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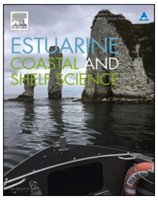

Multiscale variation in the burrow typology and abundance of *Ucides cordatus* across Atlantic mangroves: effects of time, space, and climate

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ABSTRACT

Understanding ecological processes across spatial and temporal scales is crucial for interpreting population dynamics and guiding conservation efforts. However, multiscale influences on decapod crustacean populations remain underexplored. We investigated the variability in *Ucides cordatus* burrow typologies across two protected Brazilian mangrove ecosystems: Juréia-Itatins Ecological Station (JIES) and Superagui National Park (SNP). Sampling involved 120 quadrats (5 × 5 m each), with five quadrats allocated to each mangrove zone (fringe and apicum) at both conservation units, during summer and winter seasons over three consecutive years (2016–2018). Generalised linear models tested the effects of year, season, site, and tidal zone on the abundance of five burrow types: SGL (single-opening), MLT (multi-opening), OPE (sum of SGL and MLT), CLO (closed), and ABD (abandoned). We observed marked interannual and seasonal variability, especially under climatic anomalies, along with spatial contrasts driven by tidal flooding patterns and microhabitat structure. Burrow types reflected distinct functional phases: SGL and MLT were linked to active behaviour and responded sharply to environmental variation; CLO was associated with reproduction or moulting; ABD indicated environmental stress or recolonisation. Fringe zones exhibited greater variability and reduced open burrow abundance under stressful conditions. Integrating burrow typologies with spatiotemporal factors proved an effective, non-invasive approach for detecting ecological shifts and assessing habitat quality. Our findings reinforce the role of *U. cordatus* as a bioindicator species and support the use of burrow-based metrics in the long-term monitoring and conservation of mangrove ecosystems facing increasing climatic and anthropogenic pressures.

1. Introduction

Mangrove forests are tropical and subtropical coastal ecosystems that serve as critical transitional zones between terrestrial and marine environments. These habitats provide a wide array of ecosystem services, including high primary productivity (Barbier et al., 2011), carbon sequestration (Rovai et al., 2018), shoreline stabilization (Gomes et al., 2025), and the maintenance of specialised and diverse biotic communities (Aquino-Thomas and Proffitt, 2025). Despite their ecological and economic importance, mangroves are increasingly subject to the impacts of climate change (Schaeffer-Novelli et al., 2016; Alongi, 2022), extreme weather events (Temmerman et al., 2023), anthropogenic disturbances (Duarte et al., 2016; Santos-Andrade et al., 2021), and microplastic pollution (Capparelli et al., 2025). Osland et al. (2025) emphasize that

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mangrove ecosystems, when subjected to increasing abiotic stress, may approach ecological thresholds beyond which rapid structural and functional changes can occur. Moreover, good recovery of mangrove functions after stressful conditions depends on key species, especially macrofauna that act as eco-engineers (Kristensen, 2008; Katharoyan et al., 2025).

Among the key species in these environments is the mangrove crab *Ucides cordatus* (Linnaeus, 1763), a semi-terrestrial brachyuran endemic to the Atlantic coast of the Americas and particularly abundant in Brazilian mangroves (Alves and Nishida, 2004; Pinheiro et al., 2018; Mota et al., 2023; Lima et al., 2023). As an ecosystem engineer (Marin and Tiunov, 2023), *U. cordatus* contributes significantly to habitat structure and functioning through its burrowing activity, which enhances soil aeration (Smith III et al., 1991; Pülmanns et al., 2014; Aller et al., 2024), facilitates the redistribution of organic matter and nutrients (Araújo-Júnior et al., 2016; Pereira et al., 2019; Sarker et al., 2020), and regulates biogeochemical processes (Koch and Wolff, 2002; Nordhaus et al., 2006; Kristensen et al., 2023). The species also plays a central role in detritus-based food webs (Pülmanns et al., 2016) and sustains small-scale fisheries, thus maintaining both ecological and economic relevance (Wolff, 2006; Mota et al., 2023). Given its multifaceted ecological role involving sediment properties, vegetation, and hydrology, *U. cordatus* is considered a reliable bioindicator of environmental change and stress responses, particularly under shifting climatic regimes (Osland et al., 2025).

The life history of *Ucides cordatus* depends on individual excavated burrows, which may exceed 1 m in depth and serve multiple ecological functions (Pinheiro and Fiscarelli, 2001; Nordhaus et al., 2009; Pinheiro et al., 2017). These structures provide shelter from predators (Fernandes et al., 2020), buffer individuals from temperature and salinity fluctuations (Pardo and Costa, 2021; Marin and Tiunov, 2023), offer refuges during moulting and reproduction (Wunderlich and Pinheiro, 2013; Kassuga and Masunari, 2015; Schmidt and Diele, 2024), and are used for storing organic material (Nordhaus et al., 2009; Araújo and Calado, 2012). Burrow morphology is highly variable, ranging from simple to complex, open or closed, or even abandoned, and is influenced by crab size, life stage, and behavioural traits (Wunderlich et al., 2008; Schmidt and Diele, 2009; Diele and Koch, 2010; Pinheiro et al., 2023). As proposed by Osland et al. (2025), this morphological variation may reflect not only ontogenetic stages and behavioural patterns, but also ecological shifts associated with threshold dynamics under cumulative environmental stress.

Environmental factors such as salinity, sediment characteristics, vegetation cover, and tidal regime shape burrow abundance and typology (Gomes et al., 2013; Michaud et al., 2024). Accordingly, burrow monitoring has become a widely used, non-invasive tool for estimating crab density, activity patterns, and ecological responses. It is increasingly adopted in conservation and management initiatives (Pinheiro and Almeida, 2015; Pinheiro et al., 2023; Leite et al., 2024; Pinheiro, 2025a). Incorporating burrow typologies into long-term monitoring efforts provides an effective means to detect early signals of climate-driven transformations in mangrove ecosystems, particularly those involving spatial-temporal variability.

Previous studies have demonstrated that temporal (e.g., interannual climate variability), seasonal (e.g., dry vs. wet seasons), spatial (e.g., fringe vs. inner zones), and regional (e.g., site-specific characteristics) factors influence the distribution of *U. cordatus* populations (Sandrini-Neto and Lana, 2012; Wunderlich and Pinheiro, 2013; Mota et al., 2023). However, comprehensive multiscale (i.e., fine- and larger-scale) investigations that address these dimensions simultaneously, particularly those integrating burrow typology as an indicator of population dynamics and habitat use, remain little explored. Integrating the concept of ecological thresholds into such multiscale frameworks may enhance our ability to anticipate when mangrove systems are approaching critical resilience boundaries due to ongoing climate change (Osland et al., 2025). Therefore, using burrow morphology can help better understand changes in crab population dynamics under a scenario of constant environmental impacts on Neotropical mangroves (Lacerda et al., 2019).

In this study, we examine how burrow abundance and typology vary across multiple ecological scales in two protected mangrove ecosystems located along the southeastern and southern coasts of Brazil: the Juréia-Itatins Ecological Station (JIES), a state-managed conservation unit in São Paulo State, and the Superagui National Park (SNP), a federally managed conservation unit in Paraná State. We evaluate the effects of fine and larger scales, such as year (2016, 2017, and 2018), season (summer vs. winter), site (Juréia vs. Superagui), and tidal mangrove zone (fringe vs. transition) on crab distribution and density. We hypothesise that variation in year, season, site, and tidal mangrove zone significantly influences the burrow typology of *Ucides cordatus* populations. We also expect to identify the primary drivers shaping burrow patterns and to provide an integrated framework for interpreting ecological processes that support effective conservation strategies in mangrove environments, which are increasingly subjected to environmental stressors.

