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ORIGINAL PAPER

Population density and habitat use of the yellow land crab *Johngarthia lagostoma* on the remote Trindade Island, Brazil: implications for island conservation

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Abstract

Several land crab species inhabit oceanic islands worldwide, where they often dominate terrestrial arthropod communities, and act as ecosystem engineers. In the South Atlantic, *Johngarthia lagostoma* is the only gecarcinid species, endemic to Rocas Atoll, Fernando de Noronha, Ascension, and Trindade. Despite its classification as 'Endangered', there is a gap in knowledge on the spatial and temporal distribution of this species. Here, we investigated the population density and habitat preferences of *J. lagostoma* on Trindade Island, Brazil, examining the influence of dune vegetation sectors, diel activity, and environmental variables (elevation, relative humidity, and distance from the sea). Crabs were sampled weekly across three vegetated dune areas during both day and night, over eight weeks. No significant variation in sex ratio or size was detected among areas, although males were consistently larger than females. Crab density varied significantly with vegetation dune sector and diel period. Daytime density was highest in intermediate areas where two plant species co-occurred, and crabs remained sheltered, whereas nighttime density increased closer to the shoreline during feeding activity. Elevation, humidity, and mean carapace width were positively associated with density during the day, explaining 42% of the variation in the use of vegetation for shelter. These findings highlight the importance of dune vegetation and abiotic conditions in shaping the spatial ecology of *J. lagostoma* on Trindade. By identifying habitat features that support high crab densities, this study provides insights for conservation planning and restoration actions on oceanic islands, emphasising the need to protect vegetated areas as key habitats for endangered species.

Keywords Gecarcinidae · Vegetation structure · Diel activity patterns · Insular ecosystems · Tropical oceanic islands · Conservation biology

Introduction

Land crabs of the Gecarcinoidea are commonly found on tropical oceanic islands and coastal continental habitats, and are recognised as key ecosystem engineers (Green 1997; Paulay and Starmer 2011), with numerous discoveries and phylogenetic relationships still being elucidated in recent research (Guinot et al. 2025; Guinot and Rodríguez Moreno 2026). On some islands, they may even occupy top trophic positions (Andrades et al. 2019). Their ecological importance on oceanic islands stems from their high relative abundance and their role in processing plant biomass (Green 1997), which accelerates organic matter decomposition (O'Dowd and Lake 1989) and enhances nutrient cycling (Green et al. 1999). Their influence is amplified by a wide ecological range, as they are often abundant in these

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systems (Perger et al. 2013), typically inhabiting vegetated mountainous areas and migrating to coastal environments, like beaches, rocky shores and cliffs, for reproduction (Wolcott 1988; Hartnoll et al. 2009, 2014). Although primarily herbivorous, land crabs are opportunistic generalists, feeding on carrion (Linton and Greenaway 2007) and occasionally preying on vertebrates such as birds, rodents, and turtle hatchlings (Bright 1966; López-Victoria and Werding 2008; Faria et al. 2023), while also serving as prey for some animals, such as lizards and birds (López-Victoria et al. 2011; Villegas-Retana and Picado-Masís 2021), thereby acting as a key functional component of terrestrial food webs (Estupiñán-Montaño et al. 2023).

To understand the role of land crabs in insular ecosystems, population density is a key parameter for assessing dynamics and conservation status (Green et al. 1997). Population density estimation depends on behaviour and habitat use (Kent and McGuinness 2006), being calculated preferably based on absolute abundance of individuals (absolute density) (Warren 1990), but often requiring indirect methods such as counting visibly active individuals or their burrows (apparent density) (Macia et al. 2001; Skov et al. 2002). Species-specific traits are critical to avoid biased estimates (Carmona-Suárez 2011). Most gecarcinoids build burrows and show fidelity to them (Bright 1966; Green 2004; Moraes-Costa and Schwamborn 2018). However, some species of the genus *Johngarthia* Türkay, 1970, endemic to oceanic islands, exhibit low burrow fidelity and seek shelter in rock crevices or under vegetation (Pérez-Chi 2005; Tavares and Mendonça 2022; Entringer and Srbek-Araujo 2023), reducing the reliability of burrow counts for estimating their population parameters.

Apparent density can be influenced by several factors, including species behaviour and external environmental conditions, such as reproductive aggregations, temperature, humidity, and shelter availability (López-Victoria and Werding 2008; Doi et al. 2019). In addition to environmental conditions, variation in body size may be associated with density patterns, reflecting differences in habitat use, resource acquisition, and spatial distribution among individuals (White et al. 2007). Apparent density may also vary on a diel basis, as individuals seek shelter during harsh daylight hours to avoid environmental stress. In this context, vegetation influences aggregation by offering food and shelter from heat and predators (Jiménez et al. 1994; Green et al. 1999; Lindquist et al. 2009; Paulay and Starmer 2011), and higher daytime densities of crabs occur in dense arboreal vegetation like forests, especially during fruiting periods (Jiménez et al. 1994; Green 1997). Nocturnal and crepuscular habits also help minimise desiccation (Bliss 1979; Wolcott and Wolcott 1988; Hartnoll et al. 2006a), primarily in habitats where no forest cover is found. Therefore, different sectors of the system may represent a trade-off between shelter availability and exposure to environmental stress, with intermediate zones potentially providing more favourable microhabitat conditions, where local variation in temperature and humidity is expected to influence crab density.

Accordingly, apparent density during the nocturnal activity of land crabs may not reflect the total population size, but it reveals how these crabs move during their active phase, leaving daytime shelters and moving between habitats (Goshima et al. 1978; López-Victoria and Werding 2008). This difference in habitat uses between day and night, along coastal dune systems shaped by microclimate gradients, often includes movement toward beach sand and rocky shores in search of food, and can provide insights into the behavioural requirements of these crabs. Thus, understanding distribution patterns of species with low fidelity to specific shelters provides a broader perspective on how different sectors of vegetated dune systems are occupied.

In the South Atlantic, *J. lagostoma* (H. Milne Edwards, 1837) is the only oceanic island gecarcinid, recorded on four islands: three Brazilian (Fernando de Noronha, Rocas Atoll, and Trindade) and one British (Ascension) (Melo 1996; Hartnoll et al. 2006b). This species has a narrow distribution, with genetic structure suggesting three populations: Rocas–Noronha, Ascension, and Trindade (Rodríguez-Rey et al. 2016). Studies began on Ascension (Hartnoll et al. 2006b, 2009, 2010, 2017), but key population parameters, particularly population density, remain poorly known. Research in Brazil has expanded from early larval descriptions (Colavite et al. 2021; Lira et al. 2021) to studies on population biology and reproduction (Teixeira 1996; João et al. 2021, 2022, 2023, 2024; Pinheiro et al. 2024; Santana et al. 2025).

