.856	1.006	-0.850	0.395
Trees in Acr entirely	-0.118	0.682	0.173	0.863
Trees in Acr entirely, partially in Clad"	0.015	0.651	0.023	0.982
Trees in Clad and Acr partially	-0.870	0.640	-1.358	0.174
Trees in Clad partially	0.646	0.895	0.722	0.470
Trees in Acr partially	0.093	0.630	-0.148	0.883
Forks in Clad	0.544	0.636	0.854	0.393

Forks in Crin	0.402	0.309	1.299	0.194
Fork in Acro	1.004	0.551	1.821	0.069
Forks in Crin and Acro	-0.465	0.571	-0.814	0.415
Accumulated precipitation	0.037	0.169	0.216	0.829
Rainy days	0.377	0.168	2.240	0.025
Average minimum temperature	-0.054	0.147	-0.370	0.711
Maximum tidal height	-0.359	0.135	-2.666	0.008

Table 6. Generalized Linear Mixed Model (GLMM) of adult mortality of *Formicivora acutirostris* in areas located downstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviation: SE = standard error.

Variable	Estimate	SE	z-value	p-value
Intercept	-1.362	0.180	-7.582	< 0.001

Table 7. Generalized Linear Mixed Model (GLMM) of demographic performance (DP) of *Formicivora acutirostris* in areas located upstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviations: Clad = Cladietum; SE = standard error.

Variable	Estimate	SE	z-value	p-value
Intercept	0.017	0.083	0.208	0.835
Clad area	0.163	0.049	3.335	0.001

Table 8. Generalized Linear Mixed Model (GLMM) of demographic performance (DP) of *Formicivora acutirostris* in areas located downstream in the Guaratuba Bay, Paraná, Brazil. Significant p-values are shown in bold. Abbreviations: Crin = Crinetum; L = Lagularietum; SE = standard error.

Variable	Estimate	SE	z-value	p-value
Intercept	0.068	0.069	0.979	
Area	0.079	0.065	1.222	0.222
Neighbours	0.076	0.066	1.151	0.250
Median altitude	0.106	0.115	0.925	0.355
Crin proportion	0.095	0.122	0.785	0.432
Lag proportion	0.051	0.081	0.632	0.528
Forks in Crin	-0.363	0.195	-1.857	0.134
Forks in Acro	0.589	0.293	2.013	0.124
Forks in Crin and Acro	-0.396	0.420	-0.943	0.361
Accumulated precipitation	0.088	0.010	0.883	0.377
Rainy days	0.012	0.086	0.134	0.894
Average maximum temperature	-0.120	0.085	-1.409	0.159
Average minimum temperature	-0.048	0.089	-0.540	0.589
Maximum tidal height	0.014	0.082	0.172	0.863

9. Figure legends

Figure 1. Study areas of *Formicivora acutirostris* in the Guaratuba Bay, municipality of Guaratuba, Paraná, Brazil. A. Broader view; B More detailed view. The areas are divided into upstream (Jundiaquara Island and Continente, highlighted in green) and downstream (Folharada Island, highlighted in dark blue). Background images: Geomorphometric Database of Brazil (TOPODATA), National Water and Sanitation Agency (ANA), OpenStreetMap contributors.

Figure 2. Population dynamics of *Formicivora acutirostris* per territory (colored polygons) in Guaratuba Bay, municipality of Guaratuba, Paraná, Brazil. A, C, and D represent upstream areas B, D, and F represent downstream area. A and B. Total juvenile productivity; C and D. Total adult mortality upstream; E and F. Territory dynamics. The black stars indicated the presence of considerable Cladietum area in the territory ($> 25 \text{ m}^2$). Background images: Geomorphometric Database of Brazil (TOPODATA), OpenStreetMap contributors.

Figure 3. Relationship between environmental factors and of population dynamics of *Formicivora acutirostris*, per territory, in areas located upstream in the Guaratuba Bay, Paraná, Brazil. The relationships are: A. Number of neighboring territories; B. Cladietum area; C. Vegetation density in Crinetum; and D. Acrostichetum density with annual juvenile productivity; E. Number of rainy days; F. Maximum tidal height; G. Vegetation density in Crinetum with annual adult mortality; and H. Cladietum area with annual demographic performance. The points represent observed data, the solid green lines represent the fitted GLMM models, and the shaded areas represent the 95% confidence interval around the predictions. Abbreviations: Acr = Acrostichetum; Crin = Crinetum; DP = annual demographic performance; VD = vegetation density.

Figure 4. Relationship between environmental factors and of population dynamics of *Formicivora acutirostris*, per territory, in areas located downstream in the Guaratuba Bay, Paraná, Brazil. The relationships are between: A. Forks; B. Accumulated precipitation; C. Number of rainy days; D. Average maximal temperature with annual juvenile productivity; and E. Forks with annual demographic performance. The points represent observed data, the solid blue lines represent the fitted GLMM models, and the shaded areas represent the 95% confidence interval around the predictions.