2. Materials and methods

The study was carried out in two estuarine mangrove areas located along the western Atlantic coast, within protected regions in southeastern Brazil (São Paulo State, SP) and southern Brazil (Paraná State, PR) (Fig. 1A). The first site is located within the Juréia-Itatins Ecological Station (JIES: 24°26′00″S; 47°05′58″W), in the municipality of Peruíbe (SP), which is influenced by the Una do Prelado River Estuarine System. This area is managed by the São Paulo State Forestry Foundation (SÃO PAULO, 1987; FF, 2020) and has a reduced human population (Oliveira, 1993; Duarte et al., 2016). The second site is located in Superagui National Park (SNP: 25°18′33″S; 48°10′10″W), in the municipality of Guaraqueçaba (PR), and falls within the boundaries of the Environmental Protection Area (EPA) of the Paranaguá Estuarine System. It is administered by the Chico Mendes Institute for Biodiversity Conservation (BRASIL, 1989; ICMBio, 2020), with traditional communities living from artisanal fishery (Betti, 2014). Both sites are located within the Atlantic Forest biome that includes mangrove ecosystems under formal conservation regimes, with strict restrictions on the direct use of natural resources due to their classification as strictly protected areas (BRASIL, 2000).

Although both areas share a protected status, they differ markedly in the use of the mangrove crab *Ucides cordatus* (Fig. 1-B): in JIES, the species is not exploited, and only a small resident human population is present (Duarte et al., 2016), whereas in SNP, harvesting is practised by the local traditional fishing community (Gonçalves et al., 2022). This contrast offers a valuable framework for evaluating the natural population dynamics of *U. cordatus* under distinct conservation and management regimes.

2.1. Mangrove sites: zonation and environmental settings

Davies (1964) classified regions with mean syzygy tide amplitudes below 2 m as microtidal. This classification applies to both study sites (JIES: southeastern; and SNP: southern), separated by approximately one degree of latitude. Within each site, two mangrove zones (fringe and apicum – Fig. 1-C and 1-D, respectively) were sampled based on their contrasting tidal flood levels and frequencies. In each zone, a 100 × 50 m area (5000 m^2) was established with its longer side oriented parallel to the estuarine margin, where sampling units were randomly arranged (see sampling design, Fig. 1-E).

Both study sites exhibit distinct environmental characteristics (Pinheiro, 2020). At JIES, the arboreal mangrove forest exhibited marked zonation, with *Rhizophora mangle* L. dominating the fringe zone (86.4 %) and *Laguncularia racemosa* (L.) prevailing in the apicum zone (82.7 %). In contrast, forest structure at SNP is consistently dominated

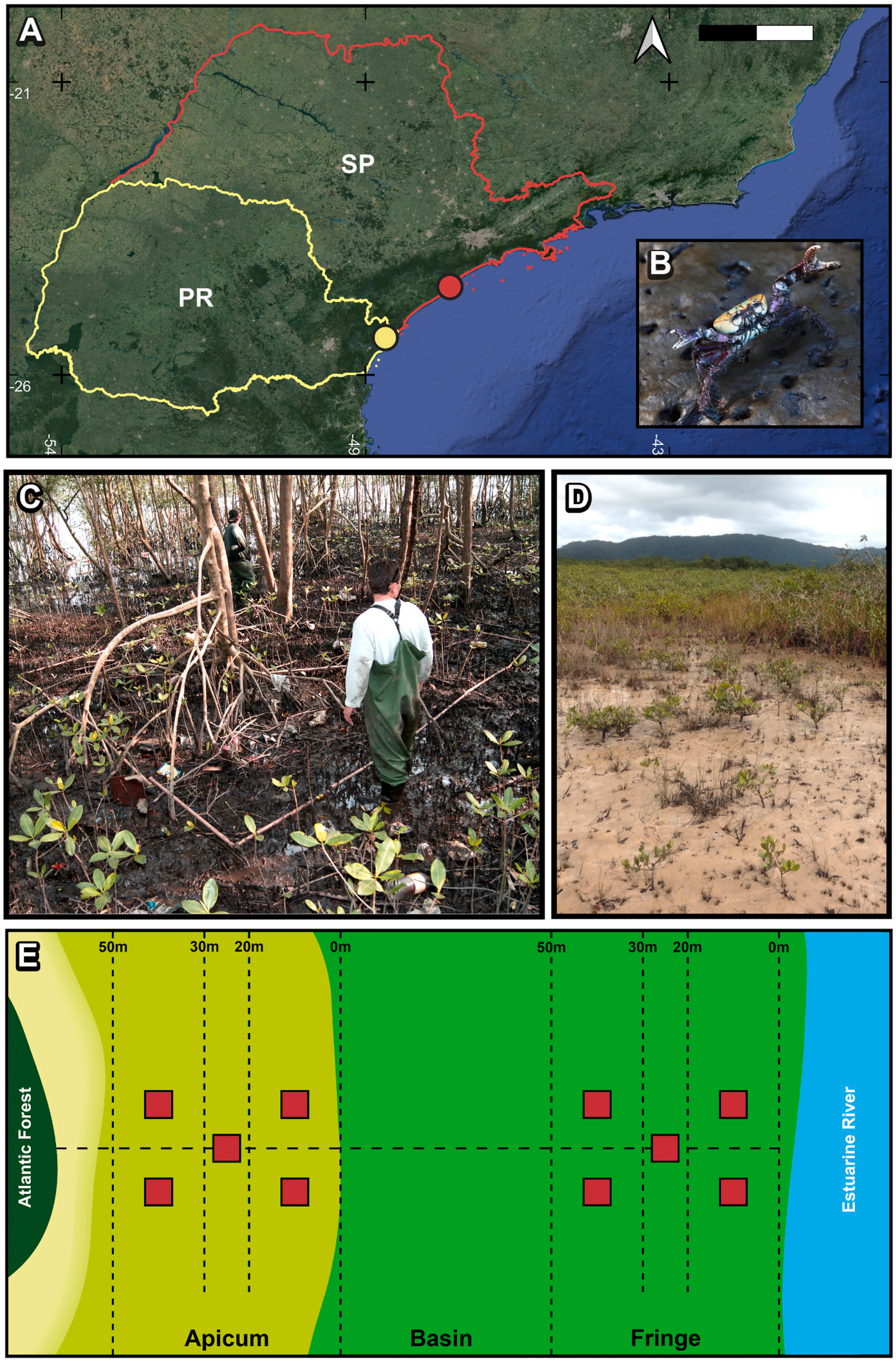

Fig. 1. (A) Geographical location of the mangrove study areas in the states of São Paulo and Paraná, Brazil (JUR, Juréia-Itatins Ecological Station: red circle; SUP, Superagui National Park: yellow circle); (B) Frontal view of a male *Ucides cordatus* on mangrove mud; (C) View of the fringe mangrove zone, showing one of the 5 × 5 m (25 m^2) sampling quadrats; (D) General view of the apicum mangrove zone; (E) Schematic representation of the position of the five quadrats in each mangrove zone (fringe and apicum), with distances from the estuarine margin and the sandier upland (three distance bands: 0–20 m, 20–30 m, and 30–50 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

by *R. mangle* across both zones, accounting for 89.9 % in the fringe and 92.5 % in the apicum. Tidal flooding is lower at JIES (fringe: 30.3 ± 4.4 cm; and apicum: 9.4 ± 2.9 cm) compared to SNP (66.2 ± 12.0 cm and 39.7 ± 7.4 cm, respectively). Additionally, sediments in the apicum zones were predominantly sandy, with sand fractions of 85.2 ± 5.2 % at JIES and 84.7 ± 5.5 % at SNP, while sediments in the fringe zones were muddier, with lower sand fractions of 33.9 ± 9.4 % at JIES and 56.6 ± 12.4 % at SNP.

2.2. *Sampling design*

A standardized sampling design was implemented to quantify the relative abundance of different burrow categories of the mangrove crab *U. cordatus* (see burrow classification) across multiple ecological scales. We compared the magnitude of burrow type abundance variation associated with fine-scale heterogeneity (<10 m; mangrove zone) with variation due to larger-scale (>1 ha) fluctuations associated with mangrove conservation (i.e., landscape-level). This design was replicated at both sites (JIES and SNP) using the same temporal structure, annually (2016, 2017, and 2018), seasonally (summer and winter), and spatially in tidal mangrove zones (fringe and apicum). This structure enabled a multiscale analysis of environmental drivers affecting burrow distribution.

