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Article

Unraveling fruit and seed morphology and seedling establishment of a narrow endemic tree species

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Abstract: Montane ecosystems in South America harbor high levels of endemism typically with species that are often threatened. Here we investigated fruit and seed morphology, germination, and early growth parameters of *Crinodendron brasiliense*, an endangered and narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. We obtained fruit and seed size and shape, number of lobes and number of seeds per fruit and evaluated germination and early growth parameters in a greenhouse. We tested the effect of different container types and parent plant on seed morphology, germination, and early growth. We also tested whether thermal scarification would improve germination rates. We showed that parent plant significantly influenced fruit and seed morphology as well as early growth rates. The germination rate of the species was extremely low (0.003–0.004%), which may be one important underlying cause of its small population size and restricted distribution. Thermal scarification was ineffective to improve the germination of seeds. Unexpectedly, container type significantly affected germination success, as seeds in trays germinated faster and in higher rates than seeds planted in seedbeds. Such result suggests a higher soil moisture could improve germination success. Our study is the first documented propagation of the species and provides essential aspects on the reproductive biology and early development of *Crinodendron brasiliense*. We highlight the urgent need for further research and collaborative conservation initiatives to prevent the extinction of this species.

Keywords: *Araucaria Forest; Brazil; Cloud Forest; Conservation; Crinodendron brasiliense; Elaeocarpaceae; Montane Forest.*

Desentrañando la morfología de frutas y semillas, así como el establecimiento de plántulas de una especie de árbol estrechamente endémica

Resumen: Investigamos la morfología de frutos y semillas, la germinación y los parámetros del crecimiento inicial de *Crinodendron brasiliense*, una especie arbórea en peligro de extinción y endémica de los bosques montanos del sur de Brasil. Obtuvimos el tamaño y la forma de frutos y semillas, el número de lóbulos por fruto y el número de semillas por fruto, además de evaluar los parámetros de germinación y crecimiento inicial – desconocidos para la especie. Demostramos que la planta madre influyó significativamente en la morfología de frutos y semillas, así como en las tasas de crecimiento inicial. La tasa de germinación de la especie fue extremadamente baja (0.003–0.004%), lo que podría ser una causa importante para explicar su pequeño tamaño poblacional y restringida distribución. La escarificación térmica fue ineficaz para la germinación de semillas. Inesperadamente, el tipo de contenedor afectó significativamente el éxito de la germinación, ya que las semillas plantadas en bandejas germinaron más rápido y en tasas más altas que las semillas plantadas en semilleros. Tal resultado sugiere que una mayor humedad del suelo podría mejorar el éxito de la germinación. Nuestro estudio es el primer registro documentado de la propagación de esta especie y proporciona aspectos esenciales sobre la biología reproductiva y el desarrollo inicial de *Crinodendron brasiliense*. Destacamos la necesidad urgente de realizar más estudios e iniciativas de conservación colaborativas para evitar la extinción de esta especie.

Palabras clave: *Bosque con Araucária; Bosque montano; Bosque nuboso; Brasil; Conservación; Crinodendron brasiliense; Elaeocarpaceae.*

Introduction

Narrow endemic species are those with a very limited geographic range, usually restricted to a specific area or habitat (Strayer 2013, Behroozian et al. 2020). These species are often vulnerable to extinction due to their restricted distribution and low population sizes, making them a conservation concern (Kier et al. 2009). Narrow endemic species are typically found in isolated habitats such as mountaintops, islands, or isolated valleys, and they are often highly adapted to the specific conditions of such environments (Lavergne et al. 2004, Nogué et al. 2013). Montane ecosystems in South America, such as the Andes (e.g., (Aagesen et al. 2012), the Guyana Highlands (e.g., (Nogué et al. 2013), and the Brazilian Subtropical Highlands (e.g., (Werneck et al. 2011, Iganci et al. 2011, Hassemer et al. 2015), harbor high levels of endemism, especially plants. High endemism in such ecosystems can result from speciation rates associated to topographical isolation (Steinbauer et al. 2016). Local persistence is also a key feature of narrow endemics survival, once they tend to be poor competitors and less tolerant to stress or disturbance than widespread species (Lavergne et al. 2004). Because of their limited range, narrow endemic species are threatened by disturbances such as wildfires, landslides, stressors such as droughts, as well as human-induced impacts such as habitat destruction and fragmentation, and climate change (Essl et al. 2009, Dirnböck et al. 2011, Hassemer et al. 2015). As such, to ensure their survival, endemic species require special conservation efforts, such as habitat protection and restoration including human-assisted propagation (Toledo-Aceves 2017). Thus, understanding biological and ecological aspects of narrow endemic species is essential for developing conservation strategies to prevent their extinction (Lavergne et al. 2004).

Critical stages in the life cycle of plants such as germination and early growth play a crucial role in population stability and ecological interactions. The comprehension of which and how much factors influence both stages is essential, as they can determine success or failure of a plant species (Miller et al. 2017) and population dynamics (Buckley et al. 2010). Soil fertility, temperature, water availability, and light intensity are among the main factors that impact the germination and early growth of plants (Bareke 2018). Besides, genetic factors can as well affect germination parameters, such as percentage of and time for germination (Bischoff et al. 2006). In addition, understanding early development stages can provide insights into the adaptive strategies employed by plants to cope with environmental challenges and can help predict how plant communities may respond to future environmental changes (Fay & Schultz 2009, Buckley et al. 2010). Therefore, the investigation of germination and early growth stages are critical aspects of ecological research that can inform conservation, restoration and management of plant populations and communities.

Crinodendron (Elaeocarpaceae) is a plant genus endemic to South America and with just four described species: *Crinodendron brasiliense* Reitz & L. B. Sm. (found only in Southern Brazil), *Crinodendron hookerianum* Gay (found only in Chile), *Crinodendron patagua* Molina (found only in Chile) and *Crinodendron tucumanum* Lillo (found in Argentina and Bolivia) (Bricker 1991, Blundo et al. 2012). *Crinodendron brasiliense* is the narrowest endemic species of its genus and occurs in a very limited geographic range in subtropical montane cloud forests in Southern Brazil (Bricker 1991, Sühs 2018, Sampaio 2020). Although described as a shrub up to 4 meters in height, it can reach up to 12 meters in height and thus be considered a tree (Sühs et al. 2019). Leaves are glossy, dark green in color and pendulous; flowers are bell-shaped and white in color (Smith & Smith 1970, Bricker 1991). Any information about the species' fruit and seed morphology, cultivation or propagation studies are still missing. Besides being narrow and endemic, *C. brasiliense* is currently classified as an "endangered" species by the International Union for Conservation of Nature standards (IUCN – Sühs 2018). It faces multiple threats, including habitat destruction, fragmentation, climate change, as well as a low known population size of < 250 adult individuals (Sühs 2018). Therefore, conservation efforts, such as habitat protection and management, in addition to basic research on biological and ecological aspects are needed to ensure the survival of this species and develop effective conservation strategies.

Biological and ecological data are crucial for the development of solid and integrated conservation programs for narrow endemic and endangered species (Lavergne et al. 2004). Considering that aspects on fruit and seed morphology, germination and early growth stages are currently unknown for the narrow endemic and endangered plant *Crinodendron brasiliense*, which are paramount for the perpetuation of the species, we aimed to examine fruit and seed morphology, determine germination rate and early growth parameters. We measured fruit and seed size and shape, number of lobes per fruit and number of seeds per fruit from several individuals and developed a greenhouse experiment to test germination and monitor early growth development. Such new data allowed us to answer the following questions: Does parent plant affect fruit and seed morphology? Does thermal scarification improve the germination of *C. brasiliense*? Does container type affect germination of *C. brasiliense*? Does parent plant identity affect early growth of *C. brasiliense*? By answering these questions and achieving the proposed goals, we believe some crucial ecological and biological information can be available, providing means for the development of conservation initiatives for this narrow endemic species.

Material and Methods

1. Study area

This study was conducted in the highlands of southern Brazil, in both the São Joaquim National Park (SJNP) and its surroundings. SJNP is a protected area with 49,500 hectares which protects Araucaria forests, cloud forests, highland grasslands, and subtropical evergreen forests. *Crinodendron brasiliense* is found in this region, in Araucaria forests / montane cloud forests, mainly in altitudes above 1500 m a.s.l. (Sühs et al. 2019). The climate between 2007 and 2020, recorded in the nearest weather station (ca. 30 km), was characterized by an annual mean rainfall of 2,822.3 mm yr^{-1}, equally distributed along the year, and an annual mean temperature of 11.1°C. The average minimum temperature for the coldest month (July) was 7.7°C and the average maximum temperature for the hottest month (January) was 14.3°C (INMET- inmet.gov.br).

2. Data collection

2.1. Fruit and seed morphology

Adult individuals (hereafter: parent plant) of *Crinodendron brasiliense* found in previous surveys and field incursions were selected based on the presence of fruits. All individuals were located within or close to the extent of the SJNP, above 1500 m a.s.l. and were no further than 8 km from each other, thus likely belonging to the same population or meta-population. We collected a minimum of 20 ripe fruits from 17 parent plant of *C. brasiliense* between January 29th and February 6th, 2022. A total of 362 fruits were collected and 350 fruits were selected for measurements. In each fruit, we measured length and width and the number of lobes and seeds per fruit was counted. Open fruits were not measured in length and width. We manually extracted seeds from the fruits and then screened them for maturity, where green seeds were considered immature and brown seeds were considered mature. A total of 350 mature seeds were selected for measurements, proportionally to the number of fruits used for each plant. We calculated fruit and seed shape and size. Shape was considered as the ratio between length and width and size was considered as the product between length and width (e.g., (Dong et al. 2023). Seeds were kept separated by parent plant and were kept refrigerated until seeding.