10. Figures

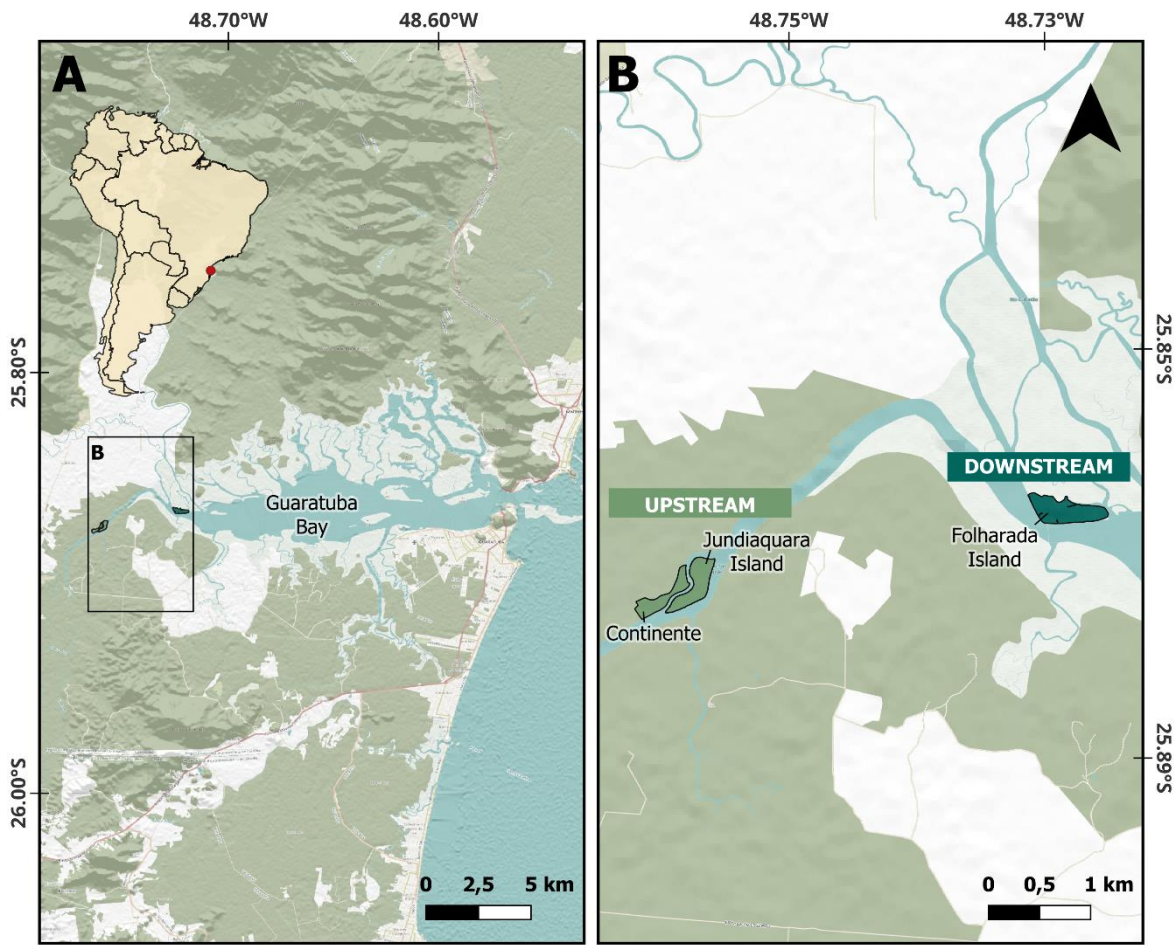


Figure 1

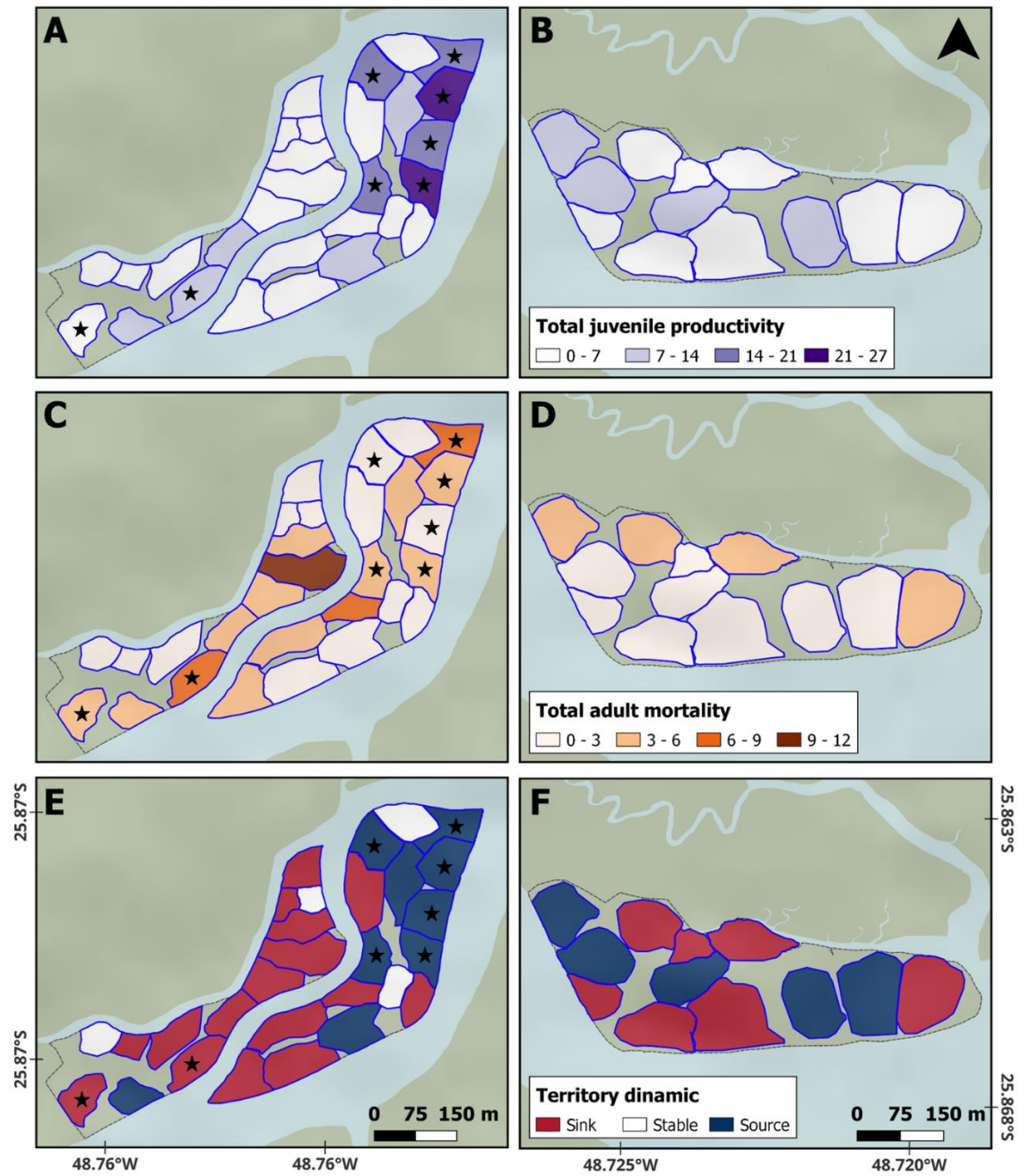


Figure 2

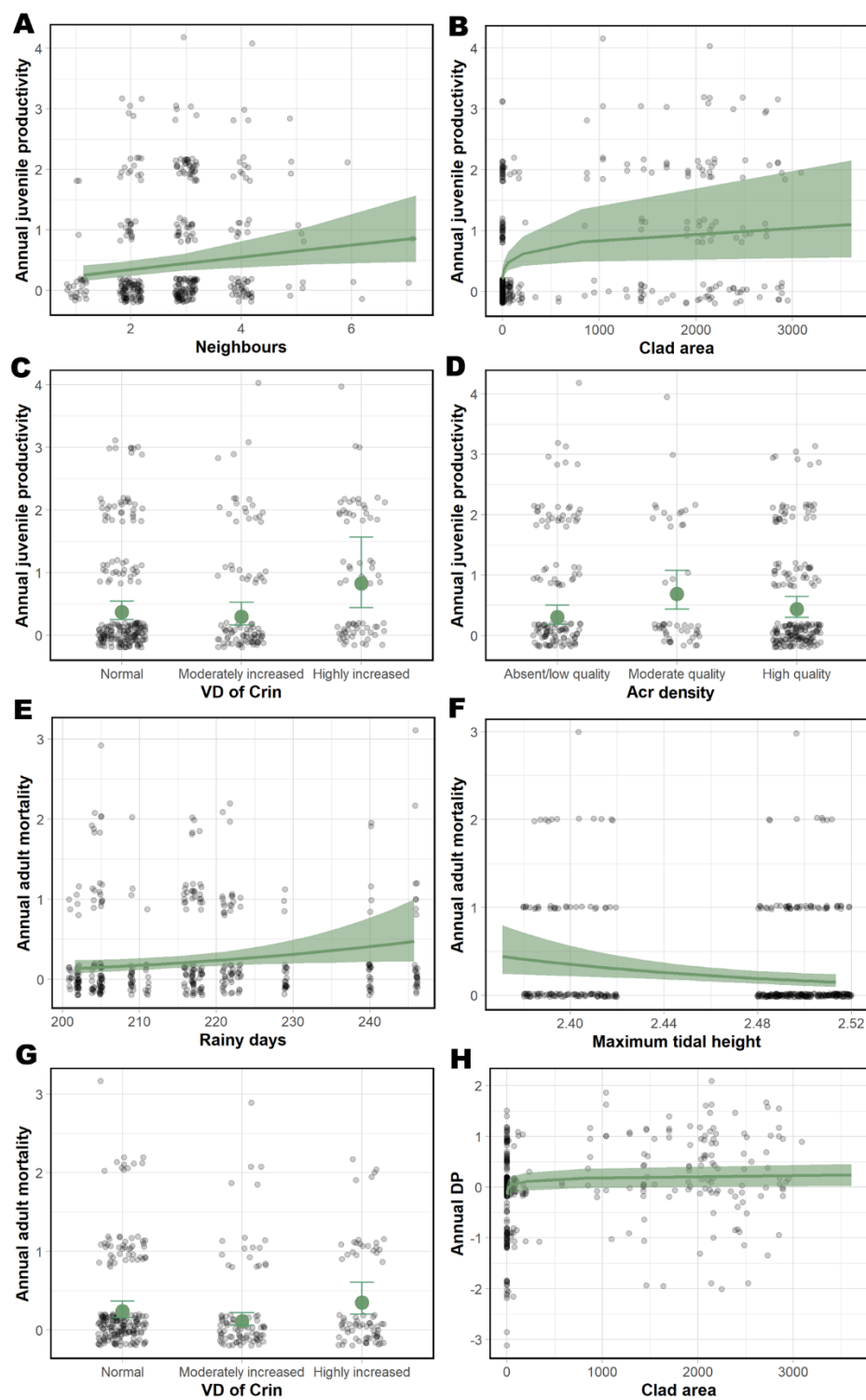


Figure 3

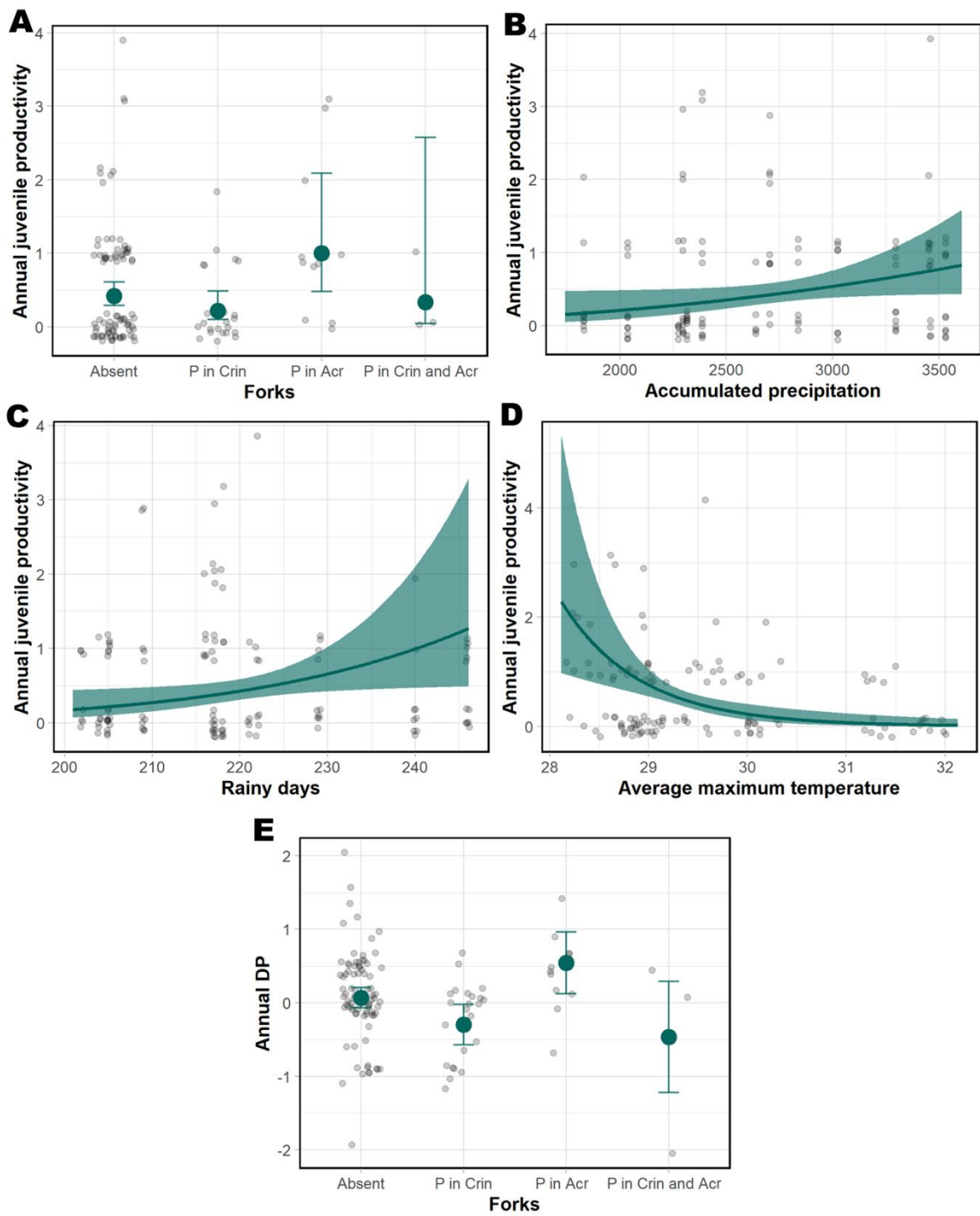


Figure 4

11. Supplementary material

ONLINE RESOURCE 1

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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Online Resource 1. Data on population dynamics for *Formicivora acutirostris* in monitored territories at Guaratuba Bay, Paraná, Brazil. There are presented juvenile productivity (first) and the number of dead adult individuals (second) during the specified period, separated by commas. Some samples were excluded from our analysis according to the sampling design to ensure that the data are comparable (see methods for details), reason why not all territories are depicted in Figure 2. Abbreviations: MPC = Multiple pair change during the breeding season (excluded from analysis); NA = Not assessed; NO = Not occupied; NRI = Non-banded adults (excluded from analysis); TEP = Non-permanent territory establishment period (excluded from analysis).

Territory	2006/ 2007	2007/ 2008	2008/ 2009	2009/ 2010	2010/ 2011	2011/ 2012	2012/ 2013	2013/ 2014	2014/ 2015	2015/ 2016	2016/ 2017	2017/ 2018	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	2022/ 2023	2023/ 2024
Jundiaquara Island																		
Acelerado	0, 0	1, 0	0, 0	0, 0	1, 1	1, 0	0, 0	1, 0	1, 1	1, 1	1, 0	1, 1	0, 0	2, 0	0, 0	0, 0	2, 0	0, 1