Johngarthia lagostoma is listed as "Endangered" in Brazil (Pinheiro and Boos 2016; MMA 2022), due to restricted range, habitat degradation mostly by human occupation, and interaction with invasive species, including herbivores that alter habitat structure through feeding (e.g., goats) and predators that actively prey on crabs (e.g., cats and rats), potentially affecting their distribution and disrupting trophic dynamics in insular ecosystems (Pinheiro et al. 2016). More recently this species was also included in the *IUCN Red List* as "Endangered", an evaluation largely based on recent data from Ascension Island, reinforcing the importance of population-level studies from other oceanic islands (Cumberlidge and Sharp 2025). However, conservation actions remain limited or poorly documented for some populations, partly due to data gaps, especially on density in insular habitats (Pinheiro et al. 2016). Density estimates underpin population size and are important for reassessing extinction risk and detecting trends (IUCN 2024). In this context, understanding density and environmental drivers is essential for conservation (Pinheiro et al. 2016), particularly on Trindade

Island, a priority area due to low human impact, strong crab populations, and genetic isolation, which may increase vulnerability (Rodríguez-Rey et al. 2016).

This study aimed to examine the spatial patterns in the density and habitat use of *J. lagostoma* along a coastal dune gradient on Trindade Island, considering both daytime (sheltering phase) and nighttime (active phase) periods. By contrasting daytime and nighttime densities, we aimed to assess shifts in habitat use along the dune gradient associated with sheltering and foraging movements. Specifically, we evaluated how crab density varied across sectors of the vegetated dune system and how, during the daytime sheltering phase, this spatial distribution was related to environmental conditions such as temperature, relative humidity, elevation, and distance from the shoreline. We hypothesized that: (1) daytime density would be higher in intermediate vegetated dune sector, where environmental conditions may provide a balance between shelter availability and exposure to thermal and desiccation stress; (2) daytime density will increase in cooler and more humid microhabitats along the dune gradient; and (3) during nighttime activity, crabs would shift their distribution toward lower vegetated dune sectors, closer to the shoreline, reflecting movement away from daytime shelters toward foraging areas.

Materials and methods

Study area

Trindade Island (20° 30′ 18″ S, 29° 18′ 27″ W) is the easternmost territory of Brazil, located in the Atlantic Ocean, approximately 1,140 km off the Brazilian coast (Fig. 1A). The island has a total land area of 13 km^2 (Nogueira et al. 2020) (Fig. 1B). It is of volcanic origin, with an estimated age of 3.9 million years, and features a rugged terrain composed of escarpments, valleys, and plateaus. Its highest point is Desejado Peak, which reaches 612 m above sea level (Clemente et al. 2018). The local climate is tropical oceanic, with a mean annual temperature of 25.3 °C (Pedroso et al. 2018). Trindade Island lacks significant arboreal vegetation, unlike many other oceanic islands, largely due to severe environmental degradation following the introduction of feral goats in the 1700s (Alves 1998). This process resulted in extensive desertification and a drastic reduction of native vegetation cover, particularly of *Colubrina glandulosa*, which formerly occupied 85% of the island (Alves 1998). However, all feral goats were successfully eradicated in 2005, and there are currently no large terrestrial herbivores, either wild or domestic, in the island, and efforts have been made to recover the island environment (Alves 1998; Martins et al. 2021).

Andradas Beach was selected due to its importance in the life cycle of *Johngarthia lagostoma*, particularly as a reproductive site, where mating (João et al. 2021), abundance of ovigerous females, spawning (João et al. 2024), and recruitment (Pinheiro et al. 2024) have been previously recorded. Sampling was restricted to the vegetated dune system of the beach, which represents relatively natural environments on Trindade Island. Areas adjacent to the Trindade Island Oceanographic Research Station (POIT) were deliberately avoided due to the presence of buildings, artificial lighting, and exotic tree species, which could influence crab behaviour.

The vegetated dune system of Andradas Beach forms a clear coastal gradient characterized by increasing elevation and distance from the shoreline. Soils are sandy and well-drained, developed under strong marine influence, high salinity, and intense wind exposure, which limit the establishment of woody vegetation and favour herbaceous plant communities (Clemente et al. 2009). As a result, the dune vegetation is composed exclusively of two species: *Canavalia rosea* (Fabaceae), a creeping vine that predominates in lower dune sectors; and *Cyperus appendiculatus* (Cyperaceae), which gradually replaces the former further inland, becoming dominant along the slope of Príncipe Hill, where it forms dense tussocks toward higher dune areas.

Based on this vegetation gradient, three sampling areas (A1 to A3) were established for comparison (Fig. 1C&D): the upper vegetated dune sector (A1) located near the slope of Príncipe Hill, 150 m from the shoreline and dominated by *Cyperus appendiculatus*; the intermediate vegetated dune sector (A2) located 120 m from the shoreline and composed of both *Canavalia rosea* and *Cyperus appendiculatus*; and the lower vegetated dune sector (A3) located 80 m from the shoreline and characterized by the presence of *Canavalia rosea*. Approximate total surface areas were ~ 6,000 m^2 for A1 and A2 and ~ 12,000 m^2 for A3, reflecting the broader and flatter extension of the lower dune sector.