A total of 120 quadrats (5 × 5 m each) were established, with five quadrats allocated to each tidal zone (fringe and apicum), in both sites (JIES and SNP), for each season and year. A stratified random sampling approach was adopted, with independent randomisation performed within each mangrove zone. Sampling units were positioned using a boomerang-throwing technique (see Pinheiro, 2025b), ensuring an approximate minimum spacing of 10 m between sampling units. This strategy minimised spatial autocorrelation and ensured representative coverage of microhabitat variability.

Zonal stratification also controlled for microtopographic variation, as each zone (fringe vs. apicum) is inherently defined by differences in elevation and tidal influence. To maintain environmental homogeneity within strata, quadrats in the fringe zone were explicitly positioned away from tidal creeks or small channels (igarapés), which are known to modify sediment composition (increasing silt content) and intensify tidal flooding, thereby introducing high variability in environmental conditions.

The spatial arrangement of quadrats within each zone is illustrated in Fig. 1

2.3. Burrow classification and assessment

Burrows were classified through visual inspection, complemented by manual verification of the number of entrances and internal status. Burrows exhibiting signs of recent biogenic activity (e.g., fresh tracks, faeces, or sediment mounds near the entrance, following Santos et al. (2009) and Pinheiro and Almeida, 2015 were classified as active.

Among active open burrows, those with a single entrance were categorised as SGL (single-opening) and those with multiple entrances as MLT (multi-opening). The variable OPE (open burrows) was obtained by summing the number of SGL and MLT burrows, regardless of the number of entrances present in each burrow.

Burrows sealed with recent or older sediment plugs were classified as closed (CLO) and were always partially excavated to confirm this status. Those showing structural degradation and lacking evidence of recent activity were recorded as abandoned (ABD).

The number of burrows in each category was recorded per sampling unit (25 m^2) and used as a proxy for the relative abundance of crabs.

However, some morphometric measurements could not be obtained due to structural constraints inherent to certain burrow types. Due to the natural sealing of closed burrows (CLO) with compacted mud plugs, it was not possible to obtain accurate measurements of their entrance diameter. Additionally, burrow depth was not assessed for any typology, as excavating individual burrows of *Ucides cordatus*, which may reach depths of up to 1.5 m, would require destructive methods and could alter the integrity of surrounding plots. Given the high energetic cost and ecological impact, such invasive measurements were beyond the scope of this study.

2.4. Statistical analyses

The relative abundance of each burrow category was organised into a data matrix, with rows representing sampling units (=quadrats) and columns corresponding to the explanatory factors. To characterise the behaviour of the response variables and to guide the selection of statistical procedures, we initially assessed the normality and homogeneity of variances of raw data using the Shapiro-Wilk and Levene's tests, respectively. Subsequently, after fitting the GLM models, we verified the normality and homogeneity of variance assumptions based on the model residuals.

To investigate how environmental and temporal factors influence the abundance patterns of *U. cordatus* burrows, we used generalised linear models (GLMs) with a negative binomial family. Separate models were fitted for each of the five burrow categories (SGL, MLT, OPE, CLO, and ABD), allowing us to evaluate whether and how the temporal (interannual variation: 2016–2017 vs. 2018), seasonal (climatic season: summer vs. winter), local (conservation unit: Juréia vs. Superagui), and spatial (tidal mangrove zone: fringe vs. apicum) factors, and their interactions, significantly affected the respective relative abundances. This approach was adopted to accommodate the discrete nature of the response variable (count data) and to address potential overdispersion by selecting the most appropriate error distribution (Poisson or negative binomial).

The full model structure tested for each burrow category was represented by ***Burrow abundance ~ year * site * season * zone***, including all main effects and their interactions. This formulation enabled the identification of the individual and combined contributions of the explanatory variables to the spatial (site and zone) and temporal (year and season) variation in the burrow distribution.

Environmental gradients related to tidal flooding, sediment texture, and arboreal vegetation were not directly included as covariates in the models, as these variables are ecologically embedded within the categorical factors' "zone" (fringe vs. apicum) and "site" (Juréia vs. Superagui). These factors reflect integrated habitat conditions shaped by flooding frequency and duration, which in turn influence sediment characteristics and mangrove forest structure (Kristensen, 2008; Wunderlich et al., 2008; Alongi, 2009). Therefore, the zone × site interaction adequately captures key environmental drivers without inflating model complexity.

Modelling each burrow category independently allowed us to detect functional and behavioural distinctions in burrow occupation and maintenance, potentially reflecting differences in crab activity, habitat preference, or life stage.

To facilitate the interpretation of third-order interaction effects (year × site × climatic season) identified in the GLMs, we constructed heatmaps to visualise adjusted mean abundances for each burrow category across all spatiotemporal combinations. This approach complements the model outputs by highlighting interaction patterns that are not easily discernible from numerical coefficients alone.

As a complementary analysis, a generalised linear model (GLM) with binomial distribution was fitted to compare the relative abundance of active burrows (i.e., SGL + MLT + CLO) versus abandoned ones (ABD), using the same fixed effects applied in the previous models (year, season, site, and mangrove zone, including all interactions). This integrated approach was conceptually consistent with the GLMs already applied to individual burrow categories, while allowing more direct interpretation through odds ratios (EC, exponentiated coefficient). The strategy is suitable for fully crossed and balanced designs, as in the present study (120 standardised quadrats). Values of EC > 1 indicate increased odds of active burrows, whereas EC < 1 suggests a higher likelihood of abandoned burrows. The outcomes of this analysis supported and reinforced patterns observed in the individual models, particularly those related to surface activity dynamics of *Ucides cordatus* in response to spatiotemporal variability.

The selection of explanatory variables and interaction terms in the generalised linear models (GLMs) followed an ecologically meaningful hierarchy (year > season > site > tidal zone), reflecting the nested spatial and temporal design of the study. Interaction terms were retained based on ecological relevance and their contribution to model performance, as indicated by reductions in AICc. To assess multicollinearity, Variance Inflation Factors (VIFs) were calculated from equivalent linear models that included only main effects and first-order interactions. This conservative approach avoids artificial inflation of VIF values caused by high-order interaction terms, which are common in fully factorial designs.

The VIFs obtained for explanatory variables and interaction terms of ecological interest ranged from 2.0 to 3.0, remaining below the commonly accepted threshold of 3. These results indicate low collinearity among predictors, supporting the adequacy of the model structure for reliable ecological interpretation (Fox and Weisberg, 2019; Zuur et al., 2010; Dormann et al., 2013).

Although floristic composition (e.g., *Rhizophora mangle* vs. *Laguncularia racemosa*) was surveyed for each quadrat, it was not included as an explicit predictor in the GLM models. This decision was based on the fact that vegetation zonation is already implicitly captured through the categorical variable "tidal zone", which reflects the typical dominance of red mangrove species (*R. mangle*) in fringe zones and white mangrove species (*L. racemosa*) in apicum zones. Therefore, including floristic composition would introduce redundancy and overparameterization.

For each model, the choice between Poisson and Negative Binomial distributions was guided by the Akaike Information Criterion (AIC), with the model presenting the lowest AIC being selected. Additionally, dispersion parameters (θ) and deviance metrics (null and residual deviance) were examined to assess the model fit and confirm the adequacy of the chosen distribution. All models were fitted using the *glm.nb* function from the MASS package in R (Venables and Ripley, 2002).

To facilitate biological interpretation, the model coefficients were exponentiated [EC = exp(coef)], representing the multiplicative change in the relative abundance of each burrow category associated with a given significant factor or interaction. Thus, the change is expressed as a percentage increase ($EC > 1$) or decrease ($EC < 1$), calculated as $(EC - 1) \times 100$ % or $(1 - EC) \times 100$ %, respectively.

As an additional step, to explore multivariate differences in burrow typology composition among environmental categories, we performed a complementary PERMANOVA based on Bray-Curtis dissimilarities using the combined abundance of four burrow types (SGL, MLT, CLO, and ABD), excluding OPE due to its derivation from SGL + MLT. The analysis included 999 permutations and was implemented in the vegan package (Oksanen et al., 2022) in R. A non-metric multidimensional scaling (nMDS) ordination was also conducted to visualise clustering patterns among zones, years, and seasons.