Territory	2006/ 2007	2007/ 2008	2008/ 2009	2009/ 2010	2010/ 2011	2011/ 2012	2012/ 2013	2013/ 2014	2014/ 2015	2015/ 2016	2016/ 2017	201/ 2018	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	2022/ 2023	2023/ 2024
Azulzinho	0, 0	2, 0	0, 0	2, 0	0, 1	1, 1	4, 0	2, 0	1, 0	3, 0	MPC	MPC	0, 1	3, 0	0, 0	1, 1	0, 0	0, 0
Boquinha	NO	NO	NO	NO	NO	TEP	TEP	0, 0	2, 1	0, 1	0, 0	0, 0	2, 0	2, 0	0, 1	NO	NO	NO
Capim-serra	0, 0	0, 0	0, 0	3, 1	0, 0	0, 0	2, 0	0, 0	2, 0	2, 0	3, 0	1, 0	1, 0	1, 0	0, 2	2, 0	1, 0	1, 0
David	NO	NO	NO	NO	NO	NO	TEP	TEP	1, 1	0, 0	0, 0	2, 0	0, 0	0, 0	0, 0	0, 0	0, 1	0, 1
Espremido	NO	NO	NO	NO	NO	NO	NO	NO	NO	TEP	TEP	0, 0	NO	NO	0, 0	NO	NO	NO
Herbacinho	0, 0	0, 1	0, 1	0, 0	0, 0	0, 0	2, 0	0, 0	0, 0	0, 0	0, 0	0, 0	0, 0	2, 0	0, 0	0, 0	0, 0	0, 1
K	TEP	TEP	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO
Mãezinha	0, 0	1, 0	0, 0	0, 1	0, 0	0, 1	0, 0	2, 0	1, 0	2, 0	0, 2	MPC	0, 1	0, 1	0, 0	0, 2	0, 0	0, 1
Magenta	0, 0	0, 0	0, 0	0, 0	0, 0	0, 2	1, 0	0, 1	MPC	0, 0	0, 0	0, 0	0, 0	2, 0	0, 0	0, 1	0, 0	0, 0
Mão-de-borracha	0, 0	0, 0	0, 0	0, 0	2, 1	2, 0	1, 0	3, 0	1, 0	3, 0	1, 2	1, 0	2, 0	1, 0	0, 0	2, 1	2, 0	2, 0
New Azulzinho	NO	NO	NO	NO	NO	NO	NO	0, 0	0, 2	0, 1	0, 0	1, 0	MPC	NO	NO	NO	NO	NO
Ponta L	0, 0	0, 0	0, 0	2, 0	2, 0	1, 0	2, 0	0, 2	0, 1	1, 1	1, 0	1, 0	2, 0	3, 0	0, 0	0, 1	1, 1	0, 1
Riozinho	1, 0	3, 0	0, 0	1, 0	2, 0	MPC	0, 0	1, 1	2, 0	1, 0	MPC	2, 0	2, 0	3, 0	0, 1	2, 0	0, 0	0, 0
Rosaldo	0, 0	0, 0	0, 0	0, 0	1, 0	2, 1	0, 0	2, 0	2, 0	1, 0	0, 0	0, 0	0, 0	3, 0	0, 0	0, 1	0, 0	0, 0
Rosinha	0, 0	0, 0	0, 0	0, 0	0, 1	0, 2	1, 0	0, 1	0, 0	1, 0	0, 0	0, 0	0, 2	0, 0	0, 0	0, 0	0, 0	NO

Territory	2006/ 2007	2007/ 2008	2008/ 2009	2009/ 2010	2010/ 2011	2011/ 2012	2012/ 2013	2013/ 2014	2014/ 2015	2015/ 2016	2016/ 2017	201/ 2018	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	2022/ 2023	2023/ 2024
Velho	1, 0	1, 1	0, 0	2, 0	3, 1	2, 0	2, 1	3, 0	2, 0	2, 0	4, 0	0, 1	2, 0	2, 0	0, 0	1, 0	0, 0	0, 1
Vigor	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	TEP	TEP	NO	NO	NO	NO
Viúva	TEP	TEP	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO	NO
Continente																		
Amarelinha	NA	NA	NA	0, 0	0, 0	NA	0, 0	0, 0	0, 0	0, 0	0, 0	NA	0, 0	0, 2	0, 0	0, 0	0, 0	0, 0
Asinha	NA	NA	NA	0, 0	0, 0	NA	0, 2	2, 1	2, 0	2, 0	1, 0	NA	0, 0	0, 0	0, 2	3, 1	0, 1	2, 0
Barbantino	NA	NA	NA	0, 0	0, 1	NA	0, 1	2, 0	2, 0	2, 1	2, 0	NA	2, 0	2, 0	NRI	0, 1	0, 0	0, 0
Beringela	NA	NA	NA	0, 1	NO	NA	2, 0	0, 1	0, 1	2, 1	0, 0	NA	0, 0	3, 0	0, 2	1, 0	2, 0	0, 0
Choquinha	NA	NA	NA	0, 0	0, 0	NA	0, 0	0, 0	0, 0	1, 0	0, 1	NA	0, 0	0, 0	0, 0	0, 0	0, 0	0, 0
Colorado	NA	NA	NA	0, 0	0, 2	NA	2, 0	1, 0	0, 1	2, 0	0, 0	NA	0, 0	0, 1	NO	NO	0, 0	0, 1
Confusão	NA	NA	NA	NO	NO	NA	NO	NO	NO	TEP	TEP	NA	0, 1	NRI	NO	NO	NO	NO
Dinha	NA	NA	NA	NO	NO	NA	NO	NO	NO	NO	NO	NA	NO	TEP	TEP	NO	NO	NO
Elisa	NA	NA	NA	NO	NO	NA	NO	NO	NO	TEP	TEP	NA	0, 0	NRI	NO	NO	NO	NO
Globo	NA	NA	NA	NO	NO	NA	NO	NO	NO	TEP	TEP	NA	0, 1	0, 2	NO	NO	NO	NO
Listrão	NA	NA	NA	0, 0	2, 0	NA	0, 0	1, 0	1, 0	0, 0	0, 1	NA	NRI	2, 0	0, 0	0, 0	0, 1	0, 1