Population sampling and analysis

In each of the three areas, eight fixed sampling units (2 × 2 m quadrats; 4 m^2 each) were established at least 5 m apart and surveyed one time per week during April and May 2022 (n = 8 weeks). In total, 24 quadrats were surveyed each week (7 days apart), during peak daylight hours (8:00 to 14:00), when the animals remain sheltered, and during the night of the same day (21:00 to 23:00), when crabs are most active. Because only 32 m^2 were sampled per sector (less than 1% of total area) and *J. lagostoma* is mobile, repeated measurements of some individuals across weeks cannot be completely ruled out. However, the limited spatial coverage and the species' movement patterns suggest that any re-sampling

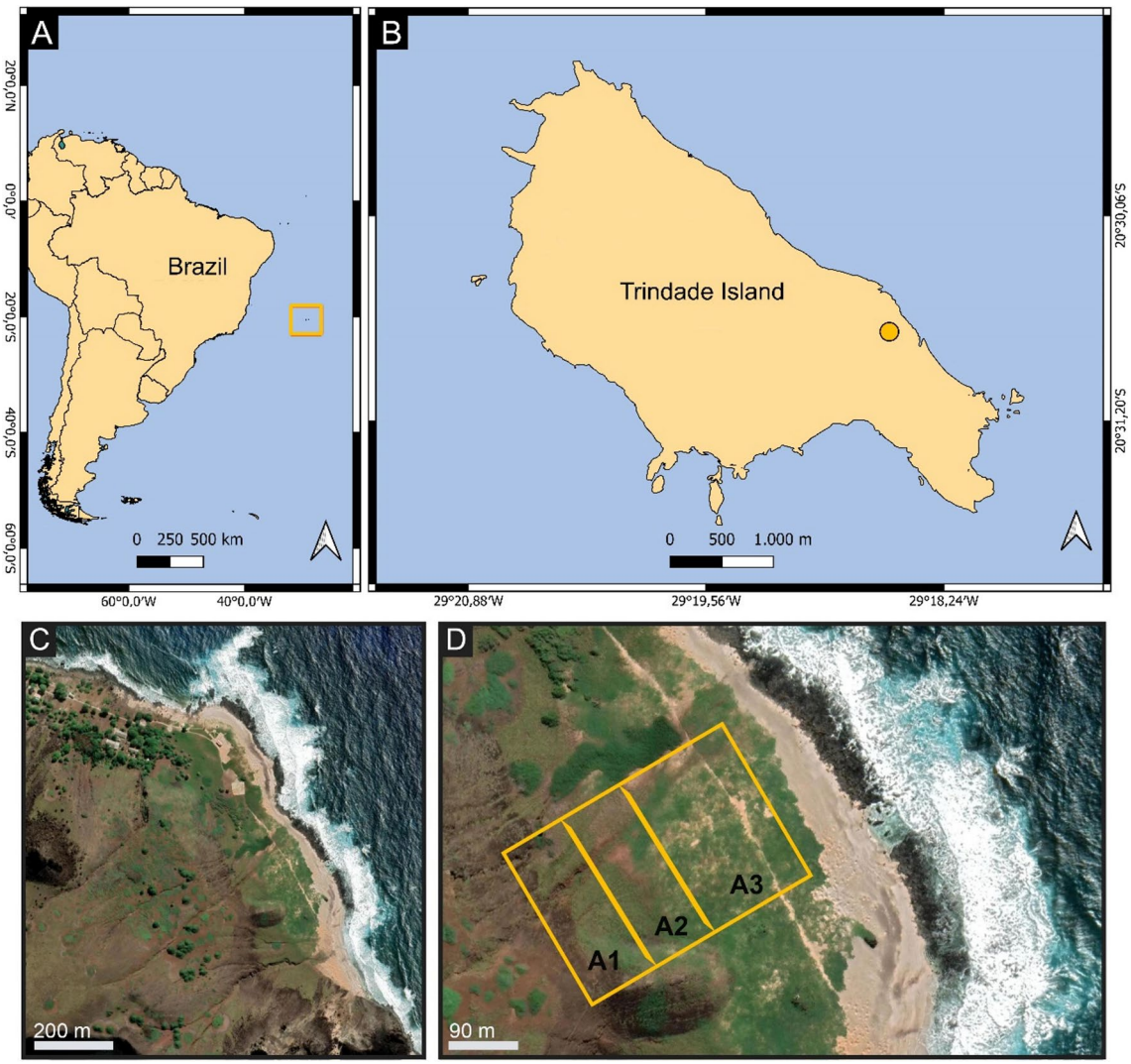

Fig. 1 Geographic location and habitat characterisation of the study site. (**A**) Trindade Island (yellow box) in relation to the Brazilian coast; (**B**) Andradas Beach sampling site (yellow dot); (**C**) Aerial view of Andradas Beach; (**D**) Delimitation of vegetation zones: Area 1 (A1), dominated by *Cyperus appendiculatus*; Area 2 (A2), with both *C. appendiculatus* and *Canavalia rosea*; and Area 3 (A3), characterised by *C. rosea* only. These zones differ in plant species composition and structural complexity, providing distinct shelter and foraging opportunities for *Johngarthia lagostoma*

is unlikely to substantially affect population-level estimates of size structure and sex ratio. Because of marked diel differences in behaviour, distinct sampling approaches were used in each period (see below), resulting in measures of absolute (daytime) and apparent (nighttime) density. The population sampling of *J. lagostoma* requires specific procedures due to its marked behavioural differences between day (more cryptic) and night (more active) periods (Hartnoll et al. 2006b). Because individuals are not permanently marked and quadrats were repeatedly sampled over time, the study was designed to characterise population-level spatial patterns rather than individual-based trajectories.

During daytime surveys, each quadrat was carefully inspected to detect all individuals, including those occupying burrows, which were manually captured and briefly held in plastic containers until carapace measurements and sex identification were completed, then released as soon as possible before moving to the next quadrat. It is important to highlight that few burrows were found, and when found, these burrows were shallow and easy to capture crabs from without destroying them; most individuals were hidden under plant litter or partially buried among the roots (see Fig. 2A-B). This active search was necessary due to the cryptic behaviour of the species, which makes observation difficult without sifting through the leaf litter, thus providing a direct estimate of density.

All captured individuals during the daytime were sexed based on pleonal morphology and the number of pleopod

Fig. 2 Habitat use and activity patterns of *Johngarthia lagostoma* in vegetated dune areas of Trindade Island. (**A**–**B**) Individuals observed during daytime surveys, sheltered under vegetation, within leaf litter, and among roots of *Cyperus appendiculatus* (photographs by Marcio João). (**C**–**D**) Actively moving crabs during nocturnal surveys, observed on *Canavalia rosea* and surrounding substrate (photographs by Nicholas Kriegler)

pairs (males: subtriangular abdomen with two pleopod pairs on the 1st and 2nd somites; females: semi-oval abdomen with four pleopod pairs from the 2nd to the 5th somites). Each individual was also measured for carapace width (CW), using a mechanical calliper with 0.05 mm precision. After measurements and recording, all crabs were released at the exact point of capture, where they readily hid under vegetation, thus avoiding sampling bias in subsequent surveys by artificial crab translocation. Because *J. lagostoma* is known to exhibit low burrow fidelity and does not maintain permanent burrows, brief handling of individuals during daytime surveys is unlikely to have affected their natural spatial distribution. This approach therefore allows the investigation of broader spatial distribution patterns rather than movements of specific individuals.