All analyses were performed in R (version 4.3.1 – R Core Team, 2023), with diagnostic plots and summary tables generated automatically. Statistical significance was set at 5 % ($\alpha = 0.05$).

3. Results

Multicollinearity diagnostics using variance inflation factors (VIFs) revealed low values for all explanatory variables and interaction terms of ecological relevance, with VIFs ranging from 2.0 to 3.0. These values are well below the conventional threshold of concern (VIF <5), confirming that collinearity did not bias model estimates.

For all generalised linear models (GLMs) conducted for each burrow category (SGL, MLT, OPE, CLO, and ABD), a better fit was achieved using the negative binomial distribution, as indicated by lower AIC values and high dispersion parameters ($\theta > 1$), confirming the presence of overdispersion across all models (Table 1). These model-based results were consistent with the observed patterns of burrow abundance across sites, seasons, and zones (Fig. 2).

3.1. Single-opening burrows (SGL)

The abundance of single-opening burrows (SGL) was significantly influenced by temporal, spatial, and seasonal factors, as well as their interactions ($n = 19$) (Table 2). A pronounced increase in abundance was observed in 2017 and 2018 compared to 2016, with increases of 857 % (EC = 9.57) and 500 % (EC = 6.00), respectively (Table 2). Similarly, higher abundances were recorded in winter (465 % increase; EC = 5.65) and at the Superagui site (443 %; EC = 5.43) compared to summer and Juréia, respectively. The fringe zone also showed a doubling of burrow abundance (EC = 2.00; +100 %) compared to the apicum zone.

These trends are depicted in Fig. 2, where the panels for SGL show elevated adjusted means in 2017 and in the winter season, especially at Superagui and in fringe zones.

However, significant negative interactions were also detected. For example, burrow abundance decreased by 88 % (EC = 0.12) and 92 % (EC = 0.08) during the winters of 2017 and 2018, respectively, compared to the baseline. Strong reductions were observed at Superagui during the same years (95 % and 89 % decreases; EC = 0.05 and 0.11, respectively), as well as in the combination of Superagui and winter (97 % decrease; EC = 0.03). Negative interactions involving the fringe zone were also notable, with reductions of 70 % (EC = 0.30) in 2017 and 86 % (EC = 0.14) in 2018.

Interestingly, some three-way interactions led to pronounced increases, such as a nearly 60-fold increase (EC = 59.64) in 2017 during winter at Superagui, and an approximately 18-fold increase (EC = 17.84) in 2018 under similar conditions. Burrow abundance also increased expressively at the fringe zone of Superagui, particularly in 2018 (EC = 8.02; +702 %), as illustrated in Fig. 2.

3.2. Multiple-opening burrows (MLT)

The abundance of multiple-opening burrows (MLT) was significantly influenced by temporal and spatial factors, with fewer significant interactions compared to single-opening burrows (SGL: $n = 6$) (Table 2). In 2017 and 2018, MLT abundance increased by 215 % (EC = 3.15) and 108 % (EC = 2.08), respectively, compared to 2016.

A sharp reduction (EC = 0.14; −86 %) was recorded in the fringe zone during 2017, as evident in Fig. 2. However, a three-way interaction among 2017, Superagui, and the fringe zone resulted in a striking local increase (EC = 18.52; +1752 %).

3.3. Total open burrows (OPE)

The total abundance of open burrows (OPE), resulting from the sum of SGL and MLT categories, was significantly affected by temporal and spatial factors ($n = 5$) (Table 2). A moderate increase of 52 % (EC = 1.52) and 126 % (EC = 2.26) was observed in 2017 and 2018, respectively. A very expressive increase (EC = 18.99; +1799 %) occurred at Superagui during summer.

This pattern is strongly reflected in Fig. 2, which shows the peak of OPE abundance associated with the Superagui site and the summer season.

Table 1

Model selection between Poisson and Negative Binomial distributions for each burrow category (ABD, abandoned; CLO, closed; MLT, multiple-opening; SGL, single-opening; and OPE, total open burrows = SGL + MLT) of *Ucides cordatus*. Where: AIC, Akaike Information Criterion; θ, dispersion parameters of the negative binomial model; SE (θ), standard error of θ. Null and residual deviances were obtained from the negative binomial model, and Fisher scoring iterations were 1 in all cases.

Burrow Category	AIC Poisson	AIC Binomial Negative	ΔAIC	θ	SE (θ)	Null Deviance	Residual Deviance
SGL	944.58	849.09	95.49	13.87	3.18	703.96	135.66
MLT	666.85	606.67	60.18	5.42	1.43	422.46	125.38
OPE	1081.99	909.20	172.79	11.42	2.29	677.20	136.16
CLO	1055.65	858.78	196.87	6.77	1.34	608.22	141.05
ABD	487.83	441.69	46.14	3.63	1.21	551.10	102.85

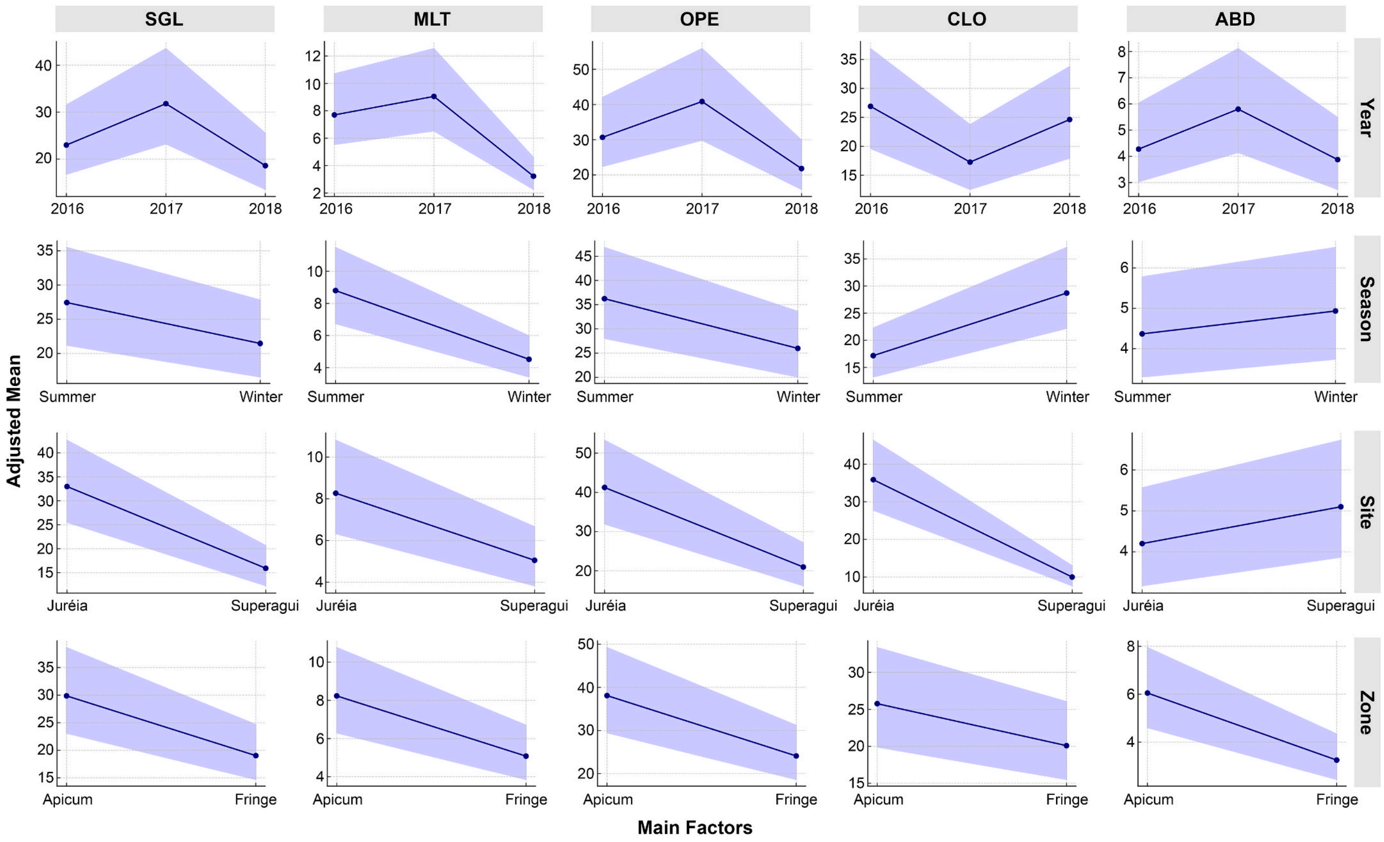

Fig. 2. Adjusted means (solid lines) and 95 % confidence intervals (shaded areas) predicted from negative binomial generalised linear models for five burrow types of *Ucides cordatus* (SGL, MLT, OPE, CLO, ABD) as a function of year, season, site, and tidal zone. Each panel shows the independent effect of one explanatory factor on burrow abundance. Models were fitted separately for each type of burrow.