2.2. *Germination*

Mature seeds were sown at a depth of two centimeters in two container types, seedbeds, and trays, containing a mixture of inert substrate and sand, in a proportion of 3 to 1, respectively. We sow 128 seeds in each seedbed, in a total of 16 seedbeds; and 36 seeds in each tray, in a total of 6 trays. The total number of seeds was 2,264 seeds, of which 2,048 were sown in seedbeds and 216 in trays. The main difference between the two containers was that trays held a larger volume of substrate, thus retaining more moisture compared to the seedbeds. The total number of seeds collected per individual was divided into two treatments: a thermal scarification treatment (“thermal scarification”) and a control treatment without scarification (“control”). For the thermal scarification, we immersed seeds in hot water (~90°C) for 60 seconds (Gray 1962). Seeds from both treatments were placed to germinate in the same seedbeds/trays. The trays and seedbeds were numbered and identified with metal tags. We keep track for each individual seed regarding the treatment, and parent plant it came from. The experiment was conducted in an open nursery with 50% shade cloth on top, on 1.5 meters high benches to prevent seed predation. The seeds were planted on 08/02/2022 with subsequent watering. During the first week, containers received daily watering, and thereafter, watering was done every 3 days. The location of seedbeds and trays was randomized in the nursery every 2 months. The germination percentage and germination time were calculated for each treatment. The duration of the germination experiment from the planting date (08/02/2022) to the end date (17/02/2023) was 374 days. We considered as germination success the emission of a cotyledon. We considered germination speed as the time needed to germinate. No seeds from the thermal scarification treatment germinated; therefore, these data were not included in the analysis. Also, 60 seeds from the control were lost for unknown causes but are unlikely to bias our results.

2.3. *Early growth*

When seedlings developed their third pair of true leaves (48 ± 11 days after germination), they were transplanted into individual 1.5 L pots. Once transplanted, seedlings were watered every two days for a period of 10 days. There were no subsequent waterings as rainfall was regular throughout the experiment period. Randomization of the location of pots was done monthly. We considered the height of the seedling/sapling as a parameter for initial growth. Initially, seedlings were measured every 15 days, and later at a monthly basis. The duration of the early growth experiment from the first transplanting date (14/12/2022) to the end date (31/05/2023) was 168 days. General aspects of the plant regarding flowers, fruits and seeds, seedling germination, seedling development, and habitat can be found in Figure 1 (A to F, respectively).

3. *Data analysis*

We evaluated fruit and seed morphology by modelling fruit and seed shape and size as a function of the parent plant. For fruit shape and size and seed size, we used generalized linear models (GLM) with a gaussian distribution because it fit the data better. For seed shape we used the Gamma distribution and log-transformed the seed shape data. Descriptive statistics for the whole data set were as well provided. To test the effect of different containers (seedbeds/trays) on the germination success (odds) of *Crinodendron brasiliense*, we used generalized linear mixed models (GLMM) with a binomial distribution, using the logit link function. We included the container nested with parent plant as a random effect variable. All models were selected by Akaike Information Criterion (AIC) by comparing models with fixed effects to an intercept-only model.

The germination parameters of germination percentage, peak germination time, mean germination rate and germination speed were calculated separately for each container type and described. We considered germination speed as the rate of germination in terms of the total number of seeds that germinate in a time interval (Aravind et al. 2023). We fit a GLMM to model plant height over time (for individuals with at least 6 measurements over time). Time was considered as days after germination. We used a gaussian distribution because it fit the data better and included the parent plant as a fixed effect term in the model. Since very few seeds germinated, only five parent plants (out of the 17) were kept for this model. The individual was included as a random effect term in the model (following recommendations of Paine *et al.* 2012).

All models were validated by means of residual evaluation. We assessed goodness-of-fit of the produced models through loglikelihood ratio pseudo-R^2. Analyses were calculated in R environment (R Core Team 2020), through the packages ‘germinationmetrics’ (Aravind et al. 2023) for calculating germination parameters, glmmTMB (Magnusson et al. 2020) for GLMM model, DHARMa (Hartig 2016) for model validation, MuMIn (Barton 2009) for goodness-of-fit, visreg (Breheny & Burchett 2017) for model visualization and ggplot2 (Wickham 2016) for data visualization.

Results

1. *Fruit and seed morphology*

Fruit length and width had similar values and varied between 1.0 cm to 3.1 cm in length and between 1.2 cm to 3.3 cm in width. The mean number of lobes per fruit was 3 (standard deviation – SD ± 0.4) and the mean number of seeds per fruit was 3.6 (SD ± 1.6). Seed length and width values were similar, with mean length of 0.5 cm (SD ± 0.04) and mean width of 0.4 cm (SD ± 0.04; Table 1). Further measurements can be found in Table 1.

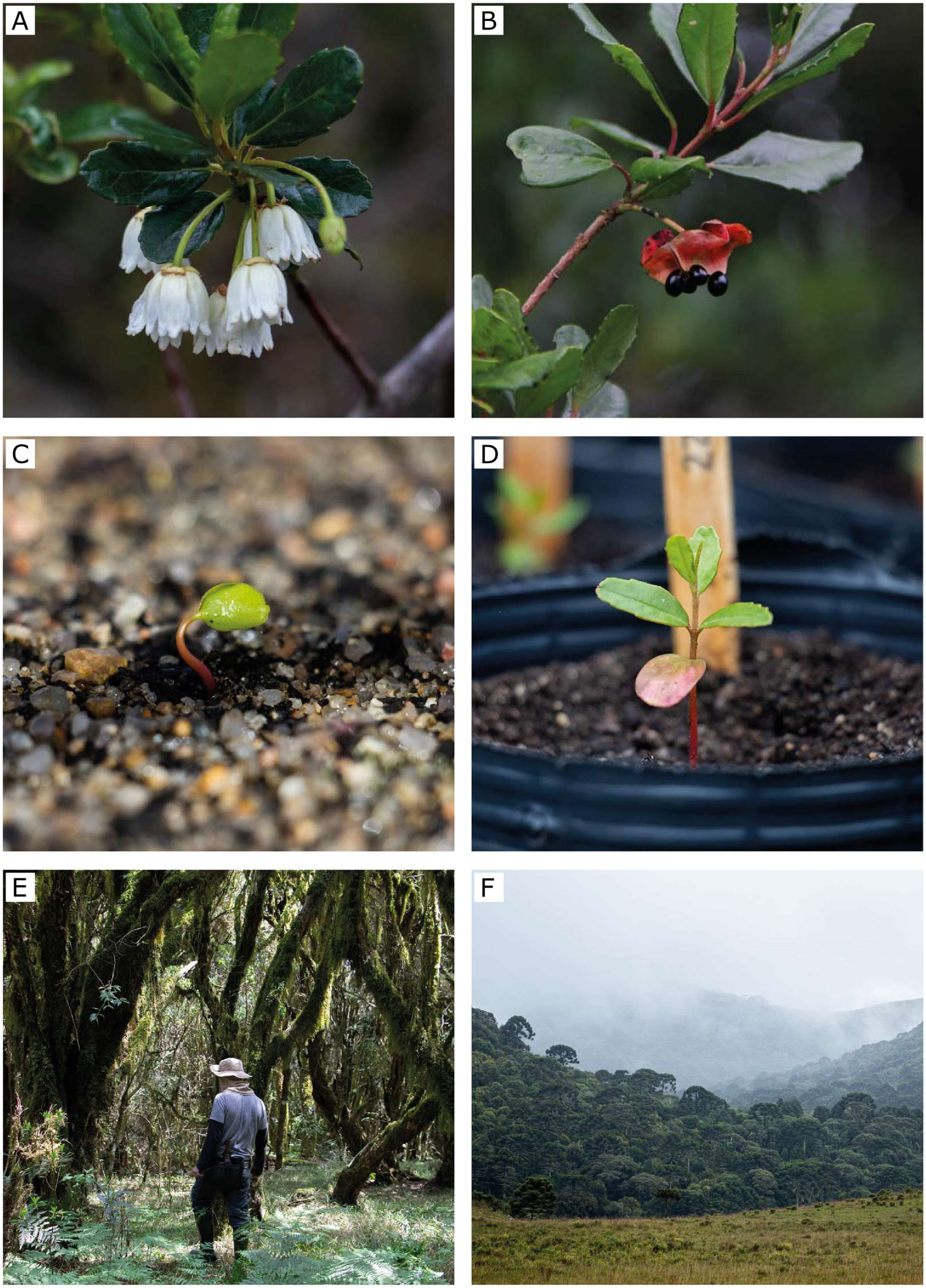

Figure 1. General aspects of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. A: flowers; B: fruit with exposed seeds; C: seedling germination; D: seedling development; E: subtropical montane cloud forest (interior); and F: subtropical montane cloud forest/ Araucaria Forest (exterior).

Table 1. Summarized values of fruit and seed morphology of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. N = sample size, MAD = median absolute deviation, SD = standard deviation, Min = minimum value and Max = maximum value.

	N	Median	MAD	Mean	SD	Min	Max
Fruit length (cm)	350	2.10	0.33	2.12	0.36	1.05	3.06
Fruit width (cm)	350	2.25	0.37	2.24	0.38	1.20	3.33
Number of lobes per fruit	362	3.00	0.00	2.95	0.42	2.00	4.00
Number of seeds per fruit	362	3.00	1.48	3.59	1.64	0.00	11.00
Seed length (cm)	350	0.52	0.04	0.52	0.04	0.40	0.81
Seed width (cm)	350	0.40	0.03	0.40	0.04	0.20	0.58
Fruit shape (cm)	343	0.95	0.13	0.95	0.13	0.62	1.33
Seed shape (cm)	350	1.30	0.08	1.33	0.14	0.87	2.38
Fruit size (cm)	343	4.73	1.44	4.85	1.51	1.60	9.66
Seed size (cm)	350	0.21	0.02	0.21	0.03	0.08	0.35

1.1. Does parent plant affect fruit and seed morphology?

Yes. The shape and size of both fruits and seeds varied according to the parent plant to which they belonged (Figure 2). The parent plant explained 35% of the variation in fruit shape and 56% of the variation in fruit size. The mean fruit shape (length/width) was 0.9 cm (SD ± 0.13), and the mean fruit size (length*width) was 4.9 cm (SD ± 1.5) (Table 1). The parent plant explained 32% of the variation in seed shape and 42% of the variation in seed size. The median seed shape (length/width ratio) was 1.3 cm (median absolute deviation – MAD ± 0.14), and the mean seed size (length*width) was 0.2 cm (SD ± 0.03) (Table 1). All models performed better than the intercept-only model and were considered valid through residual inspection. Numeric results of all models are presented in Supplementary Information – Table S1.