Additionally, to assess whether crab distribution varied with diel periodicity (day vs. night), each quadrat was also surveyed at night (21:00 to 23:00 h) on the same dates as the daytime collections. During these nocturnal visits, actively moving crabs were counted by direct observation on the substrate and vegetation (Hartnoll et al. 2009). At this time, we did not handle or collect crabs to minimise interference with the natural behaviour, in contrast with daytime when crabs remain inactive (see Fig. 2C-D). Red-light flashlights were used during nighttime sampling, due to the reduced sensitivity of crustaceans to this light spectrum (Cronin 1986). This provides a density estimate based on active individuals. This measure may (or may not) be a measure of total density at the time of survey (some crabs may remain hidden). It will be influenced by the degree of movement between sampling levels at night.

Sex and body size data obtained during daytime samplings were used to investigate potential spatial differences in the distribution of *J. lagostoma* across vegetated areas. Sex ratio was coded as a binary variable (males = 1; females = 0) and analysed using a generalised linear mixed model (GLMM) with binomial distribution and logit link function to assess differences among areas. Crab size (CW) was analysed using a GLMM fitted with a Gamma distribution and log link function, including area, sex, and their interaction as fixed effects, and sampling weeks as a random factor. This approach accounts for temporal dependence among observations collected within the same sampling week and accommodates the hierarchical structure

of sampling design (Bolker et al. 2009). Meanwhile, non-significant trends should be interpreted cautiously, as power in GLMMs can be limited by small sample sizes and unbalanced data structures (Johnson et al. 2015).

Both models were implemented using the *lme4* package (Bates et al. 2015), with sampling week included as a random effect to account for temporal variability. Sex ratio and body size analysis describe spatial differences in population structure among dune sectors and are not intended to infer individual growth or demographic rates. The significance of model terms was evaluated using the *Anova()* function from the *car* package (Fox and Weisberg 2019), and post-hoc pairwise comparisons were performed using the *emmeans* package (Lenth 2023), with *p*-values adjusted via Tukey's method. All statistical analyses were conducted in R (R Core Team 2024).

Density analysis

The density of *J. lagostoma* (individuals m^{-2}) was calculated based on the number of individuals captured in each sampling quadrat during the daytime, and the number of active individuals observed during the nighttime period. Even though these density measures are not always numerically equivalent, comparing the two metrics can provide insights into differential habitats use across diel periods.

To investigate the effects of vegetated dune gradient (three areas: A1, A2, A3) and diel period (day vs. night) on crab density, we used a generalised additive model (GAM) with a Tweedie distribution and a log link function, implemented with the *mgcv* package (Wood 2017). The model included fixed effects of area, period, and their interaction, as well as a smooth term to account for temporal variation across sampling weeks. Sampling week was included only to account for repeated measures and not to test for temporal effects. Density estimates are therefore model-predicted mean values (individuals m^{-2}), hereafter referred to as adjusted density, rather than raw observed counts, for each diel period and area.

Pairwise contrasts between combinations of factors were performed using multiple comparisons with the *emmeans* package (Lenth 2023), with *p*-values adjusted by the Tukey's method.

Environmental factors

To evaluate the potential effects of environmental factors on the daytime density of *J. lagostoma*, when using vegetated areas as shelter, mean values of air temperature (°C) and relative humidity (%) were obtained for each sampling plot using five thermo-hygrometers, positioned at the four corners and the centre of each quadrat. This procedure was repeated every survey, and used to estimate the mean values for each vegetated dune sector. Elevation and distance from mean sea level (m) were also recorded based on the central geographic coordinates of each quadrat, obtained using a Garmin® MAP70 GPS device and processed with Google® Earth® software.

Environmental variables, along with the mean carapace width of individuals, were used as predictors to explain variation in crab daytime density (dependent variable) across different dune sectors. All predictor variables were log-transformed [log(x + 1)] to meet assumptions of normality and homoscedasticity.

A multiple linear regression model was fitted using the base *lm()* function in R. Model selection was based on the Akaike Information Criterion (AIC), comparing candidate models including different combinations of the environmental predictors and mean carapace width (see Table 1). The best-supported model included elevation, relative humidity, and mean carapace width as explanatory variables.

A summary of the statistical approaches is as follows: sex ratio and carapace width were analysed using generalised linear mixed models (GLMMs) with appropriate link functions and distributions, including sampling week as a random effect. Crab daytime density was evaluated using a generalised additive model (GAM), and environmental predictors were tested using a multiple linear regression model, with model selection based on AIC. Details of each

Table 1 Results of candidate multiple linear regression models evaluating the influence of environmental variables on the daytime density of *Johngarthia lagostoma*

Predictor	Model 1	Model 2	Model 3	Model 4
Intercept	−9.13 ± 3.26 *	−8.08 ± 1.62 *	−8.51 ± 2.03 *	−1.91 ± 2.32
Distance	−0.28 ± 0.17	–	0.07 ± 0.15	–
Elevation	0.19 ± 0.06 *	0.14 ± 0.05 *	–	0.17 ± 0.05 *
Temperature	0.60 ± 0.59	–	–	−0.98 ± 0.42 *
Humidity	0.97 ± 0.29 *	0.79 ± 0.20 *	0.90 ± 0.21 *	–
Carapace width	1.19 ± 0.35 *	1.31 ± 0.35 *	1.28 ± 0.38 *	1.41 ± 0.37 *
AIC	59.57	**58.75**	67.62	68.03

Models included combinations of distance to sea, elevation, air temperature, relative humidity, and mean carapace width of individuals. Values represent regression coefficients (β ± standard error), with significance ($p < 0.05$) represented by *. Models were compared using Akaike's Information Criterion (AIC), and the most parsimonious model (lowest AIC) is highlighted in bold

model structure and implementation are provided in the corresponding sections above.

Results

A total of 698 *Johngarthia lagostoma* were sampled during daytime surveys, comprising 405 males and 293 females. Although males were generally more abundant (58.2%), the binomial GLMM (area as fixed effect; sampling week as random factor) did not detect differences in sex ratio among areas ($\chi 2_2 = 5.41$; $p = 0.067$).