In contrast, a significant decrease (EC = 0.25; −75 %) was detected in the interaction between 2018 and Superagui.

3.4. Closed burrows (CLO)

The abundance of closed burrows (CLO) was also influenced by temporal and spatial factors (n = 5) (Table 2). A 157 % increase (EC = 2.57) was recorded in 2017, and almost double the abundances were observed at Superagui compared to Juréia (EC = 1.99).

Despite these general positive effects, significant reductions were associated with interactions between year and site, especially in 2018: Superagui (EC = 0.25; −75 %) and 2017:Superagui (EC = 0.39; −61 %), as shown by decreasing adjusted means for CLO in Fig. 2.

3.5. Abandoned burrows (ABD)

The abundance of abandoned burrows (ABD) was shaped by temporal, seasonal, and spatial factors (n = 5) (Table 2). A significant increase (EC = 3.33; +233 %) occurred in 2017, with a particularly strong increase during summer (EC = 13.17; +1217 %). A positive effect was also recorded at the Superagui site (EC = 4.16; +316 %).

Conversely, the interaction between 2018 and Superagui resulted in a sharp reduction (EC = 0.06; −94 %), indicating the near absence of this burrow type, a pattern evident in Fig. 2.

Fig. 3 illustrates the adjusted mean abundance of each burrow category across all combinations of site, year, and climatic season, providing a visual representation of the third-order interaction effects identified in the GLMs. In Juréia, the heatmaps reveal a progressive increase in the adjusted mean abundance of SGL and OPE burrows from 2016 to a peak in summer 2017, followed by a decline in 2018. MLT burrows showed a more subtle temporal pattern, with a slight peak during winter 2018. CLO burrows exhibited higher adjusted means during the winter months across all years, especially in winter 2018. No consistent temporal pattern was evident for ABD burrows at Juréia. In contrast, Superagui exhibited more fluctuating temporal patterns across all burrow types, without clear annual trends. This higher variability may reflect the ongoing harvesting pressure in this site.

A complementary binomial model confirmed patterns consistent with the results obtained for individual burrow categories. When comparing the relative abundance of active burrows (SGL + MLT + CLO) versus abandoned ones (ABD), higher proportions of active burrows were recorded in Juréia, particularly during the summers of 2017 and 2018 (Fig. 4). In contrast, the lowest values occurred during the winters of 2016 and 2018 in Superagui. The binomial GLM identified significant interactions between year, season, site, and mangrove zone, with predictive patterns largely coherent with those revealed by the independent models per burrow type (Table 3; Fig. 4).

A complementary multivariate analysis reinforced the patterns observed in the GLMs. The PERMANOVA revealed significant differences in burrow typology composition across all tested environmental factors: site (F = 22.87, R^2 = 0.162, P = 0.001), year (F = 4.16, R^2 = 0.066, P = 0.001), season (F = 8.31, R^2 = 0.066, P = 0.001), and mangrove zone (F = 4.16, R^2 = 0.034, P = 0.003). These results suggest that burrow composition is influenced by both spatial and temporal variables, with site accounting for the largest proportion of explained variance.

The non-metric multidimensional scaling (nMDS) ordination corroborated these findings. When all sampling units were plotted together (Fig. 5A), a tendency for clustering by mangrove zone was observed, with partial but consistent separation between fringe and apicum. This pattern was particularly evident in samples from the winter season. Faceted ordinations by year and climatic season (Fig. 5B)

Table 2

Significant terms ($p < 0.05$) from generalised linear models (GLMs) with negative binomial distribution evaluating the effects of year (2016–2018), season (summer vs. winter), site (Juréia vs. Superagui), and mangrove zone (fringe vs. apicum) on the relative abundance of *Ucides cordatus* burrows. Burrow categories: ABD (abandoned), CLO (closed), MLT (multiple-opening), SGL (single-opening), OPE (total open = SGL + MLT). Columns: Coef = Estimate (log), log-transformed coefficient; SE, standard error; P-value (expressed in scientific notation); EC, exponentiated coefficient [exp(Estimate)], representing the multiplicative change; and significance level (*P < 0.05; **P < 0.01; ***P < 0.001).

Burrow Category	Model Term	Coef	SE	*P*-value	EC
SGL (n = 19)	(Intercept)	2.00	0.20	2.66E-05 ***	7.40
	2017	2.26	0.24	2.00E-16 ***	9.57
	2018	1.80	0.25	3.05E-13 ***	6.00
	Superagui	1.69	0.25	6.83E-12 ***	5.43
	Winter	1.73	0.25	2.06E-12 ***	5.65
	Fringe	0.69	0.26	8.50E-03 **	2.00
	2017:Superagui	−3.06	0.32	2.00E-16 ***	0.05
	2018:Superagui	−2.19	0.32	6.41E-12 ***	0.11
	2017:Winter	−2.12	0.31	8.77E-12 ***	0.12
	2018:Winter	−2.51	0.32	6.81E-15 ***	0.08
	Superagui:Winter	−3.37	0.35	2.00E-16 ***	0.03
	2017:Fringe	−1.20	0.32	2.21E-04 ***	0.30
	2018:Fringe	−1.98	0.34	8.86E-09 ***	0.14
	Superagui:Fringe	−1.18	0.33	3.86E-04 ***	0.31
	2017:Superagui: Winter	4.09	0.45	2.00E-16 ***	59.64
	2018:Superagui: Winter	2.88	0.47	1.34E-09 ***	17.84
	2017:Superagui: Fringe	0.10	0.46	2.92E-02 *	2.72
	2018:Superagui: Fringe	2.08	0.46	5.09E-06 ***	8.02
	2018:Winter:Fringe	1.68	0.46	2.39E-04 ***	5.35
MLT (n = 6)	(Intercept)	1.70	0.23	2.00E-14 ***	5.49
	2017	1.15	0.27	2.30E-05 ***	3.15
	2018	0.73	0.27	7.60E-03 **	2.08
	Superagui:Summer	1.77	0.47	2.00E-04 ***	5.87
	2017:Fringe	−1.98	0.38	2.10E-07 ***	0.14
	2017:Superagui: Fringe	2.92	0.68	1.60E-05 ***	18.52
OPE (n = 5)	(Intercept)	2.27	0.20	2.00E-16 ***	9.67
	2017	0.42	0.17	1.22E-02 *	1.52
	2018	0.82	0.17	1.40E-06 ***	2.26
	Superagui:Summer	2.94	0.44	2.00E-11 ***	18.99
	2018:Superagui	−1.41	0.23	2.50E-09 ***	0.25
CLO (n = 5)	(Intercept)	2.27	0.23	2.00E-16 ***	9.66
	2017	0.94	0.28	9.00E-04 ***	2.57
	Superagui	0.69	0.28	1.33E-02 *	1.99
	2018:Superagui	−1.40	0.30	2.50E-06 ***	0.25
	2017:Superagui	−0.95	0.33	4.30E-03 **	0.39
ABD (n = 5)	(Intercept)	1.51	0.31	1.10E-06 ***	4.53
	2017	1.20	0.57	3.45E-02 *	3.33
	Summer	2.58	0.57	1.40E-05 ***	13.17
	Superagui	1.43	0.57	1.16E-02 *	4.16
	2018:Superagui	−2.80	0.64	1.00E-05 ***	0.06

further revealed interactive patterns, highlighting shifts in burrow composition over time and clearer zonal segregation in the winters of 2017 and 2018.