2. Germination

2.1. Does hot water seed scarification improve the germination of C. brasiliense?

No. Seeds scarified with hot water did not germinate (therefore we do not present any further result regarding this question).

2.2. Does container type affect germination of C. brasiliense?

Yes. Seeds sown in trays had a greater chance to germinate than seeds sown in seedbeds ($z = 3.98$, $p < 0.001$). The odds of a seed to germinate in trays were 36 times greater than the odds of a seed to germinate in seedbeds. The odds for a seed to germinate in seedbeds was 0.0028, while the odds for a seed to germinate in trays was 0.1016 (Figure 3). The produced model explained 19% of data variation (pseudo-R^2 theoretical variance = 0.188).

2.3. Germination parameters

A total of 31 seeds from the control group germinated (2.9% of 1,071 seeds). Seeds planted in trays germinated faster (Figure 4) and in a higher rate than seeds sown in seedbeds. The germination parameters of germination percentage, peak germination time, mean germination rate and germination speed were calculated separately for each container type and are described in Table 2.

3. Early growth

3.1. Does parent plant affect early growth of C. brasiliense?

Yes. The height of seedlings varied according to the parent plant to which they belonged (Figure 5A). The produced model with parent plant and number of days after germination (Figure 5B) as fixed effects explained 78% of data variation (marginal pseudo-$R^2 = 0.78$, conditional pseudo-$R^2 = 0.88$).

Discussion

Beyond showing basic aspects on the morphology of fruits and seeds, we found that the parent plant plays an important role in fruit and seed morphology by affecting shape and size of fruits and seeds. Thermal scarification of seeds was completely ineffective to improve germination of the species, possibly indicating that when passing through the digestive tract, particularly of large animals, seeds will not germinate. Seeds planted in trays germinated faster and in a higher rate than seeds sown in seedbeds, suggesting higher success rates when using containers that retain more moisture. Parent plant also influenced the development of the individuals by affecting seedling height in early growth development stage.

1. Fruit and seed morphology and early growth

We found parent plant played a significant role in fruit and seed morphology (shape and size of fruits and seeds) as well as in early growth. Such intraspecific variation was unexpected, especially considering that individuals likely belong to the same population, occur in very similar environmental conditions, and were planted within similar conditions of soil and light availability. In general, intraspecific variation in fruits and seeds can occur across gradients (e.g., Guja et al. 2014) and across spatial scales (e.g., Cavazos 2022). This variation can be a result of genotypic variations and phenotypic plasticity (Cavazos 2022), likely triggered by environmental factors or biotic interactions (Herrera 1992, Albert et al. 2010, Johnson et al. 2019). Intraspecific variations in fruit and seed morphology and in early growth can influence both dispersal mechanisms and fitness, affecting the species' overall

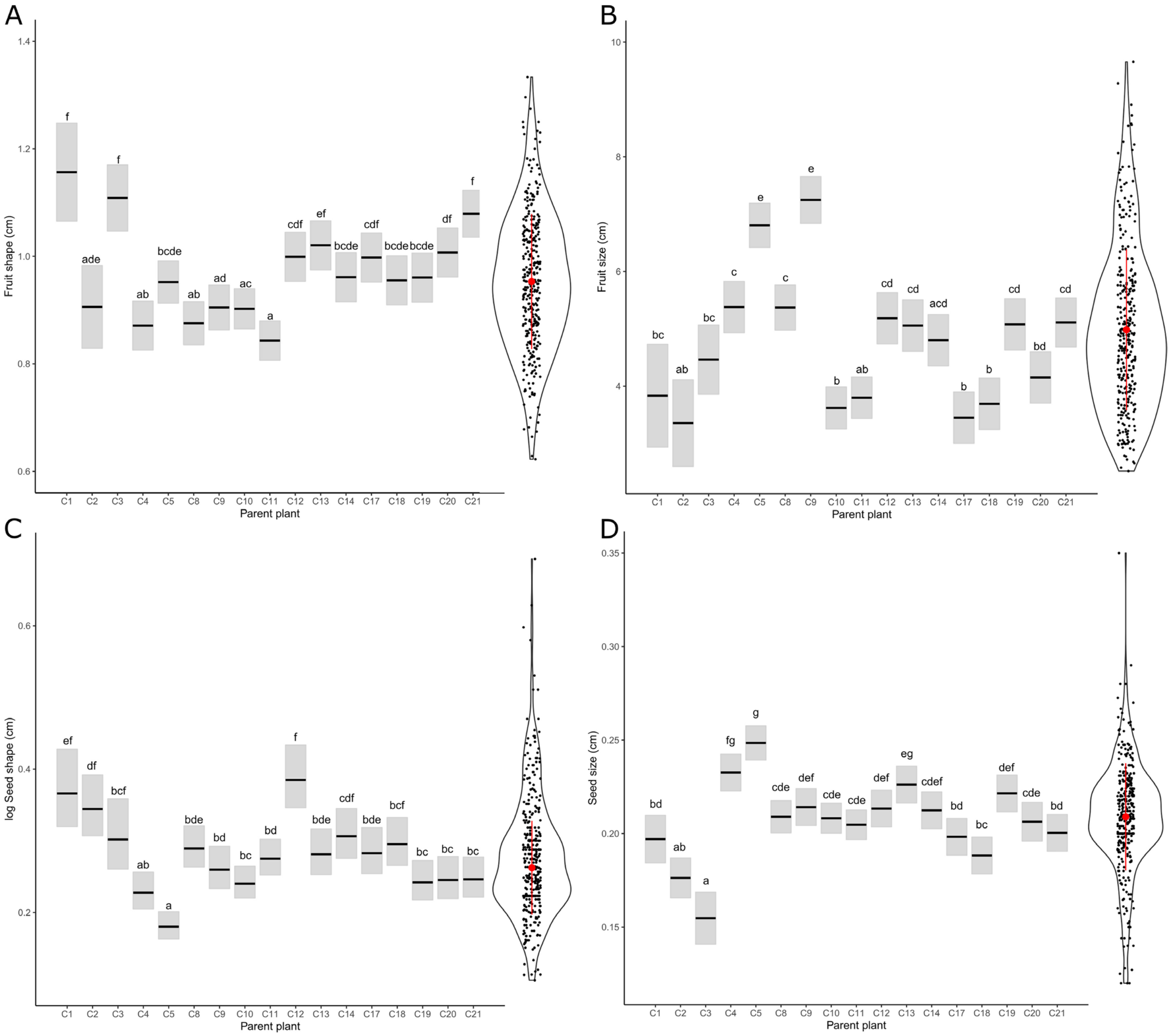

Figure 2. GLMM model results for evaluating the effect of parent plant on fruit and seed morphology of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. A and B represent shape (length/width ratio) and size (length * size) of fruits, respectively; C and D represent shape and size of seeds, respectively. Boxplots not sharing any letter are significantly different (Tukey test at the 95% level of significance). A violin plot with all sampled values (black dots) is displayed in the right of each graph. The red dot indicates the mean (A, B and D) and median (C); red lines indicate standard deviation (A, B and D) and median absolute deviation (C).

reproductive success and population dynamics (Buckley et al. 2010, Galetti et al. 2013, Johnson et al. 2019). Since parent plant was important to explain fruit and seed morphology as well as seedling development, we strongly recommend future studies to consider evaluating genetic diversity (e.g., Xu et al. 2016) and whether fruit and seed morphology can affect dispersal and development of the species.

2. *Germination*

The unsuccessful germination of seeds subjected to thermal scarification reveals the inefficacy of this technique for enhancing germination in *C. brasiliense*. This result was not a surprise given that *C. brasiliense* seeds lack a rigid coat or any hard structure that could require scarification or interruption of dormancy. Still, the fact that none of the seeds germinated after the thermal scarification suggests germination will unlikely improve with scarification methods applied for similar purposes (such as immersion in sulphuric acid; Gray 1962). This result possibly applies for other *Crinodendron* species that share similar seed structure (Bricker 1991). Although germination was higher in trays than in seedbeds, the germination rate of *C. brasiliense* can be considered extremely low compared to other unrelated species from tropical montane forests in Mexico (Toledo-Aceves 2017), Brazil (Dos Santos et al. 2023), and Colombia (Vásquez et al. 2012). Considering

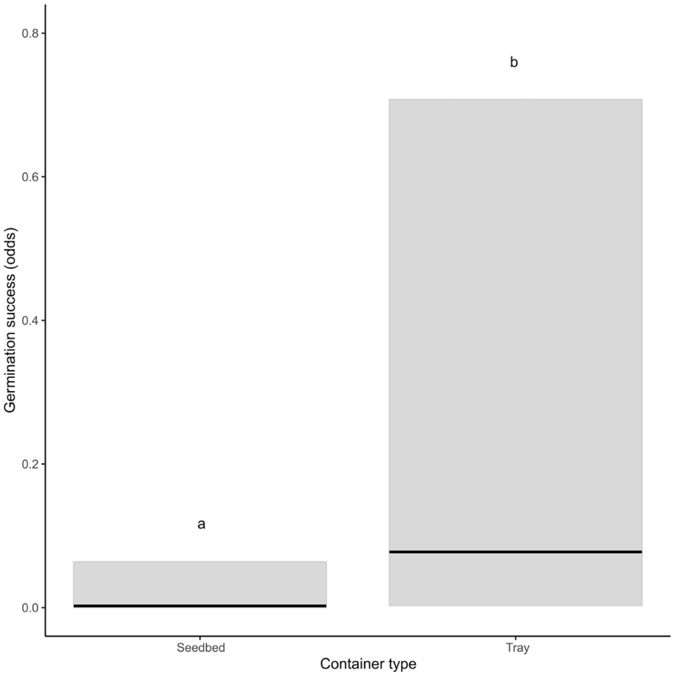

Figure 3. Germination success (odds) for seeds of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil, sown in seedbeds and trays. Different letters indicate significantly different results between groups (Binomial GLMM at 95% level of significance).