Carapace width (CW) ranged from 20.5 to 105.7 mm in males (mean ± SD: 82.7 ± 14.2 mm) and from 23.8 to 102.4 mm in females (77.5 ± 15.1 mm). The size-frequency distribution of crabs considering all sampled individuals (Fig. 3A) and for each sampling sector (Fig. 3B) shows a negatively skewed distribution, illustrating that the sample is primarily composed of larger individuals. A Gamma GLMM with a log link indicated that males were significantly larger than females at population level ($\beta = 5.20 \pm 1.15$ SE, $t = 4.52$, $\chi 2_1 = 20.61$; $p < 0.001$). No significant differences in carapace width were detected among areas ($\chi 2_2 = 3.28$; $p = 0.194$), nor was there a significant interaction between sex and area ($\chi 2_2 = 2.13$; $p = 0.344$).

A generalised additive model (GAM) with Tweedie distribution and log link was fitted to model crab density as a function of area (A1 *vs*. A2 *vs*. A3), diel period (daytime density *vs.* nighttime density), and their interaction, including a smooth term for sampling week. The model-estimated density of *J. lagostoma* varied significantly among vegetated areas (GAM, $F = 69.0$, $p < 0.001$), between diel periods ($F = 8.8$, $p = 0.003$), and in their interaction ($F = 27.9$, $p < 0.001$) (Fig. 4). Compared with A1 (baseline), daytime density was significantly higher in A2 ($\beta = 1.847 \pm 0.181$ SE, $t = 10.22$, $p < 0.0001$) and A3 ($\beta = 0.680 \pm 0.205$ SE, $t = 3.31$, $p = 0.001$). Relative to the daytime period (baseline), density was lower at night ($\beta = -1.103 \pm 0.372$ SE, $t = -2.97$, $p = 0.0033$), with this reduction being more pronounced in A2 ($\beta = -1.328 \pm 0.407$ SE, $t = -3.26$, $p = 0.0012$). Conversely, nighttime density increased markedly in A3 relative to the daytime baseline ($\beta = 1.785 \pm 0.408$ SE, $t = 4.37$, $p < 0.0001$). The smooth term for sampling week was also significant (edf = 2.78, Ref.df = 2.96, $F = 47.76$, $p < 0.0001$), indicating consistent temporal variation in density throughout the sampling period. During

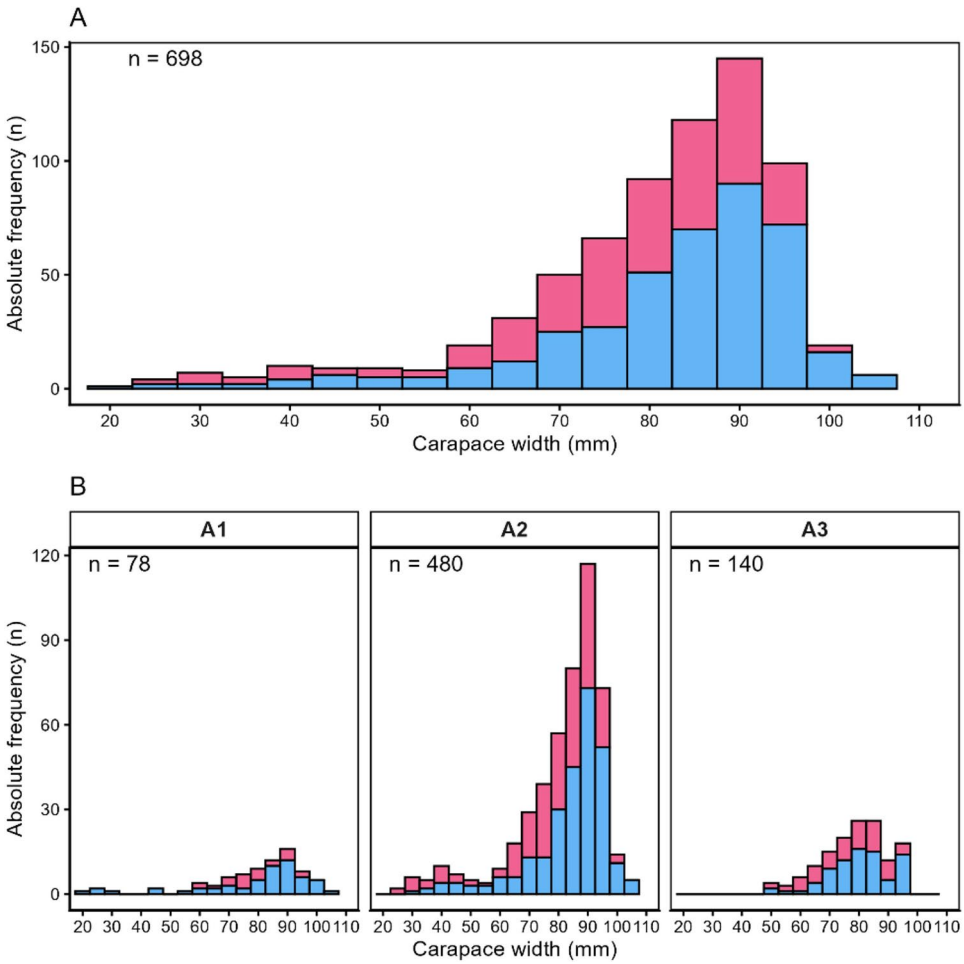

Fig. 3 Size-frequency distribution of the land crab *Johngarthia lagostoma*, separating males (blue) and females (pink), based on carapace width (CW) measured during daytime surveys at Andradas Beach, Trindade Island, Brazil. (**A**) Size-frequency distribution considering all sampled individuals pooled across sectors. (**B**) Size-frequency distributions for each sampling sector (A1, A2, and A3) within Andradas Beach. Histograms represent 5-mm CW classes, with tick marks on the x-axis shown at 10-mm intervals