Territory	2006/ 2007	2007/ 2008	2008/ 2009	2009/ 2010	2010/ 2011	2011/ 2012	2012/ 2013	2013/ 2014	2014/ 2015	2015/ 2016	2016/ 2017	201/ 2018	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	2022/ 2023	2023/ 2024
Vermelhinha	NA	NA	NA	0, 0	0, 1	NA	0, 0	1, 1	0, 1	0, 0	NRI	NA	0, 0	2, 0	0, 1	NRI	1, 0	0, 0
Vitório Pai	NA	NA	NA	0, 0	0, 2	NA	0, 0	1, 0	0, 1	0, 3	0, 0	NA	0, 2	0, 3	0, 1	0, 0	0, 0	0, 0
Vizinho	NA	NA	NA	0, 0	0, 0	NA	0, 0	2, 0	0, 0	1, 2	1, 0	NA	1, 0	0, 0	0, 2	2, 0	0, 0	NRI
Folharada Island																		
Alemão	NA	NA	NA	NO	NO	NO	NO	NO	NO	NO	NO	NA	NO	TEP	NO	NO	NO	NO
Brasileiro	NA	NA	NA	1,0	0,0	2,1	0,1	0,0	0,0	NRI	NO	NA	NO	NO	NO	NO	NO	NO
Canalito	NA	NA	NA	0,0	0,0	2,0	0,0	0,0	0,1	1,1	0,0	NA	0,1	1,0	0,1	1,0	0,1	1,0
Capivara	NA	NA	NA	NO	NO	NO	TEP	TEP	NRI	NO	NO	NA	NO	NO	NO	NO	NO	NO
Denirson	NA	NA	NA	NO	NO	TEP	TEP	NRI	NO	0,1	NO	NA	NO	NO	NO	NO	NO	NO
Desrrabado	NA	NA	NA	0,0	0,1	1,0	0,1	0,0	2,1	1,1	0,0	NA	0,0	0,1	0,0	0,0	0,0	NRI
Dezinho	NA	NA	NA	0,0	1,0	1,0	1,0	0,0	1,0	1,0	0,1	NA	0,0	1,0	0,0	0,0	1,0	2,0
Dividido	NA	NA	NA	NO	NO	NO	NO	NO	NO	NO	NO	NA	TEP	TEP	NO	NO	NO	NO
Hibisquito	NA	NA	NA	0,1	NRI	NRI	0,0	0,1	0,1	0,0	0,0	NA	0,0	1,1	1,1	NRI	1,0	1,0
Jamaicano	NA	NA	NA	1,0	4,0	1,0	1,0	1,0	0,0	0,0	0,0	NA	0,0	0,1	NRI	0,0	1,0	1,0
Kalito	NA	NA	NA	NO	NO	TEP	NO	NO	NO	NO	NO	NA	NO	NO	NO	NO	NO	NO

Territory	2006/ 2007	2007/ 2008	2008/ 2009	2009/ 2010	2010/ 2011	2011/ 2012	2012/ 2013	2013/ 2014	2014/ 2015	2015/ 2016	2016/ 2017	201/ 2018	2018/ 2019	2019/ 2020	2020/ 2021	2021/ 2022	2022/ 2023	2023/ 2024
Manguito	NA	NA	NA	0,0	MPC	0,0	1,1	0,0	2,0	0,0	0,0	NA	0,1	NRI	NRI	NRI	NO	NO
Primeirinho	NA	NA	NA	1,0	1,0	3,1	3,0	1,0	0,0	1,1	2,0	NA	0,0	1,0	0,0	0,2	0,0	1,0
Salsicha	NA	NA	NA	0,0	1,0	2,0	0,0	0,0	3,0	0,1	1,0	NA	0,0	0,0	0,0	NRI	0,0	1,1
Tremilique	NA	NA	NA	NO	NO	TEP	TEP	0,0	0,2	0,0	NRI	NA	NRI	NO	NO	NO	NO	NO
Ypsilone	NA	NA	NA	1,0	0,0	0,0	0,0	1,1	1,0	1,0	0,0	NA	0,0	NRI	NO	NO	NO	NO

ONLINE RESOURCE 2

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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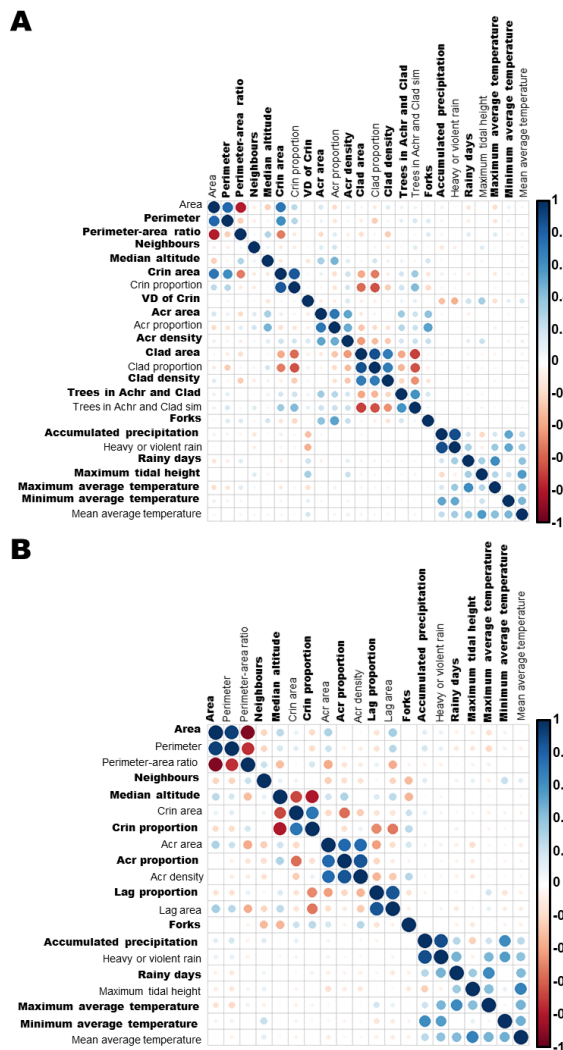
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Online Resource 2. Correlation matrix heatmaps of the fixed effect variables used in the Generalized Linear Mixed Models (GLMMs) for the population dynamics of *Formicivora acutirostris* in Guaratuba Bay, Paraná, Brazil. A. Variables of upstream area models. B.