Table 2. Germination parameters of *Crinodendron brasiliense* in an experiment conducted in an open nursery, Southern Brazil.

	Trays	Seedbeds
Number of seeds	126	945
First Germination Time (days)	79	267
Peak Germination Time (days)	246.5	273
Mean Germination Rate (%)	0.0042	0.0035
Germination Speed (% days)	0.1034	0.0354

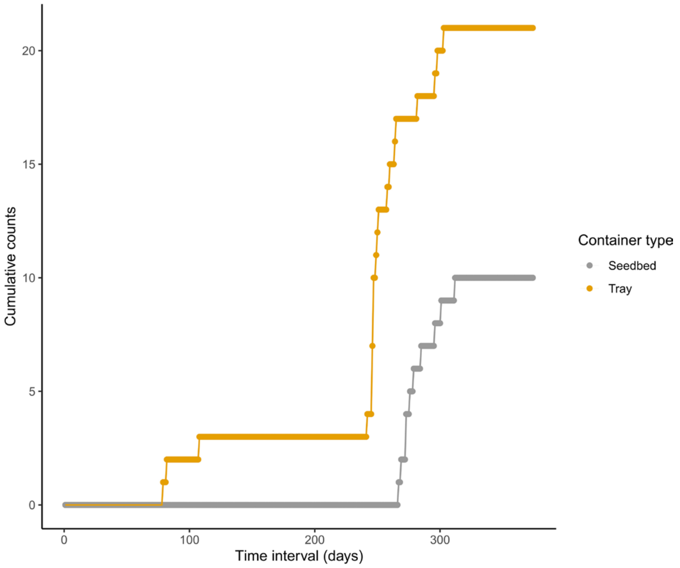

Figure 4. Cumulative germination curves of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. Grey color indicates seeds sown in seedbeds and orange color indicates seeds sown in trays.

both the low germination rate and the long-time seeds took to reach peak germination (246 days – 8 months), we believe the low population size of *Crinodendron brasiliense* can be a consequence of recruitment failure (Volis 2019). Moreover, the temperature fluctuations spanning from fruit-ripening in summer, passing by the cold and frosty winter, until seed germination in spring can be important for the species. It is thus possible that the species' germination can occur after exposure to a cold period, thus benefiting from a cold stratification treatment. Besides temperature, moisture levels also seem to be important. We showed a strong effect of container type on germination rates underscores the importance of substrate moisture retention provided by container volume, suggesting that container choice during propagation can be crucial to improve germination success rates and plant development (NeSmith & Duval 1998). These results are particularly relevant for species propagation efforts. We recommend propagating *C. brasiliense* by carefully extracting seeds from fruits and directly sowing them into individual containers capable of retaining good amounts of moisture. These containers should have a minimum volume of 1.5 liters of soil, and precautions should be taken to prevent the soil from becoming excessively dry. Also, future studies could investigate whether a cold stratification treatment could trigger germination of *C. brasiliense* and the causes of a possible recruitment failure.

3. *Conservation implications*

Species with limited distribution and small population sizes, such as narrow endemic species, usually rely on local persistence for survival (Lavergne et al. 2004), are often at risk of extinction (Essl et al. 2009), and require priority conservation efforts (Kier et al. 2009, Hassemer et al. 2015). Consequently, safeguarding the existence of endemic species demands conservation measures, such as species monitoring and management (Robinson et al. 2018), including human-assisted propagation in some cases. To meet conservation goals, it is crucial to know basic aspects on the biology of the species. In this sense, our study provides new and important insights into the biology and ecology of *Crinodendron brasiliense* – most if not all information previously unknown. By addressing questions related to fruit and seed morphology, germination and early growth, our findings contribute to the understanding of the species biology and marks the first investigation directed to this species and the first documented propagation of the species. This achievement not only sheds light on important aspects of the species' life cycle but also holds profound significance for enhancing its persistence and survival. Our effort lays a foundation for future programs aimed at increasing the population size of *C. brasiliense* (e.g., Volis 2019), underscoring its importance for conservation initiatives and biodiversity conservation (Toledo-Aceves 2017). Conservation of montane cloud forests, the main habitat in which *C. brasiliense* occur, are also extremely important. Despite being within a protected area (São Joaquim National Park), *Crinodendron* populations are threatened by wildfires that occur mainly because of fire exclusion in adjacent grasslands (Sühs et al. 2020). Therefore, controlled fire in grasslands can be considered to prevent montane cloud forests from burning with wildfires.

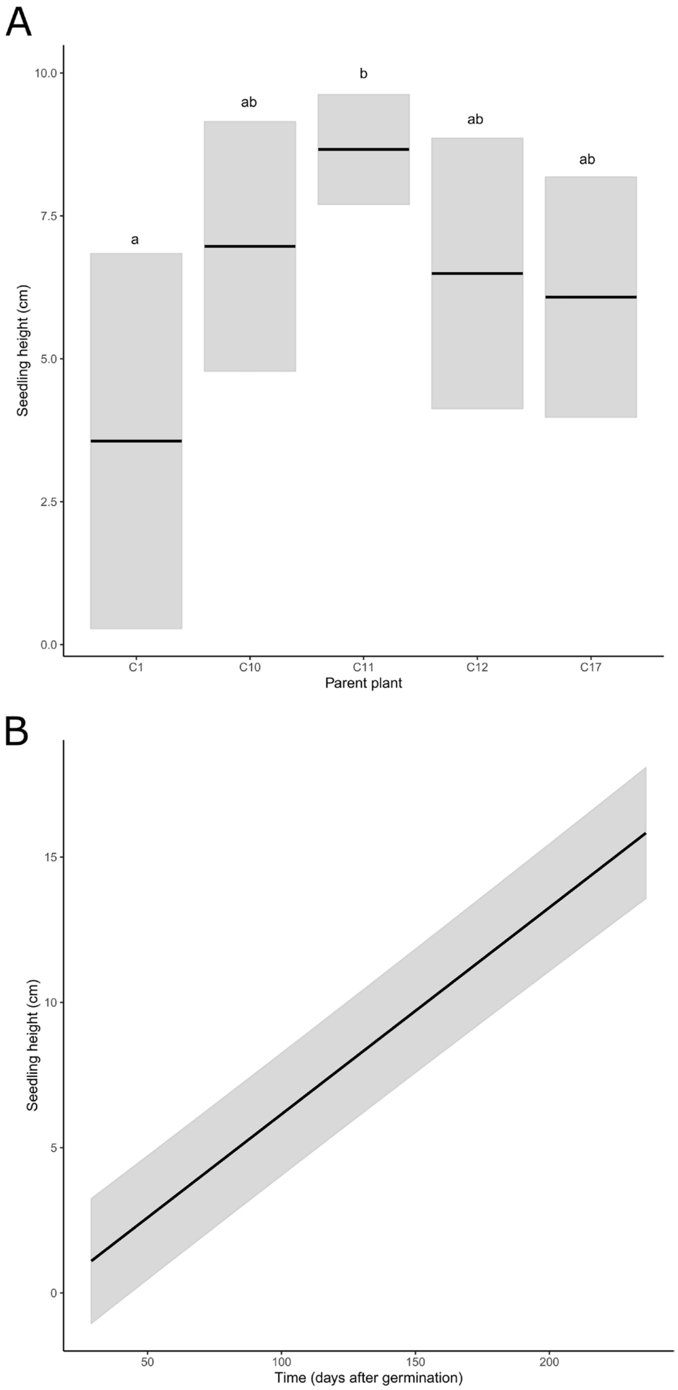

Figure 5. GLMM model results for evaluating the effect of parent plant (A) and time (B) on seedling height of *Crinodendron brasiliense*, a narrow endemic tree species of subtropical montane cloud forests in Southern Brazil. Boxplots not sharing any letter are significantly different (Tukey test at the 95% level of significance).

Considering the small distribution range and the extinction risk status (Sühs 2018), *Crinodendron brasiliense* still lacks dedicated conservation programs, and there are no active propagation efforts in place. The absence of *C. brasiliense* from the list of threatened plants in its home-state (State of Santa Catarina, Brazil), as of the last update in 2014, underscores the urgency for a more recent assessment to accurately determine and address its current conservation status. Consequently, the species is still unknown to many authorities, conservationists, and non-specialists. Thus, urgent attention and concerted efforts are required to address the critical conservation needs of this species.

This study provides essential aspects on the reproductive biology and early development of *Crinodendron brasiliense* and highlights the urgent need for future research and collaborative conservation initiatives. We appeal to the scientific community, conservation managers, and the general population to join forces in developing targeted strategies to ensure the survival and long-term sustainability of this narrow endemic and endangered plant species.

Supplementary Material

The following online material is available for this article:

Table S1 - Models produced to evaluate the effect of parent plant (C1:C21) on fruit and seed morphology of *Crinodendron brasiliense*, a narrow endemic tree species of southern Brazilian highlands. CI = confidence interval. Note that the P-Values provided changed after adjustment for multiple comparison tests.

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Author Contributions

Rafael B. Sühs: designed the experiment; analyzed and interpreted the data and wrote the main part of the manuscript; collected the data, performed the experiment, discussed the results, reviewed, and edited the manuscript.

Sofía Casali: collected the data, performed the experiment, discussed the results, reviewed, and edited the manuscript.

Sophia K. Novaes: collected the data, performed the experiment, discussed the results, reviewed, and edited the manuscript.

Jonata Silveira: collected the data, performed the experiment, discussed the results, reviewed, and edited the manuscript.

Eduardo L.H. Giehl: supervisioned the experiment, discussed the results, reviewed, and edited the manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Data Availability

Supporting data are available at <https://doi.org/10.5281/zenodo.10664507>.