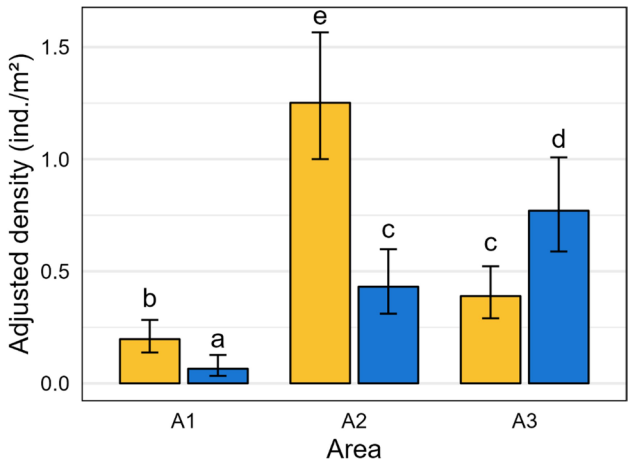

Fig. 4 Predicted *Johngarthia lagostoma* densities across vegetation zones and diel periods. Mean adjusted densities (individuals m^{-2}) from the generalised additive model (GAM) are shown for daytime (yellow) and night-time (blue) sampling. Error bars represent 95% confidence intervals (CI). Different letters above bars indicate statistically significant differences ($p<0.05$). The results show that crabs aggregated in the structurally complex vegetation of A2 during the day, but shifted towards the shoreline area (A3) at night

Table 2 Daytime air temperature and relative humidity across the three vegetated dune sectors (A1–A3)

Sector	Temperature (°C)		Relative humidity (%)	
	min–max	mean ± SD	min–max	mean ± SD
A1	26.1 – 42.6	32.9 ± 3.5	29.4 – 77.6	59.1 ± 10.1
A2	25.9 – 50.9	38.1 ± 4.6	25.6 – 77.6	48.0 ± 11.0
A3	29.0 – 44.4	35.2 ± 3.8	30.8 – 74.4	50.5 ± 11.4

the daytime, model-estimated density was highest in A2 (1.25 ± 0.14 individuals m^{-2}), followed by A3 (0.39 ± 0.06 individuals m^{-2}) and A1 (0.20 ± 0.04 individuals m^{-2}). At night, this pattern was reversed, with the highest density in A3 (0.77 ± 0.11 individuals m^{-2}), followed by A2 (0.43 ± 0.07 individuals m^{-2}) and A1 (0.07 ± 0.02 individuals m^{-2}).

Model comparison based on AIC (Table 1) indicated that the model including elevation, relative humidity, and mean carapace width provided the best fit to the data, outperforming alternative models that also included distance to sea and/or air temperature. The selected multiple linear regression model was significant ($F_{(3.59)}=15.86$, $p<0.001$) and explained approximately 42% of the variation in *J. lagostoma* daytime density (adjusted $R^2=0.418$). The intercept was significantly negative ($\beta_0=-8.083\pm1.622$ SE, $t=-4.99$, $p<0.001$). Crab density showed a positive relationship with all predictors: elevation ($\beta=0.145\pm0.048$ SE, $t=3.03$, $p=0.0037$), relative humidity ($\beta=0.793\pm0.200$ SE, $t=3.97$, $p<0.0002$), and mean carapace width ($\beta=1.306\pm0.350$ SE, $t=3.74$, $p<0.0004$). Across vegetated dune sectors, mean daytime air temperature was highest in A2 (38.1 ± 4.6 °C), followed by A3 (35.2 ± 3.8 °C) and A1 (32.9 ± 3.5 °C). In contrast, relative humidity was highest in A1 (59.1 ± 10.1%), and lower in A3 (50.5 ± 11.4%) and A2 (48.0 ± 11.0%) (Table 2). Consistently, the partial effects of the selected predictor (Fig. 5) show a clear positive increase in crab density with increasing elevation, humidity, and mean body size.

Discussion

Population structure and density patterns

The population of *J. lagostoma* at Andradas Beach was dominated by adults (> 56 mm CW; João et al. 2022) across all vegetated dune sectors, consistent with previous observations of mating, ovigerous females, and recruitment in this area (João et al. 2021, 2024; Pinheiro et al. 2024), reinforcing its role as a key reproductive site. Although sampling occurred at the end of the reproductive season, when ovigerous females were no longer observed, the predominance of large adults supports this interpretation. Although a slight male bias was observed, the sex ratio did not differ significantly from parity in our sample, which is consistent with previous studies on Trindade Island (João et al. 2024). This pattern differs from findings reported during the peak reproductive season (Hartnoll et al. 2010), when female mortality associated with reproductive migrations can lead to a statistically significant sex-ratio bias (Turner et al. 2011; Doi et al. 2019). Males were consistently larger than females, a general pattern in land crabs (Turner et al. 2011) and previously reported for *J. lagostoma* on Trindade and Ascencion islands (Hartnoll et al. 2009; João et al. 2023). Overall, population structure followed expected patterns and provides a consistent biological context for interpreting spatial and diel variation in density.

Daytime densities were highest in the intermediate vegetated dune sector (A2), whereas at night crabs concentrated in the lower dune sector near the shoreline (A3). Notably, the upper sector (A1), despite its denser vegetation and higher humidity, consistently supported lower densities across diel periods, suggesting that vegetation alone does not determine habitat use. This nocturnal movement likely reflects active movement across sectors, with individuals spreading into flatter and more accessible areas during foraging periods. This interpretation is supported by field observations of crabs moving across sandy substrates and using non-vegetated microhabitats, as well as aggregating around marine-derived food resources such as fish (*Melichthys niger*) and green-turtle (*Chelonia mydas*) carcasses, and occasional predation on hatchling turtles (Nicholas Kriegler, pers. obs.). Although foraging appears to be a primary driver of this redistribution, additional factors such as water balance