4. Discussion

Variations in the burrow morphology of *Ucides cordatus* reflect both behavioural and ontogenetic differences within the species, modulated by environmental dynamics that significantly influence their distribution (Santos et al., 2009). Understanding the spatiotemporal variability in the abundance and typology of *Ucides cordatus* burrows in mangrove ecosystems is essential for assessing the ecological status of populations and the environmental quality of their habitats. Our findings demonstrate that burrow categories are sensitive indicators of temporal fluctuations, spatial heterogeneity, and behavioural phases, providing valuable insights into the functioning of mangrove ecosystems under various climatic and habitat conditions. We structure our discussion into four analytical **themes**: (1) temporal patterns driven by climatic stress and biological plasticity; (2) spatial heterogeneity resulting from microhabitat variability; (3) burrow categories as proxies of ecological and behavioural phases; and (4) broader ecological and conservation implications.

(1) Temporal patterns: plasticity and climatic stress

Data from the Oceanic Niño Index (ONI) available from NOAA (2025) indicate a strong El Niño in early 2016, followed by a La Niña later that year. In contrast, 2017 and 2018 were climatically neutral years, although short-term ONI fluctuations occurred without meeting the thresholds for formal ENSO classification (Trenberth, 1997; L'Heureux et al., 2017). These climatic transitions may have contributed to observed interannual fluctuations in burrow abundance. About burrow typology, single-opening (SGL) and multiple-opening (MLT) burrows showed marked increases in 2017 and 2018, whereas closed (CLO) and abandoned (ABD) burrows exhibited more variable, site-dependent responses. For example, CLO burrows increased significantly in 2017, especially at Superagui (+99 %), but declined sharply in 2018:Superagui (−75 %), potentially indicating suppression of reproductive or moulting activity in response to climatic or site-specific stressors (Diele and Koch, 2010; Pinheiro et al., 2022).

A seasonal surge in ABD burrows was observed in summer (+1217 %), which may reflect elevated environmental stress (e.g., hypersalinity, high sediment temperatures), mortality (natural or fishery), or for reproductive purposes ("andada" events). These patterns suggest a high degree of temporal plasticity in burrow dynamics, highlighting the importance of incorporating seasonality and interannual variability into monitoring frameworks. During reproductive periods, seasonal increases in open burrow types may also relate to ovigerous female behaviour. Santos et al. (2009) proposed that females orient their burrows toward the river margin to facilitate larval release. This may partly explain higher open burrow frequencies in fringe zones under particular

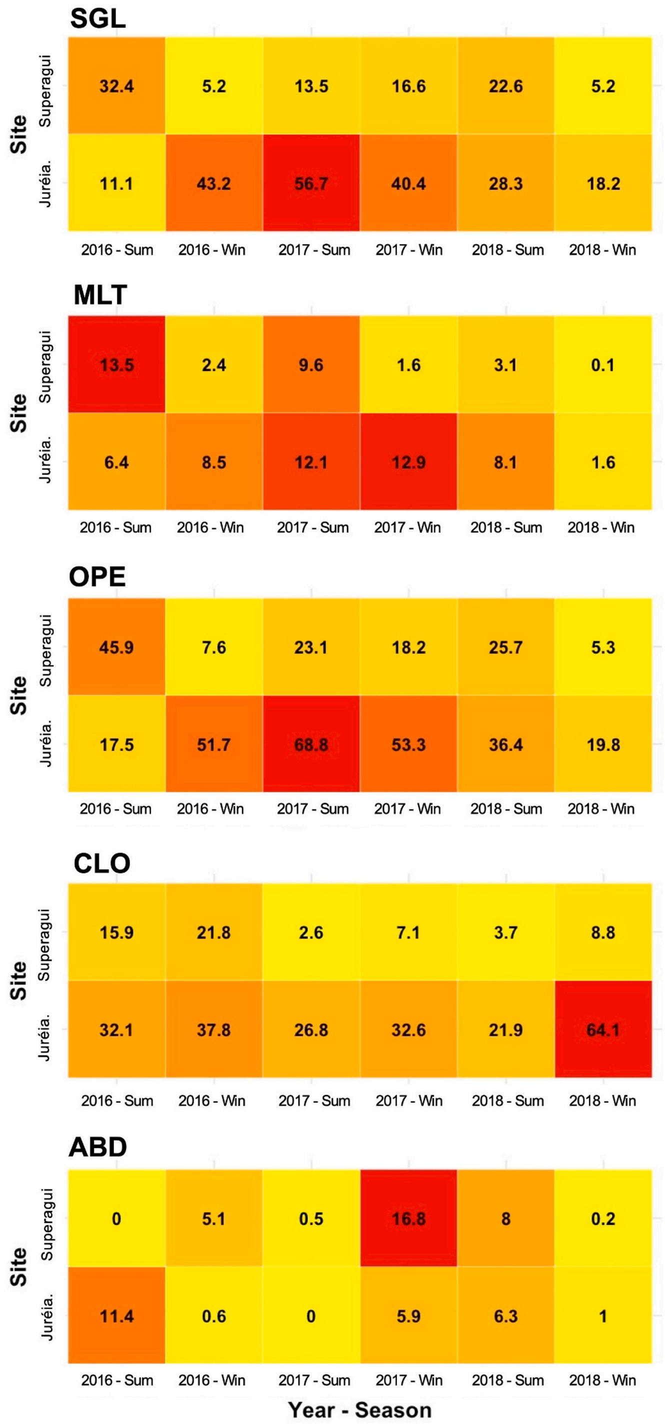

Fig. 3. Heatmaps showing adjusted mean abundances of *Ucides cordatus* burrow categories (SGL, single-opening; MLT, multiple-opening; OPE, total open = SGL + MLT; CLO, closed; and ABD, abandoned) across all combinations of site (Juréia, Superagui), year (2016–2018), and climatic season (Sum, summer; Win, winter). Values represent model-adjusted means per 25 m^2 quadrat, derived from generalised linear models (GLMs) with negative binomial distribution. Warmer colours indicate higher burrow abundance. These visualisations highlight the spatiotemporal complexity of third-order interaction effects, revealing site-specific and seasonal shifts in burrow typology patterns. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

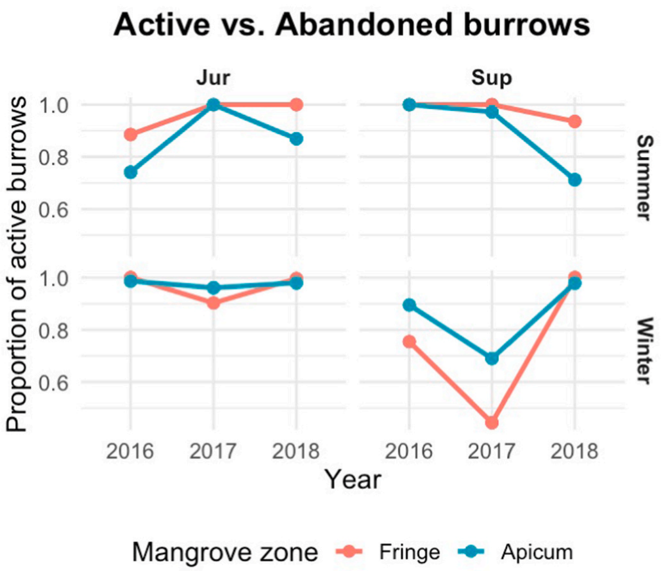

Fig. 4. Predicted proportion of active burrows (SGL + MLT + CLO) relative to abandoned ones (ABD) for *Ucides cordatus*, based on the binomial generalised linear model. Patterns are shown by year (2016–2018), season (summer vs. winter), site (Juréia vs. Superagui), and mangrove zone (fringe vs. apicum). Higher values indicate greater odds of active burrows, reflecting increased surface activity. Note the contrasting winter patterns in Superagui, especially in 2016 and 2017, which showed markedly lower proportions of active burrows.

climate conditions.