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Article

Assessment of distribution of two sympatric mud crab species – *Panopeus americanus* and *Panopeus austrobesus* – in a Western Atlantic estuarine intertidal zone

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Abstract: Sympatric mud crab species *Panopeus americanus* and *Panopeus austrobesus* are found in intertidal environments associated with muddy and rocky habitats in the Western Atlantic coast. Therefore, they are a suitable model system to be used in studies focused on investigating biological coexistence aspects between close species, such as population structure and habitat. The aims of the current study are to describe and compare the distribution of two sympatric mud crab species – *P. americanus* and *P. austrobesus* – based on their spatial and temporal distribution, in a low human impact estuarine complex area. The hypothesis that these two species show similar distribution, although one species is more abundant than the other, was herein tested. Sampling was carried out in the intertidal zone of a specific area in Cananeia estuarine complex, São Paulo State, Southeastern Brazil, in different periods of time for two years. Both species presented similar pattern distribution and frequency, with predominance in the middle and high intertidal zones, including all demographic categories. However, *Panopeus americanus* was more abundant and presented smaller mean size in all sampling zones. The pronounced disparity in size between the species suggests divergent dietary preferences, potentially related to prey size allowing the coexistence of these sympatric and syntopic species. The predominance of these two species in the upper intertidal zones was understood as a strategy for avoiding competition with the intertidal alpheid shrimps.

***Keywords*:** *Brachyura; coexisting species; microhabitat distribution; Panopeidae.*

Avaliação da distribuição de duas espécies simpátricas de caranguejo-da-lama – *Panopeus americanus* e *Panopeus austrobesus* – em uma zona intertidal estuarina do Atlântico Ocidental

Resumo: As espécies simpátricas de caranguejo-da-lama *Panopeus americanus* e *Panopeus austrobesus* são encontradas em ambientes entremarés associados a habitats lamacentos e rochosos, bem como em simpatria na costa do Atlântico Ocidental. Portanto, constituem um sistema modelo adequado para ser utilizado em estudos focados na investigação de aspectos de coexistência biológica entre espécies semelhantes, como estrutura populacional e habitat. Os objetivos do presente estudo são descrever e comparar a microdistribuição de duas espécies simpátricas de caranguejo-da-lama – *P. americanus* e *P. austrobesus* – com base na avaliação de sua distribuição espacial e temporal, em uma área estuarina complexa e com baixo impacto antrópico. A hipótese de que estas duas espécies apresentam microdistribuição semelhante, embora uma espécie seja mais abundante que a outra, foi testada. A amostragem foi realizada na zona entremarés de uma área específica do complexo estuarino de Cananeia, Estado de São Paulo, Sudeste do Brasil, em diferentes períodos durante dois anos. Ambas as espécies apresentaram microdistribuição e frequência semelhantes, principalmente nas zonas entremarés média e alta. Entretanto, *Panopeus americanus* foi mais abundante e apresentou menor tamanho médio em todas as zonas amostrais. A pronunciada disparidade de tamanho entre as espécies sugere preferências alimentares divergentes, potencialmente relacionadas ao tamanho das presas possibilitando a coexistência dessas espécies simpátricas. A predominância dessas duas espécies nas zonas intermareais superiores também indica uma estratégia para evitar a competição com os camarões alfeídeos.

Palavras-chave: *Brachyura; espécies coexistentes; distribuição de microhabitat; Panopeidae.*

Introduction

Species interactions in a given community are of major importance to gather information about the function and dynamics of ecosystems. This knowledge is essential to support decision-making for conservation, biodiversity management and overall health of natural systems (Neylan et al. 2019). Coexistence among congeneric species is a key aspect to help better understanding their influence on communities' spatial and temporal distribution. Biological processes capable of interfering with this coexistence process are scale-dependent (Hart et al. 2017). Divergence among niches is a factor capable of explaining species interaction at local scale (Kneitel and Chase 2004). Traits, such as selecting different habitats and consuming food deriving from different sources, may avoid competition between species and enable their coexistence (Stearns 1976). Investigating the coexistence of species living in mangroves, as well as their habitats, can be a fruitful environmental assessment aspect given their richness, specificity and diversity (Amaral et al. 2010). Analyzing ecological roles played by crabs and their impact on crab abundance, diversity, distribution and coexistence, at both spatial and temporal scale, as well as assessing mangrove features, can provide information on habitat quality and indicate likely changes in mangroves (Lee et al. 1999, Krausman 1999, Macintosh et al. 2002, Freitas et al. 2021).

Estuarine complex areas encompass mangroves that, in their turn, form habitats typical of coastal wetlands found in intertidal zones along tropical and subtropical latitudes (Tomlinson 1986, Beger et al. 2010). These environments are essential to both aquatic and terrestrial organisms, since they are one of the most productive ecosystems in the world (Goessens et al. 2019, Hamilton 2020). This ecosystem is acknowledged for providing several ecosystem services, such as biodiversity maintenance, nutrient cycling, breeding and nursery habitat, flood control, shoreline stabilization and erosion control, storm protection and pollution control filter (Junk et al. 2014, Barbier 2017).

Information on species richness and interaction are essential to help featuring and assessing this ecosystem, given its high diversity level (Rog et al. 2017). Crabs play essential ecological role in mangroves due to their large number of species and abundance (Nagelkerken et al. 2008, Mokhtari et al. 2015). In addition, they are seen as ecosystem engineers in mangroves because they can affect energy flow, as well as sediment structure and chemistry (Kristensen 2008). Furthermore, crabs form an important link between the basal food web components and the highest trophic levels, consequently, they are capable of affecting different fish and bird species, among other taxa (Macintosh et al. 2002).

Sympatric crab species like *Panopeus americanus* de Saussure, 1857 and *Panopeus austrobesus* Williams, 1983 are widely distributed in intertidal enviroments throughout the Western Atlantic (Melo 1996, 2008), including São Paulo State coast (Mantelatto et al. 2020). Oliveira-Rogeri et al. (2023) recently performed an integrative study focused on explaining the taxonomy and distribution range of mud crab species belonging to genus *Panopeus* in the Southwestern Atlantic zone. Their findings have evidenced six different *Panopeus* species in the investigated region. According to the aforementioned authors, *Panopeus austrobesus* presented wide distribution in almost all Brazilian states and in all marine provinces bordering the country. On the other hand, morphologically similar species, such as *Panopeus occidentalis*, presented a more limited range; its Southern incidence was observed between Southern Pernambuco and Northern Rio de Janeiro states. Consequently, the aforementioned study suggested that previously studies focused on investigating *P. occidentalis* along the Brazilian Southeastern coast likely analyzed *P. austrobesus* populations.

The sympatric crab species *P. americanus* and *P. austrobesus* are suitable to investigate coexistence between similar species, since they inhabit the same ecosystem although they have different reproduction patterns (Peres et al. 2018 and Vergamini and Mantelatto, 2008a,b, both the references as *P. occidentalis*). Habitats occupied by *P. americanus* and *P. austrobesus* comprise algae and roots, and both species can be found under rocks and gravel, or buried in sand (Melo 1996, 2008).

The aims of the current study were to describe and compare the distribution of the sympatric mudcrab species *P. americanus* and *P. austrobesus,* based on assessing their spatial and temporal distribution in an estuarine intertidal zone located in a well-preserved estuarine complex in Western Atlantic coast. We hypothesized that the investigated species show similar distribution in the intertidal zones, although one species is more abundant than the other. Species size and distribution based on demographic categories, juveniles, adults and ovigerous females were also analyzed.

Material and Methods

1. Study site

Sampling was done in the intertidal zone of the intertidal zone in Cananeia estuarine complex, São Paulo State, Southeastern Brazil (25°04'11.2"S, 48°03'08.9"W); this site is a well-preserved area and is considered one of the most productive estuaries in the world (Diegues 1987, Cunha-Lignon et al. 2011) (Figure 1). The substrate of this site is mainly composed of a mixed sediment of sand and mud, on which randomly distributed gravels and boulders are laid. Although these gravels remain exposed to the air during the low tide, small water puddles provide a moisture refuge to *Panopeus americanus* and *P. austrobesus*. The estuarine complex edges hold a dense mangrove forest (Figure 2A-B).

2. Sampling and data analysis

Sampling was carried out in an area of approximately 600 m^2. Collections were performed in June, July, August, October and December 2015, as well as in February 2016, during spring low-tide