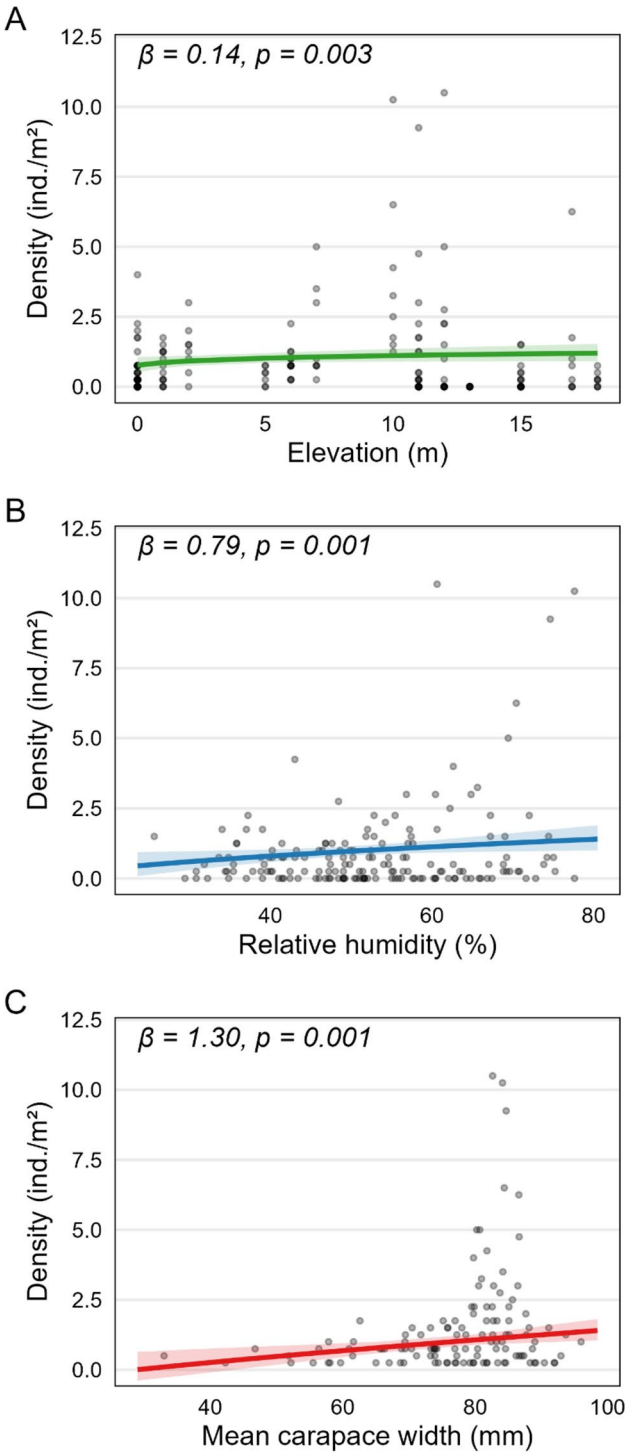

Fig. 5 Relationships between key environmental variables and *Johngarthia lagostoma* daytime density. Panels show partial effects from the multiple linear regression model relating crab density (individuals m^{-2}) to (**A**) elevation, (**B**) relative humidity, and (**C**) mean carapace width. Points represent individual sampling units (quadrats), solid lines represent model-predicted partial effects, and shaded areas indicate 95% confidence intervals. All predictors showed positive effects on crab density

may also be involved, as individuals may benefit from higher moisture availability in lower sectors. However, as sampling was restricted to vegetated dune areas, the extent to which adjacent habitats contribute to these movements remains uncertain.

At a broader spatial scale, *J. lagostoma* is distributed across the island during the reproductive season, from coastal zones to high elevations (up to 600 m above sea level), with previous studies reporting spatial segregation of life stages, where adults are concentrated in coastal reproductive areas and juveniles are more abundant inland (João et al. 2024). Although no natural predators of *J. lagostoma* adults occur on Trindade Island, some bird species may opportunistically prey on juveniles during daytime (López-Victoria and Werding 2008; Entringer and Srbek-Araujo 2023). While nocturnal activity is often associated with reduced exposure to visually oriented predators in other land crab species (Lavalli and Spanier 2015), this is unlikely to be a primary driver in this system. Competition appears limited, as the only other abundant species at Andradas Beach is the diurnal sally-lightfoot crab, *Grapsus grapsus*, primarily restricted to rocky shores (Gianuca and Vooren 2007), with only occasional overlap in transitional areas.

Gecarcinoid crabs are predominantly nocturnal, showing contrasting movement strategies, from burrow-centred site fidelity (e.g., *Cardisoma guanhumi*—Moraes-Costa and Schwamborn 2018) to high vagility and long-distance movements (e.g., *J. malpilensis*—López-Victoria and Werding 2008, and *Tuerkayana hirtipes*—Goshima et al. 1978). In this context, *J. lagostoma* appears to align more closely with highly mobile species, exhibiting extensive nocturnal movements and relying less on fixed refuges, which may reflect its use of spatially separated resources across dune and beach habitats. Burrow construction by *J. lagostoma* is uncommon on Trindade Island. During the day, individuals sheltered by partially burying in sediment or hiding under vegetation and within rock crevices (Tavares and Mendonça 2022), similar to *Gecarcinus ruricola*, which uses both burrows and alternative refuges associated with vegetation (Britton et al. 1982; Hartnoll et al. 2007; Rodríguez-Fourquet et al. 2025). This reduced reliance on permanent burrows likely contributes to greater mobility and continuous habitat use across the landscape in this species, reducing the need for large-scale migrations compared to more burrow-dependent gecarcinoids such as *Cardisoma* spp. and *Gecarcoidea* spp.

On Trindade, most *J. lagostoma* were found beneath vegetation, within leaf litter, and among the roots of *Cyperus appendiculatus*, the most abundant herbaceous plant on Trindade and Martim Vaz (Alves 1998). This pioneer species dominates the island's vegetation cover, colonising bare niches (Alves et al. 2011), so creating favourable

microclimates by reducing wind exposure and facilitating the establishment of other plants (Martins et al. 2021).

Despite the historical loss of forest vegetation caused by human occupancy, the vegetated dune system on Andradas Beach still provides important shelter and microclimatic buffering for *J. lagostoma*, particularly in the intermediate sector (A2), where *Cyperus appendiculatus* and *Canavalia rosea* co-occur. Crab aggregation appears to be associated not only to vegetation presence but also to plant richness and structural complexity, whether in clumps (grasses, creeping plants) or forests (arboreal species), which are critical for shelter and food (e.g., leaf litterO'Dowd and Lake 1989; Marin and Tiunov 2023). Although structural complexity was not quantified, the presence of both species in the intermediate sector (A2) increases habitat heterogeneity and refuge availability compared with sectors dominated by a single plant species. Juvenile *J. lagostoma* also co-habit shelters occupied by adults, particularly in vegetated areas, suggesting these microhabitats support both recruitment and adult survival (Pinheiro et al. 2024).

Vegetation can also influence burrow morphology and stability, as in the burrowing Chinese salt marsh crab, *Helice tientsinensis*, where plant species altered burrow architecture and microhabitat quality (Wang et al. 2015). Similarly, *H. tientsinensis* acts as an ecosystem engineer, enhancing soil properties and habitat quality (Qiu et al. 2019). On Socorro Island (Mexico), *J. planata* reached twice the densities in structurally complex vegetation, such as dense forests with high fruit availability (Jiménez et al. 1994).