Additionally, the oxidative stress modulation described by Santos et al. (2019) highlights the influence of seasonality on the physiological condition of *U. cordatus*, reinforcing the role of seasonal stressors in modulating crab activity and potentially affecting burrow typology. These findings are consistent with the ecological threshold framework proposed by Osland et al. (2025), which suggests that mangrove ecosystems may exhibit nonlinear responses to cumulative climatic stress. The abrupt shifts observed in burrow typology may therefore reflect underlying tipping points in system dynamics, reinforcing the need for early-warning indicators in conservation planning.

The physiological susceptibility of *U. cordatus* to degraded environmental conditions has already been evidenced by immunological alterations, such as hemocyte depletion, even in the absence of histopathological signs or direct mortality, as demonstrated by Valentim-Neto and Gesteira (2020) in the Jaguaribe River estuary (Ceará State, Brazil) under the influence of shrimp farming.

This broader temporal sensitivity is further exemplified by an exceptional anomaly recorded in Superagui during the winter of 2017. A remarkable surge in SGL burrows was detected in Superagui during winter 2017, with a 59-fold increase compared to the baseline. Although this anomaly may reflect a natural recolonisation process or behavioural shift, it is plausible that extreme climatic conditions (e.g. ENSO-related events) contributed to this abrupt increase. However, the absence of local meteorological stations and the limited spatial resolution of regional datasets hindered the incorporation of ENSO indicators as explanatory covariates in the current GLMs. Nevertheless, this pattern highlights the potential of burrow typologies as indicators of environmental fluctuations. A dedicated analysis integrating remotely sensed climatic data (e.g. from NOAA and INMET) is planned for a future study specifically focused on climate-burrow interactions.

(2) Spatial heterogeneity: microhabitat variability and tidal regime

Although Juréia and Superagui are both microtidal systems (Davies, 1964), marked zonal contrasts, particularly between fringe and apicum

Table 3

Significant terms ($P < 0.05$) from a generalised linear model (GLM) with binomial distribution comparing the relative abundance of active (ACT = SGL + MLT + CLO) versus abandoned (ABD) burrows of *Ucides cordatus*, based on the fixed effects of year (2016–2018), season (summer vs. winter), site (Juréia vs. Superagui), and mangrove zone (fringe vs. apicum), including all interaction terms. Columns: Estimate (log), log-transformed coefficient; SE, standard error; P-value (scientific notation); EC, exponentiated coefficient [exp(Estimate), representing multiplicative change in the odds of active burrows]; and significance level (***$P < 0.001$).

Burrow Category	Model Term	Estimate (log)	SE	P-value	EC
ACT vs. ABD (n = 2)	Intercept	2.043	0.180	5.74E-30 ***	7.71
	Apicum	−0.992	0.222	8.00E-06 ***	0.37

zones, modulate burrow distribution at finer spatial scales. Flooding frequency, sediment characteristics, and vegetation structure are the primary drivers of these differences. Juréia consistently exhibited higher abundances of open (SGL, MLT) and closed (CLO) burrows, likely associated with favourable fringe zone conditions (greater oxygenation, moderate flooding, organic-rich sediment). Conversely, the higher flooding levels at Superagui promoted reductions in open burrow counts, particularly under the interaction between the fringe zone and the winter season, potentially due to sediment compaction and lower redox potential characteristic of apicum zones (Schmidt et al., 2010; Gomes et al., 2024; Soares et al., 2024).

These patterns align with the findings of Wunderlich and Pinheiro (2013), who demonstrated that *U. cordatus* exhibits sex- and size-specific habitat partitioning, driven by flooding levels and mangrove composition. Additional support comes from Gomes et al. (2013) and Schmidt et al. (2010), who linked substrate characteristics and inundation regimes to crab density and recruitment zones, respectively. Fringe zones exhibited higher variability in open burrow counts, often with significant declines (e.g., −70 % in SGL burrows in 2017:Fringe). These findings reinforce previous studies indicating that fringe environments are less stable and more exposed to physical disturbance, which may reduce burrow persistence and visibility. This pattern has implications for crab behaviour and habitat partitioning, particularly during stressful seasons or climatic anomalies (Schmidt et al., 2010; Wunderlich and Pinheiro, 2013).

Mangrove structure also differed notably between zones: fringe zones featured fewer, taller trees and open canopies, while apicum zones had high-density thickets with smaller individuals, consistent with scrub forest formations. These structural and edaphic gradients influence crab activity, burrow construction, and persistence.

The interaction between spatial heterogeneity and climate exposure may also define the vulnerability of specific zones to threshold transitions. Osland et al. (2025) highlighted that microhabitat-scale differences can determine whether ecosystems buffer stress or undergo abrupt change, further supporting the use of burrow typologies to detect early ecological responses.

Among these factors, tidal flooding represents the primary ecological driver, as it conditions both sediment granulometry and the establishment of mangrove tree species. This hierarchical influence defines the abiotic and biotic attributes of each zone × site combination and explains much of the observed variation in burrow abundance and typology (Cintrón and Schaeffer-Novelli, 1984; Kristensen, 2008; Alongi, 2009; Osland et al., 2025).

A potential limitation of our modelling strategy is the omission of tree species composition as an explicit covariate. Nonetheless, this factor is indirectly captured by the "tidal zone" variable, which reflects the ecological contrasts between *Rhizophora*-dominated fringe zones and *Laguncularia*-dominated apicum zones. Including both predictors would likely result in collinearity and reduced model parsimony, offering limited additional explanatory power within the ecological scope of this study.

(3) Burrow categories as indicators of ecological phases and disturbance

Each burrow type provides a proxy for behavioural or ecological stages in *U. cordatus*. Open burrows (SGL, MLT) are typically associated with active foraging, movement, and territoriality. Their increases in 2017:Superagui:Fringe (EC = 18.52) and declines in 2017:Fringe (EC = 0.30) reflect the species' behavioural plasticity and responsiveness to local habitat conditions. To complement the interpretation of functional phases, Fig. 6 presents the typological classification of the burrows, illustrating how morphology relates to ecological roles.

Closed burrows (CLO) are interpreted as signs of cryptic phases, such as moulting (e.g., buffering of chemicals in water) or protection during reproduction (e.g., pleopodal egg incubation). Their site- and year-

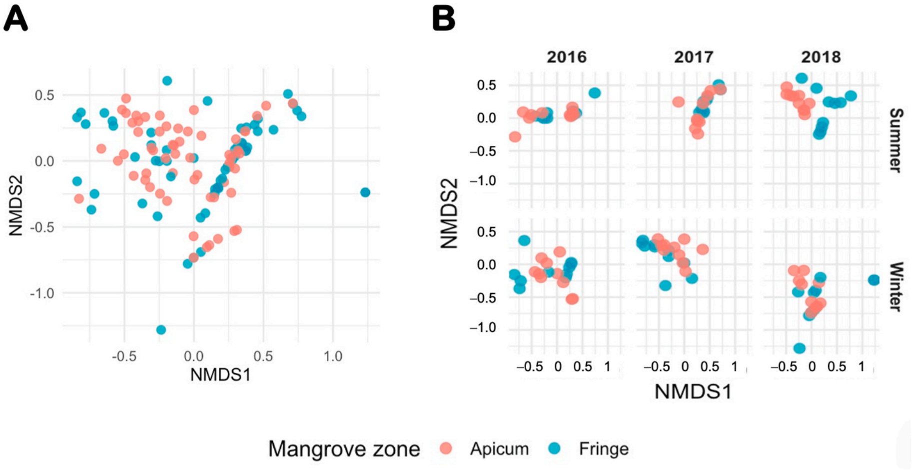

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination of *Ucides cordatus* burrow typology composition based on Bray-Curtis dissimilarities. Each point represents a 25 m^2 quadrat. **(A)** Overall ordination showing multivariate compositional differences between mangrove zones (fringe vs. apicum), with points coloured by zone. **(B)** Faceted ordination by year (2016–2018) and climatic season (summer vs. winter), highlighting interactive effects of time and space on burrow structure. Together, the panels reveal multiscale variation in burrow typology and the influence of environmental gradients on spatial clustering.