Variables of downstream area models. Variables in bold were selected for inclusion in the complete model. Abbreviations: Acr = Acrostichetum; Clad = Cladietum; comp = complete; Crin = Crinetum; DP = annual demographic performance; JP = annual juvenile productivity; Lag = Laguncularietum; M = annual adult mortality; VD = vegetation density.

ONLINE RESOURCE 3

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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Online Resource 3. Importance of non-structural random effect variables included in the Generalized Linear Mixed Models (GLMMs) of population dynamics of *Formicivora acutirostris*. The intercepts from the Mixed Effects Random Forest (MERF) models for each random effect variable and their order of importance (1 to 4, in parentheses) used to guide model selection are showed. The values are reported for each response variable within each study area. Abbreviations: DP = annual demographic performance, JP = annual juvenile productivity, M = annual adult mortality.

Variable	Upstream			Downstream		
	JP	M	DP	JP	M	DP
Female ID num	0.059 (4)	0.020 (3)	0.048 (4)	0.054 (3)	0.059 (3)	0.186 (3)
Male ID num	0.071 (3)	0.012 (4)	0.060 (3)	0.038 (4)	0.046 (4)	0.154 (4)

Female age	1.319 (1)	3.797 (1)	4.602 (1)	0.361 (1)	0.096 (2)	0.727 (1)
Male age	0.807 (2)	1.513 (2)	1.924 (2)	0.332 (2)	0.589 (1)	0.500(2)

ONLINE RESOURCE 4

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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Online Resource 4. Importance of fixed effect variables included in the Generalized Linear Mixed Models (GLMMs) of population dynamics of *Formicivora acutirostris* in areas located upstream in the Guaratuba Bay, Paraná, Brazil. The table presents the percent of increase in mean squared error (%IncMSE) from the Mixed Effects Random Forest (MERF) models for each fixed effect variable and their order of importance (in parentheses) used to guide model selection. The values are provided for each response variable Abbreviations: Acr = Acrostichetum; Clad = Cladietum; Crin = Crinetum; DP = annual demographic performance; JP = annual juvenile productivity; M = annual adult mortality; VD = vegetation density.

Variable	JP	M	DP
Perimeter	0.006 (10)	0.004 (11)	0.004 (12)
Perimeter-area ratio	0.001 (13)	0.024 (1)	0.020 (3)
Neighbours	-0.003 (16)	0.005 (10)	0.001 (15)
Median altitude	-0.006 (17)	0.022 (2)	0.008 (6)
Crin area	0.022 (6)	0.009 (4)	0.023 (2)
VD of Crin	0.009 (8)	0.002 (16)	-0.000 (17)
Acr area	0.004 (12)	0.022 (3)	0.008 (8)
Acr density	0.005 (11)	0.006 (5)	0.005 (11)

Clad area	0.140 (1)	0.006 (6)	0.047 (1)
Clad density	0.015 (7)	0.002 (15)	0.016 (4)
Trees in Acr and Clad	0.007 (9)	0.002 (14)	0.002 (13)
Forks	0.001 (15)	0.005 (8)	0.002 (14)
Accumulated precipitation	0.026 (5)	0.006 (7)	0.008 (7)
Rainy days	0.039 (4)	0.005 (9)	0.009 (5)
Average maximum temperature	0.063 (2)	0.001 (17)	0.006 (9)
Average minimum temperature	0.045 (3)	0.004 (12)	0.005 (10)
Maximum tidal height	0.001 (14)	0.003 (13)	0.001 (16)

ONLINE RESOURCE 5

Effects of environmental heterogeneity on the population dynamics of a threatened bird endemic to subtropical salt marshes

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Online Resource 5. Importance of fixed effect variables included in the Generalized Linear Mixed Models (GLMMs) of population dynamics of *Formicivora acutirostris* in areas located downstream in the Guaratuba Bay, Paraná, Brazil. The table presents the percent of increase in mean squared error (%IncMSE) from the Mixed Effects Random Forest (MERF) models for each fixed effect variable and their order of importance (in parentheses) used to guide model selection. The values are provided for each response variable Abbreviations: Acr = Acrostichetum; Crin = Crinetum; DP = annual demographic performance; JP = annual juvenile productivity; L = Lagularietum; M = annual adult mortality; VD = vegetation density.