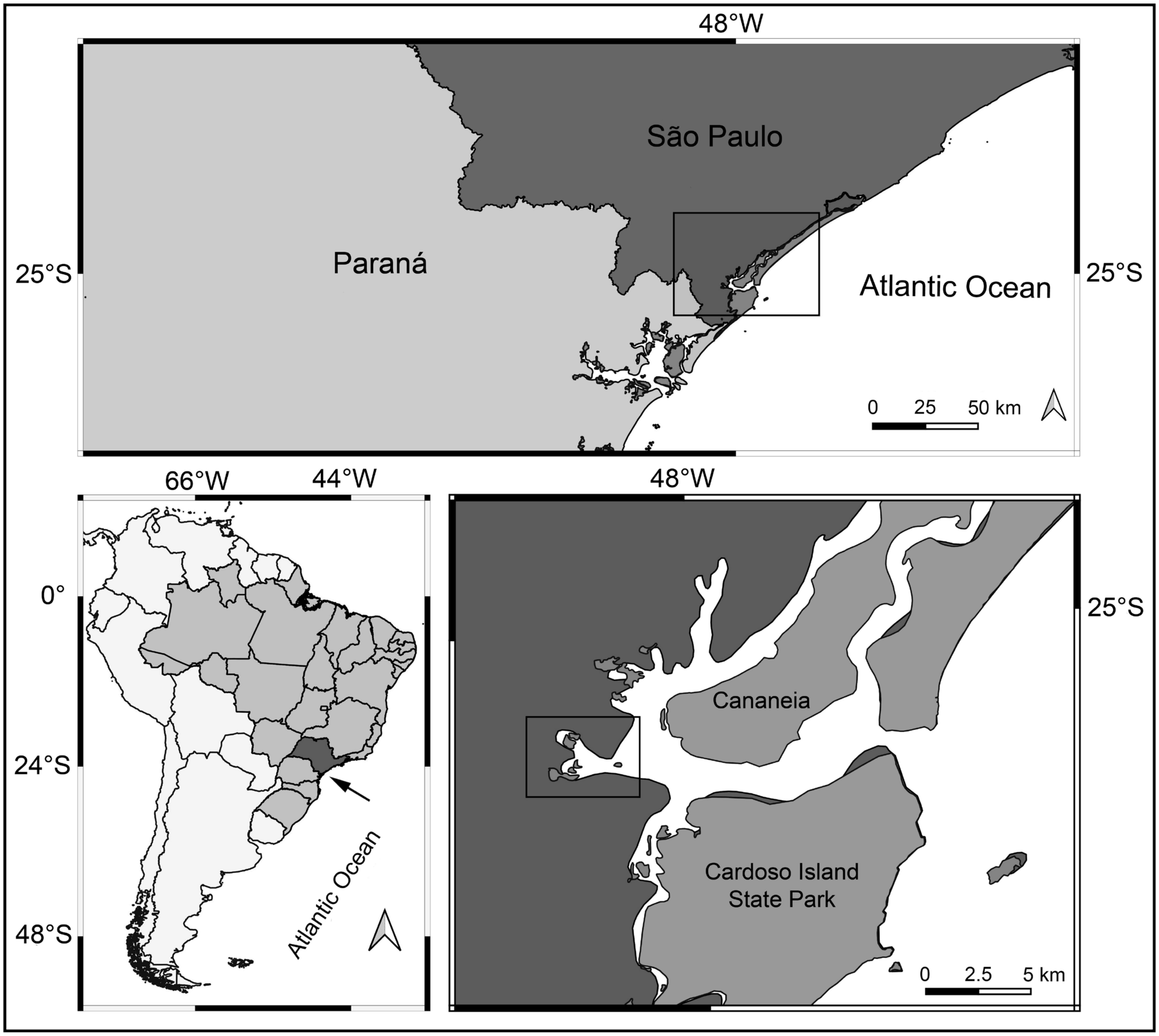

Figure 1. Location of the study area in the intertidal estuarine complex of Cananeia, São Paulo, Southeastern Brazil. Adapted from Pescinelli et al. (2021).

periods. These dates were selected due to good weather conditions, as well as to the ease of access and the longer low tide time during the collection.

The intertidal area was divided into three sub-areas parallel to the waterline, in the following zones according with the position of the sampling area relative to the waterline at high and low tide: low intertidal zone (the nearest to the waterline), middle intertidal zone (that between the low and high zones) and high intertidal zone (the adjacent to the supralittoral zone and the farthest from the waterline). Three 1-m^2 sampling units were established in each sub-area; in total, nine sampling units were obtained per month. Sampling units in each sub-area were equidistant from each other, based on the methodology adapted from Vergamini et al. (2008b) and Costa-Souza et al. (2014) (for further details, see Pescinelli et al. 2017).

Two people have manually collected the crabs in a 2-h catch effort per person (one hour before and one hour after the exact lowest tide time in the day). Gravel, boulders sediments were removed from the collection spot in order to enable capturing the specimens. All *Panopeus americanus* and *P. austrobesus* individuals found in each sampling unit were collected. Then, crabs were placed in coolers filled with crushed ice. All collected individuals were identified in laboratory, according to Melo (1996) and Oliveira-Rogeri et al. (2023). The sex of each crab was identified based on pleon morphology and on paired males'gonopods. Carapace width (CW) was measured with digital caliper (0.01 mm). Crabs were classified into juveniles and adults, based on morphological sexual maturity values estimated by Carvalho-Batista et al. (2015) and Santos et al. (2017).

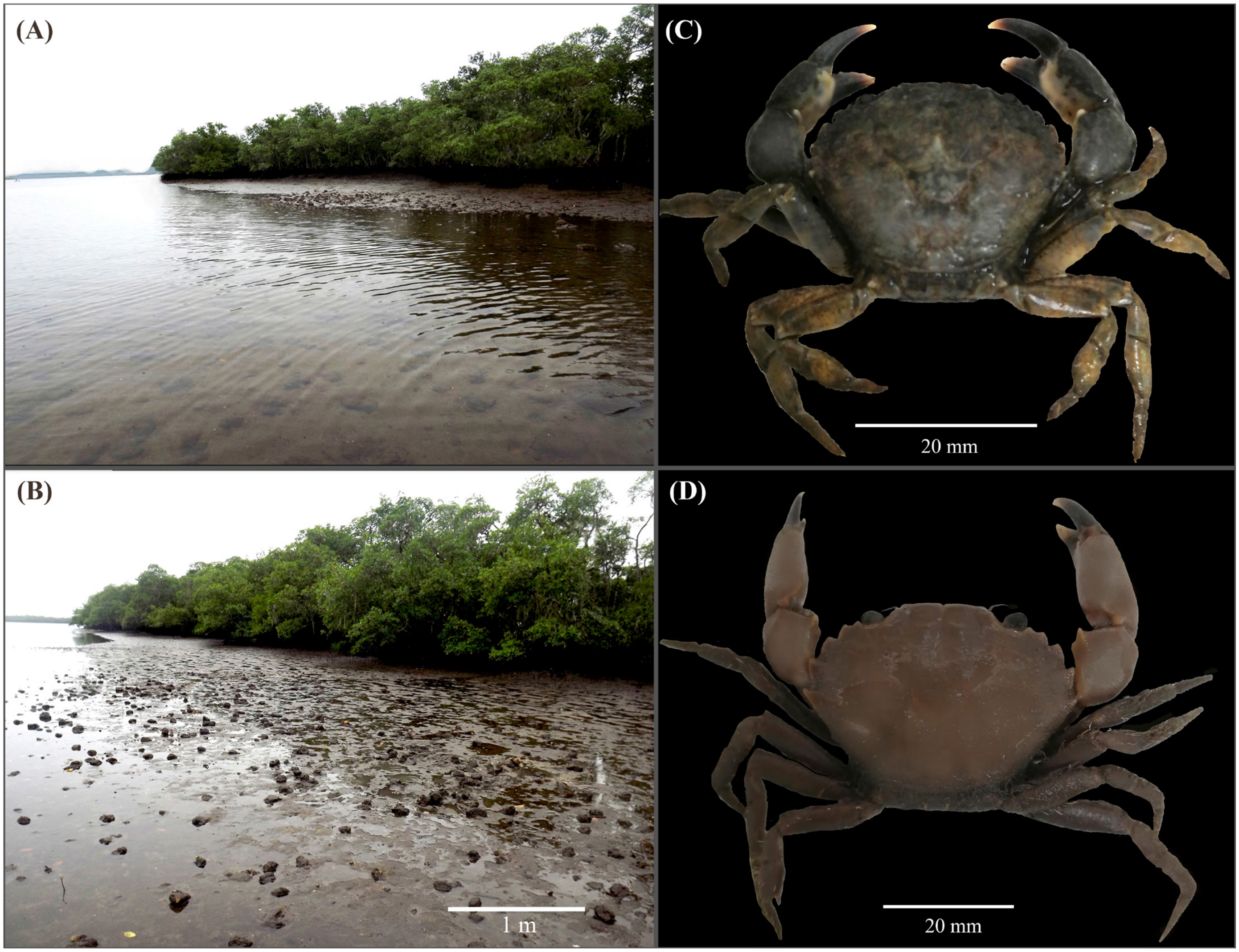

Figure 2. (A-B) view of the sampling area, intertidal zone of the estuary of Cananeia, São Paulo, South-eastern Brazil. (C) dorsal view of a male of *Panopeus americanus* and (D) *Panopeus austrobesus*. Photograph by Pescinelli RA.

Homoscedasticity (Levene) and normality (Shapiro–Wilk) tests were carried out as statistical analysis prerequisites (Zar 1996). Temporal distribution was analyzed based on species' incidence in the sampled months. Mann-Whitney test ($\alpha = 0.05$) was used to investigate differences in CW mean (mm) between *Panopeus americanus* and *P. austrobesus*, in each intertidal zone. Generalized linear model (GLM) was used to analyze the effect of zones (low, middle and high) on crabs' mean abundance value. Similarity in spatial distribution (intertidal zones) was analyzed through non-metric multidimensional scaling analysis (NMDS). ANOSIM test was used to compare the separation degree between intertidal zones.

Results

In total, 211 crabs were collected: 133 *Panopeus americanus* (63%) and 78 *P. austrobesus* (37%). Although crabs of both species were collected in all monthly-sampling and in the three intertidal zones, *P. americanus* was the most abundant both in the collection months and in those zones (Figure 3). Abundance data did not present normal distribution (Shapiro-Wilk, $P < 0.05$). However, both species showed similar spatial distribution and frequency (%) rates: presence in all intertidal zones with gradual increase of abundance towards the intertidal high zone (Table 1, Figure 4A). Moreover, ovigerous females were only collected in the middle and high intertidal zones (Figure 4A).

There was a significant difference in the mean CW between *P. americanus* and *P. austrobesus* (Mann-Whitney test $P < 0.05$). Despite its higher abundance, *P. americanus* presented smaller mean CW in all sampled zones (Figure 4B).