Environmental drivers

Environmental factors shaped daytime shelter use, with higher densities in more humid areas, particularly A2, where larger individuals were also more frequent, although mean carapace width did not differ among areas. Unexplained variability likely reflects additional drivers not modelled here, such as fine-scale vegetation structure, shelter availability, and behavioural processes. Similar patterns have been reported for other land crabs, such as *Gecarcinus ruricola*, typically associated with shaded and humid coastal environments (Bigelow et al. 2025).

Elevation influenced *J. lagostoma* aggregation indirectly by modulating environmental conditions. Across the dune system, it is associated with changes in soil, exposure, and habitat structure that affect microclimatic conditions. Similar patterns have been reported for other decapods, such as *Ucides cordatus* (Saher et al. 2018) and *Hartnollius quadratus* (Griffiths et al. 2004). Despite its significant effect, elevation had a modest influence on density, with highest values in the intermediate dune sector (A2), indicating that local habitat conditions can override simple altitudinal gradients.

Relative humidity constrains land crab activity due to their dependence on moist branchial chambers for respiration (Marin and Tiunov 2023). Despite behavioural and physiological adaptations to reduce desiccation, terrestrial decapods remain associated with humid microhabitats (Wolcott 1992; Thurman 1998). Reduced daytime activity and shelter use minimize water loss, whereas nocturnal activity allows resource exploitation under less restrictive conditions (Bliss 1968; Morris 2002; McGaw et al. 2019).

The positive relationship between crab size and density observed here aligns with general patterns linking body size and abundance, although the specific nature of this relationship can vary depending on ecological context (White et al. 2007). Here, aggregations of larger individuals are likely facilitated by resource availability. Although plant material is abundant but low-quality (Wolcott 1988), nocturnal foraging expands access to animal-derived resources such as carrion (McGaw et al. 2019). Field observations (see Sect. "Population structure and density patterns") showed aggregation around marine-derived resources, with no evidence of agonistic behaviour, suggesting low interference competition.

The use of spatially and temporally variable resources highlights the trophic flexibility of *J. lagostoma*, which adjusts its feeding strategy according to local resource availability rather than occupying a fixed trophic position. This flexibility allows *J. lagostoma* to exploit both plant and animal-derived resources across habitats, consistent with isotopic evidence showing variable trophic position in island systems (Andrades et al. 2019). In insular environments, such behaviour likely enhances trophic connectivity between terrestrial and marine systems (Estupiñán-Montaño et al. 2023). Thus, beyond its role as an herbivore, *J. lagostoma* may act as an ecological connector linking detrital pathways and marine-derived resources to higher trophic levels. These patterns suggest that its success in terrestrial ecosystems is driven by the integration of multiple traits, including nocturnal behaviour, association with vegetation, and an omnivorous diet, rather than by a single specific adaptation.

Conservation implications

This is the first study to examine *J. lagostoma* population density and its relationship with environmental factors influencing distribution. Despite the history of environmental degradation on Trindade Island, dune vegetation proved crucial, serving as both food (Hartnoll et al. 2006b) and shelter from solar radiation, reducing desiccation risk. However, the vegetation remains structurally simple, with low

stature and limited litter accumulation, likely constraining organic matter retention and associated biota.

Despite such degradation, this association with vegetated zones likely influences soil organic carbon dynamics through sediment turnover and organic matter processing (Sherman 2006), consistent with the higher crab densities observed in vegetated sectors (particularly A2). Land crabs may also affect plant dynamics by predation on seeds and seedlings (Green et al. 1997; Lindquist et al. 2009), while seasonal variation in crab activity can reduce leaf litter availability and alter soil moisture and nutrient retention (Green et al. 1999; Lindquist et al. 2009).

Land crabs from the brachyuran families Gecarcinidae and Cardisomatidae, and the anomuran family Coenobitidae, are particularly abundant on tropical oceanic islands, where their success reflects the integration of behavioural, physiological, and ecological traits that facilitate the use of heterogeneous habitats. This success may be linked to reduced predation pressure, although island populations remain more vulnerable to disturbance (Paulay and Starmer 2011). On Trindade Island, where habitat structure is still simplified following past degradation, such vulnerability is especially relevant. Human occupation, habitat modification, and invasive species (e.g., rats and pigs) have been associated with population declines, as observed for *J. planata* on Clipperton Atoll (Pitman et al. 2005), and even local extinctions, such as *Geograpsus severnsi* in Hawaii (Paulay and Starmer 2011). Although information on invasive species impacts on *J. lagostoma* remains limited, competition and predation on juveniles are considered potential threats (João et al. 2023; Cumberlidge and Sharp 2025).

These findings support conservation measures prioritising vegetated zones, such as those at Andradas Beach. Given the association with *C. appendiculatus*, mapping and protecting areas with this species could indirectly support conservation. Data on *J. lagostoma* densities from other oceanic islands remain scarce. In Rocas Atoll, vegetation is sparse and dominated by *Cyperus*, whereas Fernando de Noronha retains only 5% of its original Atlantic Forest cover (Serafini et al. 2010; Claudino-Sales 2019), reinforcing the importance of vegetation structure and complexity for suitable habitats.

Although vegetation recovery is challenging, these findings support prioritising the conservation and restoration of vegetated beach-adjacent areas. Habitat management could also include small-scale interventions inspired by the engineering role of land crabs, mimicking microtopographic and sediment-disturbance effects generated by their activity. In other coastal systems, such modifications improve soil moisture, reduce salinity, and enhance habitat suitability for crabs, as demonstrated for the saltmarsh crab *Helice tientsinensis* (Qiu et al. 2019), suggesting similar process-based effects may occur in *J. lagostoma*, particularly in areas of higher crab density.

Although *J. lagostoma* does not rely exclusively on burrows, its sediment turnover and defecation may modify soil properties and improve habitat quality. Integrating habitat protection (e.g., preservation of dune sectors), restoration of native vegetation, invasive species control, and process-based management may therefore be particularly important for sustaining populations on oceanic islands.

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Author contributions Nicholas Kriegler: Conceptualization (lead); Methodology (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). Marcio João: Methodology (supporting); Writing – review and editing (equal). Richard Hartnoll: Writing – review and editing (equal). Marcelo Pinheiro: Conceptualization (supporting); Writing – review and editing (equal); Supervision (lead); Funding Acquisition (lead).

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Data availability Data will be made available on request.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Ethics approval Sampling activities were authorised under permit #65446, issued by the *Sistema de Autorização e Informação em Biodiversidade* (SISBIO).

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