Variable	JP	M	DP
Area	0.001 (9)	-0.009 (12)	0.003 (7)
Neighbours	0.004 (8)	0.000 (6)	0.000 (8)
Median altitude	0.021 (5)	-0.007 (10)	-0.002 (10)
Crin proportion	0.075 (1)	0.006 (2)	0.021 (2)
Acr proportion	-0.012 (12)	-0.002 (9)	-0.007 (12)
Lag proportion	0.021(4)	0.009 (1)	0.025 (1)
Forks	-0.003 (11)	-0.007 (11)	-0.002 (11)
Accumulated precipitation	0.020 (6)	-0.001 (7)	0.004 (5)

Rainy days	0.015 (7)	0.002 (4)	0.004 (6)
Average maximum temperature	0.049 (3)	0.000 (5)	0.006 (4)
Average minimum temperature	0.054 (2)	0.004 (3)	0.008 (3)
Maximum tidal height	0.001 (10)	-0.002 (8)	-0.000 (9)

CONCLUSÕES

Investigamos a adoção de estratégias comportamentais adaptativas na nidificação e os principais fatores ambientais que influenciam a produção de filhotes independentes, a mortalidade de adultos e o desempenho demográfico em territórios de uma ave de brejos salinos subtropicais, *Formicivora acutirostris*. Os dados foram coletados ao longo de quase duas décadas, o que permite uma visão abrangente e realística do comportamento reprodutivo e parâmetros demográficos e evita vieses de condições atípicas temporárias. As análises ambientais foram realizadas em escala 1:1, possibilitando boa compreensão da interação entre a espécie e seu ambiente.

No Capítulo 1, testamos a existência de aprendizado pela adoção da estratégia “win-stay, lose-switch” na nidificação de *F. acutirostris* e analisamos seu potencial significado adaptativo. Nossos resultados mostraram que a espécie ajusta os atributos dos ninhos que são importantes para o seu destino, com base nos resultados no ninho prévio, como altura para alagamento, espessura para tombamento e posição para predação e tombamento. Demonstramos a estratégia WSLs para mais um dos ocupantes do desafiador ambiente dos brejos salinos, mas, no presente caso, tratando-se de uma ave de uma família de espécies essencialmente florestais (Zimmer e Isler, 2003), com somente dois membros restritos aos brejos (Buzzetti et al. 2013; Winkler et al. 2020). Embora mudanças adaptativas sejam adotadas, elas nem sempre resultam em maior sucesso reprodutivo, e, por isso, são insuficientes para superar todos os desafios oferecidos pelos brejos salinos em obter sucesso reprodutivo. As pressões sinérgicas de alagamento, predação e tombamento dos ninhos apresentam impactos complexos para *F. acutirostris* e afetam sua viabilidade a longo prazo (Sandretti-Silva et al. 2024).

No Capítulo 2, avaliamos a influência de fatores de habitat, maré e clima sobre a produtividade de filhotes, a mortalidade de adultos e o desempenho demográfico dos territórios de *F. acutirostris*. Nossos resultados destacam variáveis ambientais tais quais a extensão, densidade e características de micro-habitat da vegetação, o número de territórios vizinhos e condições de clima e maré como importantes para a reprodução e sobrevivência da espécie. A interação entre condições climáticas adversas e características do ambiente, como a estrutura de refúgios e densidade de outras espécies de aves parece ser determinante para a exposição de *F. acutirostris* a predadores, impactando a produtividade de filhotes e a mortalidade de adultos. Cladietum representa um ambiente crucial para a *F. acutirostris*, pois oferece condições ideais de altura para a nidificação e de densidade para a proteção contra predadores.

Condições climáticas extremas, como altas temperaturas, alterações nos padrões de precipitação, alagamentos mais intensos e ventos fortes, afetam diretamente a reprodução e a sobrevivência dos indivíduos e podem aumentar sua exposição a predadores, impactando negativamente a dinâmica populacional. Embora seja impossível manejar diretamente as mudanças climáticas localmente, o manejo contra a invasão de plantas exóticas em habitats essenciais, como o Cladietum, e o controle das populações de predadores, são estratégias complementares que recomendamos para a conservação da espécie. Sugerimos o controle das populações de predadores para diminuir as pressões sinérgicas sobre *F. acutirostris*. Controlar as populações de *P. nigricans* e *R. rattus* pode melhorar diretamente o sucesso reprodutivo da espécie pela redução do principal fator de insucesso de ninhos, bem como indiretamente, por melhorar as relações de recompensa após estratégias de plasticidade comportamental adotadas para alagamentos e tombamento de ninhos. Também recomendamos a proteção de habitats que apresentam desempenho demográfico satisfatório e podem assegurar a viabilidade da espécie. Essa abordagem complementa a proposta de zonas mínimas para a conservação da espécie (zonas livres de exóticas), de Bornschein et al. (2024).

Reforçamos a importância do monitoramento de longo prazo para prover os dados em qualidade que permitiram as análises aprofundadas efetuadas. Ainda assim, gerou-se pouco dado de algumas situações para permitir que dois conjuntos de análises fossem feitas. Também reforçamos pela continuidade no monitoramento, fundamental para entender as dinâmicas populacionais frente à mudança climática, tropicalização e invasão crescente de espécies exóticas, bem como para monitorar ações de manejo e outras estratégias de conservação em curso e que desejamos sejam executadas com a máxima brevidade. Pesquisas adicionais que explorem condições de microclima e micro-habitat são desejáveis por poderem fornecer dados que ajudem na compreensão dos fenômenos a nível não explorado no presente trabalho, além de permitirem o refino das estratégias de conservação propostas.

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