The generalized linear model (GLM) revealed a significant association between the mean abundance and spatial distribution of both species. The significant association was observed between the zones (GLM $P < 0.05$). As there was no difference in the spatial distribution between the species (GLM $P > 0.05$) (Figure 5A), Non-Metric Dimensional Scaling (NMDS) with the Bray-Curtis index was performed for the grouped species. It revealed a significant difference between the zones low *vs*. middle zones, and between low *vs*. high intertidal zones (ANOSIM $P < 0.05$). The NMDS showed no significant difference between the zones middle *vs*. high intertidal zones (ANOSIM

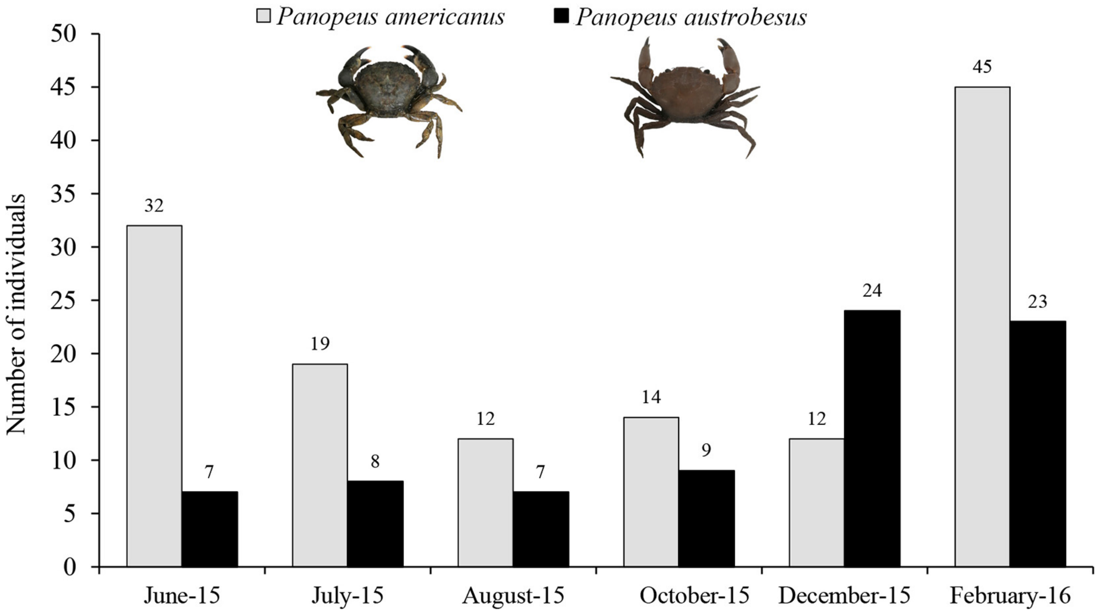

Figure 3. Temporal distribution of *Panopeus americanus* and *Panopeus austrobesus* during the sampling period in the estuarine complex of Cananeia, São Paulo, Southeastern Brazil.

Table 1. Abundance, carapace width (CW) (mm) and frequency (%) of *Panopeus americanus* and *Panopeus austrobesus* according to sampling zones in the estuarine complex of Cananeia, São Paulo, Southeast Brazil.

Zones	*Panopeus americanus*				*Panopeus austrobesus*			
	N	Min–Max	Mean ± SD	%	N	Min–Max	Mean ± SD	%
Low intertidal	28	5.91–18.95	12.94 ± 2.92	21.3	13	5.83–43.67	20.76 ± 11.81	16.6
Middle intertidal	43	7.11–26-44	13.80 ± 4.13	32.4	29	7.84–45.85	21.96 ± 9.71	37.2
High intertidal	62	6.42–26.75	14.33 ± 4.44	46.3	36	5.38–45.71	24.41 ± 11.69	46.2
Total	133	5.91–26.75	13.80 ± 4.07	100	78	5.38–45.85	22.89 ± 10.97	100

$P > 0.05$), revealing a higher similarity of these zones with overlapping clusters (Figure 5B).

Discussion

The current study has comprehensively assessed the distribution patterns of two sympatric mud crab species – *Panopeus americanus* and *P. austrobesus* – in a Western Atlantic estuarine intertidal zone. The present findings substantiated the initial hypothesis and confirmed that both species share the same distribution and coexist within identical intertidal zones (middle and high levels). However, *P. americanus* was more abundant than *P. austrobesus* in all sampled zones. Despite this discrepancy in abundance, the distribution and frequency of both species remained similar in all investigated zones – the highest abundance was observed in the middle and high intertidal zones.

Different demographic categories (juveniles, as well as adult male and female individuals) have also evidenced the preference of both species for middle and high intertidal zones. Assumingly, competition in ecological contexts is higher when species have niche overlapping, i.e., use similar resources in space and time (Rosenfeld 2002). This competition type can lead to likely exclusion of one species from the community. Results in the current study have evidenced that not only both species are present in the intertidal ecosystem, but that they have also same distribution pattern in the intertidal zone (high abundance in middle and high zones). This pattern was also observed for *P. americanus* by Vergamini and Mantelatto (2008b) who analyzed a crab population in the remnant mangrove of Araçá, near São Sebastião Channel, on the Northern coast of São Paulo State, Brazil. Interestingly, although both investigated areas (Araçá and Cananeia), are located along the same São Paulo State coast, they are approximately 400 km away from each other and, present different geomorphological features. However, their mud-crab populations present the same genetic and taxonomic aspects (Oliveira-Rogeri et al. 2023), as well as show similar distribution pattern.

The temporal distribution also showed the same pattern for both species. Despite the higher abundance of *P. americanus* specimens during all sampling period, *P. austrobesus* increased in abundance in December and February. These results may be correlated to different reproductive periods, especially during December, when *P. austrobesus*' abundance surpassed that of *P. americanus*. According to Peres et al.

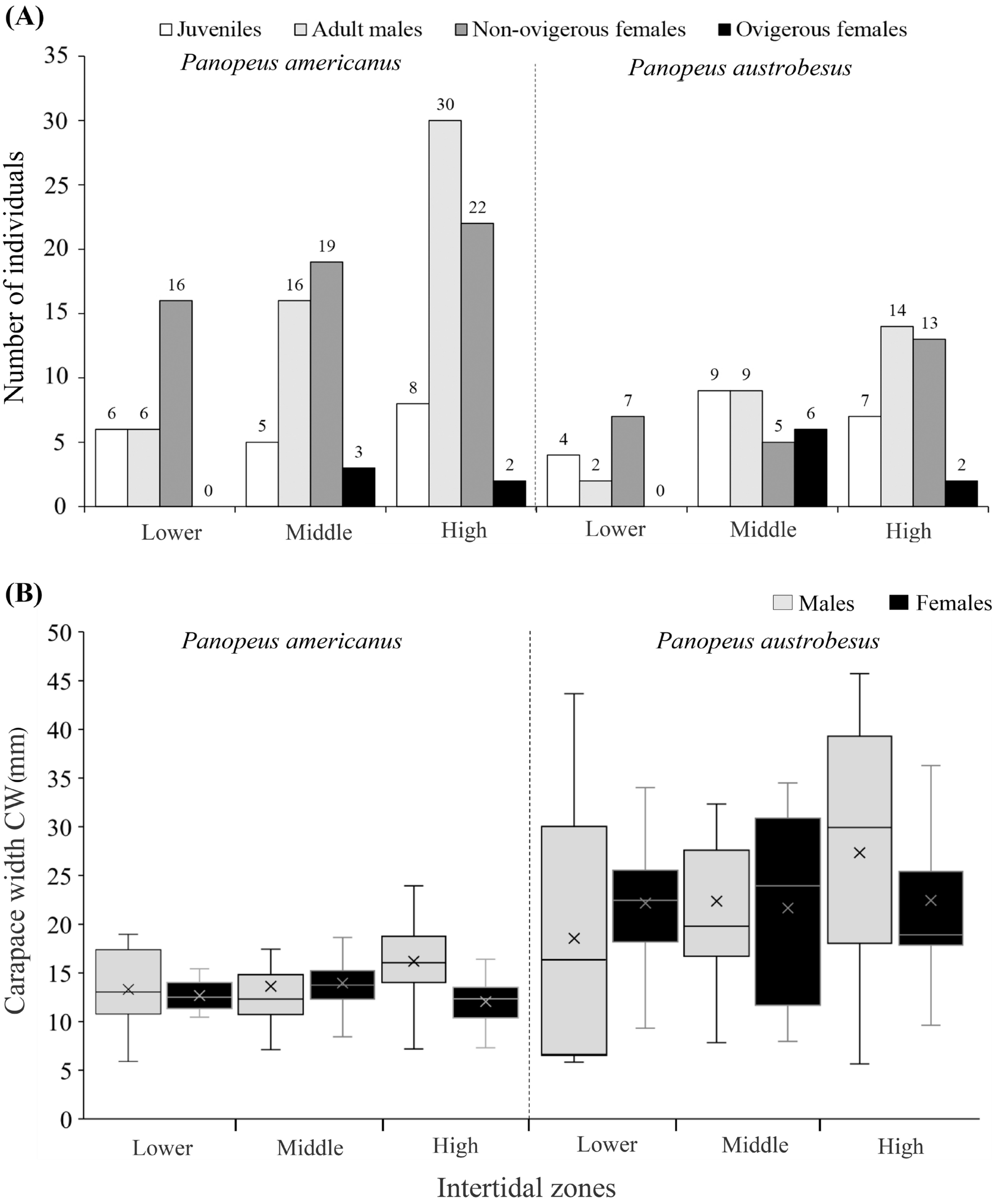

Figure 4. (A) Spatial distribution of juveniles, males, non-ovigerous females and ovigerous females of *Panopeus americanus* and *Panopeus austrobesus* in the intertidal zones in the estuarine complex of Cananeia, São Paulo, Southeastern Brazil. (B) Minimum, maximum (whiskers), median (horizontal lines) and mean (x) of the CW of both species are also plotted.

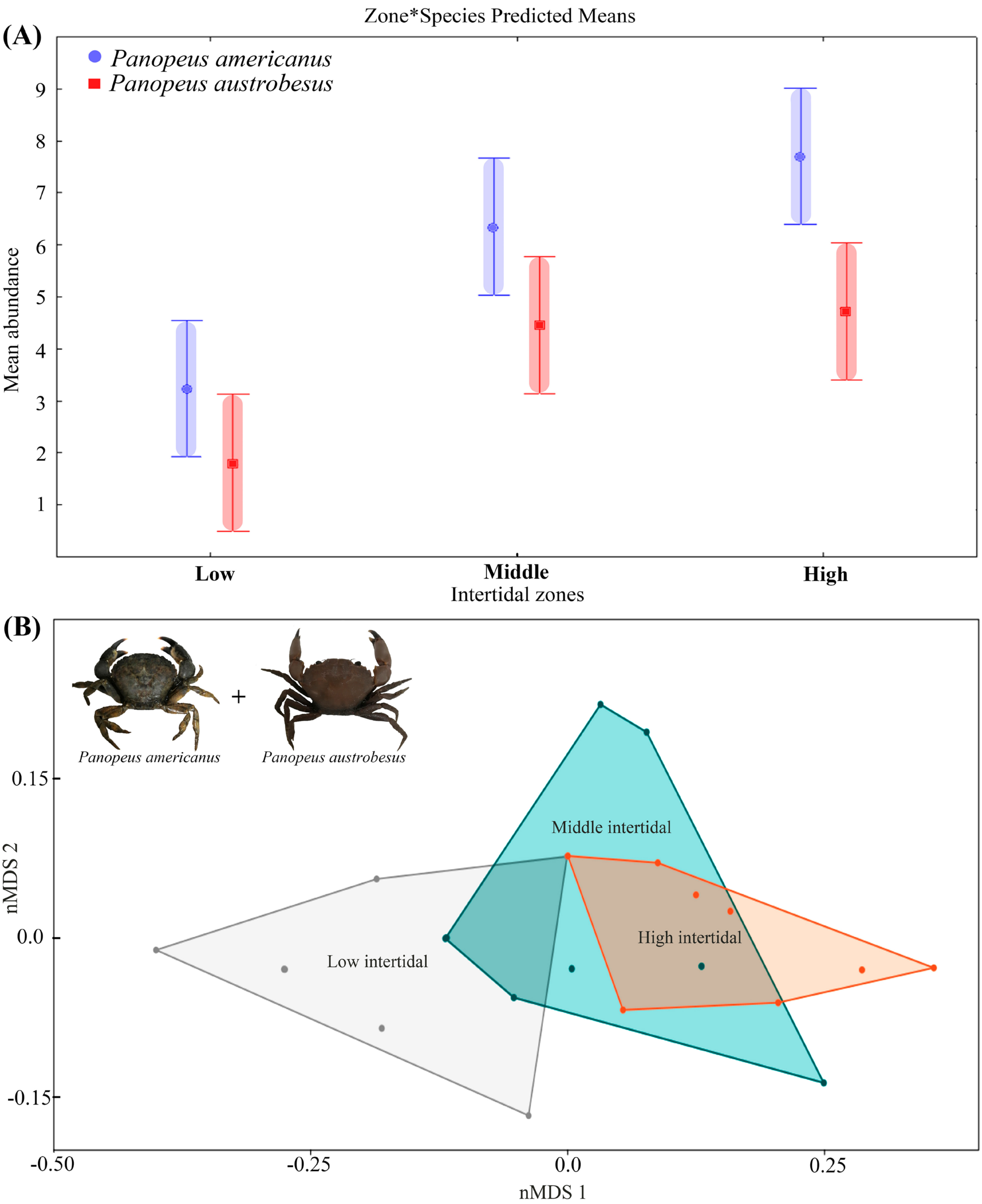

Figure 5. (A) Generalized linear models (GLM) showing the relationship between the mean abundance of *Panopeus americanus* and *Panopeus austrobesus* in the spatial (zones) scale. (B) Non-metric multidimensional scaling (NMDS) showing the distribution of grouped species in the intertidal zones.

(2018), *P. americanus* presents continuous reproduction, whereas *P. austrobesus* (assessed as *P. occidentalis*) presents seasonal reproduction between September and March – our results corroborate these authors' observation. Considering both species have similar spatial distribution, the following question arises: How can one explain their interspecific coexistence? The explanation for this factor may lie on poorly-explored niche features that go beyond temporal and spatial distribution aspects. Niche specializations can happen in the least obvious ways, such as varying activity patterns (Albrecht and Gotelli 2001). Although the diet of other panopeid crabs includes barnacles, oysters, mollusks and other crabs (Guida 1976, Brown and Haight 1992, Milke and Kennedy 2001), unfortunately, no data are available about the natural diet of *P. americanus* nor *P. austrobesus*. Certainly, the pattern of spatial distribution observed in the present study may be associated with different diet and/or food of different sizes, as their body size is quite different.

The pronounced disparity in size of the two species suggests divergent dietary preferences, potentially related to prey size, in this syntopic setting. It is conceivable that *P. americanus* predominantly preys upon smaller organisms, whereas *P. austrobesus*, prey larger items. While direct dietary analysis was not conducted in this study, the observed size variation is indicative of potential dietary specialization based on prey dimensions. The substantial difference in average size between the two species, and consequent consumption of prey of differing sizes, likely contributes significantly to their coexistence within the middle and high intertidal zones. A study on the diet of both species, as well as a morphological analysis on the mouth morphology and size of structures related to feeding habit, could confirm the difference in feeding between the species studied here.

Another aspect to be evaluated would be different reproductive traits. Peres et al. (2018) reported that sympatric congeneric species can adopt life history strategies to avoid competition and to enable coexistence, such as females from the same area that do not share same reproductive features. According to results by Peres et al. (2018), *P. americanus* has shown higher fecundity and reproductive output, as well as smaller embryo size, than *P. austrobesus.* Certainly, these contrasting characteristics allow these two populations from Cananeia estuarine complex to share the same habitat.

Based on the current findings, the different demographic categories followed the same spatial distribution of the species. The coexistence of ovigerous females of both species corroborates the results observed by Peres et al. (2018), according to whom, different reproductive traits may be mainly accountable for avoiding juvenile competition.

The spatial distribution pattern observed in the present study may be also correlated to availability of cracks and refuges amongst boulders and gravels, as well as to the presence of other decapods in the intertidal zone, as shown by Generalized linear models (GLM) and Non-metric multidimensional scaling (NMDS). In the study site, rocks are exposed to the air during low tide periods (See Figure 2A-B), but certainly small water puddles around them provide refuge an immediate water to *Panopeus americanus* and *P. austrobesus*.

Mud crabs are not the only organisms using these habitats throughout the intertidal zone. *Alpheus* snapping shrimps were observed in high abundance during collection procedures in the present study (data not shown), mainly in the low intertidal zone. Previous studies focused on alpheid shrimps in this same area have shown that many of them inhabit the same intertidal zone, but in highest abundance in the low intertidal zone (Pescinelli, pers. obs.). Thus, *Panopeus* predominance in the middle and high intertidal zones may be a strategy to avoid competition for space with alpheid shrimps. *Alpheus brasileiro* (Pescinelli et al. 2017, 2018) and *Alpheus carlae* (Ghizelli-Fraga et al. 2021) were the most abundant snapping shrimp species found in the study site, whereas *Alpheus buckupi*, *Alpheus petronioi* and *Alpheus estuariensis*, the least abundant (Almeida et al. 2018). Pescinelli et al. (2017) conducted a study on social monogamy of *A. brasileiro* in this same area and observed male and female individuals living together in the same space, besides their high territorialism and territorial defense (Mathews 2002). This behavior and the strong weaponry of these shrimps are factors likely influencing *Panopeus* species' distribution in the intertidal zone. In addition, species of the genus *Panopeus*, as *P. americanus* studied by Carvalho-Batista et al. (2015) show evidences of cryptic/non-cryptic color pattern in males and females and relationships to morphological and functional sexual maturity, which is another variable in the life strategy in this complex intertidal system.

Considering that studied populations of *P. americanus* and *P. austrobesus* coming from Cananeia mangrove and from São Sebastião Channel show the same pattern of spatial distribution in the intertidal zone, certainly, biological factors such as competition, reproductive trait and social organization are stronger that physical features in determining such pattern. Cananeia mangrove is one of the five least degraded and most productive estuaries worldwide (Schaeffer-Novelli et al. 1990), and it is supposed that it provides abundant food resources and diverse habitat refuges. In contrast, São Sebastião Channel is in frequent influence of water pollution and urban development.

On top of that, the availability of refuges can also be a decisive factor in the investigated intertidal zone. Rocks distributed throughout the intertidal zone, as well as their use as refuge by crabs and snapping shrimp species, creates a scenario featured by high competition for space, which is essential to enable species survival. This refuge not only provides protection from desiccation, but also from nekton predators during the high tide, as well as from birds and other predators during the low tide.

The hypothesis of species coexistence within intertidal zones, although with different abundance was confirmed. Furthermore, differences in the crabs' mean size were observed. Despite the similarity in space occupied by each species, the current findings have suggested that different activity patterns, such as divergent dietary preferences, allow the same distribution of crabs. Due to the great importance of Cananeia mangrove, data on crab populations living in the intertidal zone are essential to help monitoring this ecosystem. Thus, the current findings on the distribution and abundance of sympatric mud-crab species *P. americanus* and *P. austrobesus* can be used as indicators to help detecting and assessing disturbances in this important ecosystem.

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Author Contributions

Gabriel L. Saraiva: led the writing and analyzed the data; read and approved the final manuscript.

Leonardo Moreira: led the writing and analyzed the data; read and approved the final manuscript.

Fernando L. Mantelatto: participated in revising of the manuscript; read and approved the final manuscript.

Rogerio C. Costa: conducted the fieldwork sampling; participated in revising of the manuscript; read and approved the final manuscript.

Régis A. Pescinelli: led the writing and analyzed the data; conducted the fieldwork sampling; participated in revising of the manuscript; read and approved the final manuscript.

Conflicts of Interest

The author(s) declare(s) that they have no conflict of interest related to the publication of this manuscript.

Ethics

The present study was conducted in compliance with current Brazilian laws; specimens were obtained under collection permits (permanent license to RCC for the collection of Zoological Material N. 23012-1 MMA/IBAMA/SISBIO and SISGEN AE942E3).

Data Availability

Supporting data are available at <https://doi.org/10.48331/scielodata.T4SALV>.

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