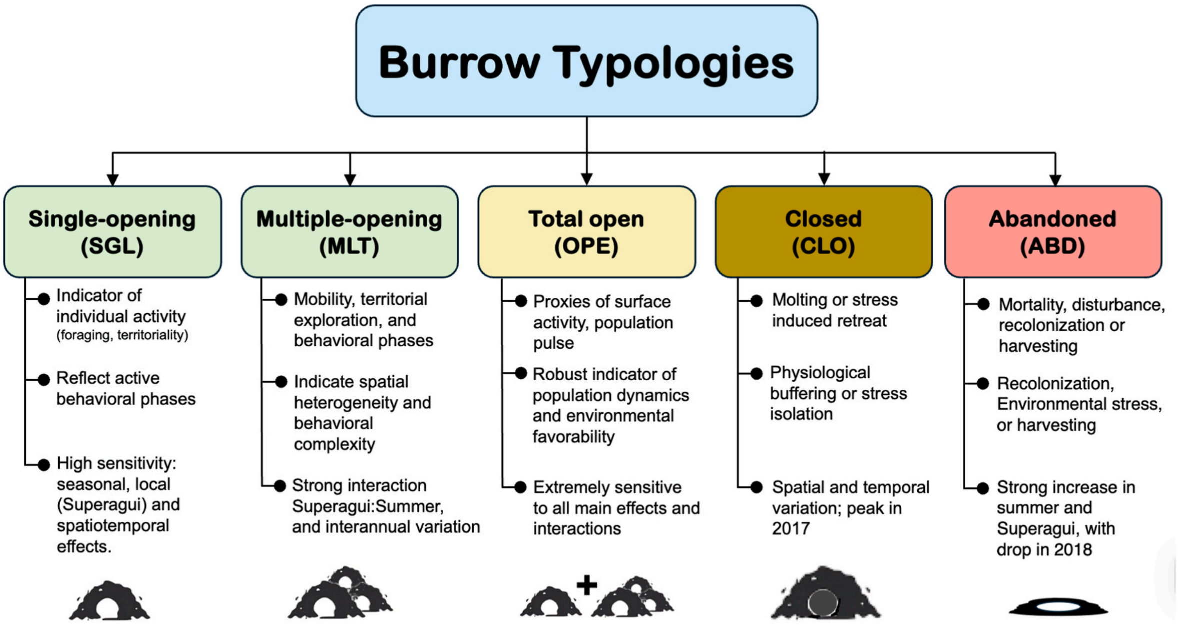

Fig. 6. Typological classification of burrows excavated by *Ucides cordatus* based on morphological features and associated ecological functions. Burrow types include single-opening (SGL), multiple-opening (MLT), total open (OPE), closed (CLO), and abandoned (ABD) forms, each reflecting distinct behavioural or physiological states. Open burrows (SGL, MLT, and OPE) are typically associated with foraging and movement; closed burrows (CLO) indicate sedentary phases such as moulting; and abandoned burrows (ABD) suggest mortality, recolonisation, or environmental disturbance. This typology provides a framework for interpreting population dynamics and assessing habitat quality.

specific fluctuations support their use as indicators of environmental buffering or physiological commitment (João and Pinheiro, 2019).

Although the functional interpretation of CLO burrows as shelters for reproduction or moulting is well supported (Diele and Simith, 2007; Schmidt et al., 2012), our study did not permit direct measurement of their morphology. The natural sealing of these burrows and their potential depth (up to 1.5 m) precluded non-invasive access, especially in protected areas. While this is a methodological limitation, the interpretation remains valid given behavioural evidence and ecological patterns. Future studies could adopt non-destructive imaging or endoscopic tools to examine internal structures, despite the added challenge posed by the muddy substrate, typically found in *U. cordatus* habitats, which may compromise lens clarity and operational efficiency.

Abandoned burrows (ABD), often linked to mortality, recolonisation, or human disturbance, displayed sharp reductions in 2018:Superagui (EC = 0.061). The higher frequency of ABD burrows in Superagui may partially result from traditional crab harvesting practices that persist in the region (Costa, 2025), unlike Juréia, where crab harvesting is absent due to local cultural practices and conservation regulations (Souza and Pinheiro, 2021, 2022; Lima et al., 2023). These patterns are also consistent with observations from Aviz et al. (2020), who demonstrated the recovery of *U. cordatus* populations in restored mangroves.

The multivariate structure of burrow typologies further reinforces their value as functional ecological indicators. The nMDS ordinations highlighted subtle yet consistent differences between fringe and apicum zones, particularly under certain temporal conditions such as the winter of 2018. These results, coupled with the PERMANOVA findings, suggest that environmental filtering linked to tidal inundation and vegetation structure influences the spatial and temporal configuration of burrow types. The integration of multivariate analyses thus enhances diagnostic resolution and supports the ecological relevance of burrow typology monitoring.

Table 4 summarises the morphological characteristics, ecological significance, and the main significant effects detected for each burrow category of *Ucides cordatus*. Incorporating burrow typology into early detection frameworks is aligned with recent calls to identify functional indicators of ecological stress before irreversible system shifts occur.

Table 4

Summary of typological, functional, and ecological interpretations for each burrow category of *Ucides cordatus*, based on morphology and generalised linear model results. Burrow categories: SGL (single-opening), MLT (multiple-opening), OPE (total open = SGL + MLT), CLO (closed), ABD (abandoned).

Burrow category	Morphological description	Ecological significance	Functional interpretation	Sensitivity and main effects
SGL	Single entrance with recent biogenic activity	Individual foraging and territoriality	Reflects behavioural plasticity and active life phases	Sensitive to year, season, site, zone, and interactions
MLT	Multiple interconnected entrances used by one individual	Mobility, territorial exploration	Indicates spatial adaptation and behavioural complexity	Interaction Superagui: Summer; interannual variation
OPE	Sum of SGL and MLT; proxy of surface activity	Juvenile and adult surface activity; population pulse	Robust indicators of population dynamics	Extremely sensitive to all main effects and interactions
CLO	Plugged burrows, confirmed by manual inspection	Moulting, reproduction, or stress-induced retreat	Represents physiological buffering and stress isolation	Spatial and temporal variation; peak abundance in 2017
ABD	Degraded, inactive burrows without biogenic signs	Mortality, disturbance, recolonisation, or harvesting	Indicators of habitat degradation and disturbance history	Substantial increase in summer and Superagui; sharp drop in 2018

Osland et al. (2025) emphasize that monitoring bioindicator traits, such as behaviourally linked structures, can offer insight into ecosystem trajectories under stress.

The results from the unified binomial modelling reinforce the relevance of burrow typologies as sensitive ecological indicators of environmental conditions. The high proportion of active burrows in Juréia during summer 2017 suggests enhanced behavioural activity under favourable microhabitat conditions, whereas the predominance of abandoned burrows in Superagui during the winters of 2016 and 2018 may reflect environmental stress, disturbance, or mortality (Diele and Koch, 2010; Pinheiro et al., 2023). These findings corroborate the trends identified by the individual GLMs, validating the use of aggregate approaches as complementary tools for ecological diagnosis.

Diagnostic checks, including assessments of multicollinearity, supported the reliability of the generalised linear models (GLMs). All variance inflation factors (VIFs) for the explanatory variables and ecologically meaningful interaction terms were below the commonly accepted threshold of 3, confirming low collinearity among predictors. This result strengthens the interpretability of the models and validates the inclusion of interaction effects based on ecological hierarchy and model parsimony.

Furthermore, multivariate analyses provided converging evidence for the ecological relevance of burrow typologies. The PERMANOVA confirmed statistically significant variation in burrow composition across spatial and temporal factors, with the strongest effect observed between sites. These findings were visually supported by the nMDS ordinations, which showed subtle yet consistent differences between fringe and apicum zones, especially during the winters of 2017 and 2018. This multivariate structure highlights how environmental filtering, likely driven by tidal inundation and vegetation structure, influences the spatial and temporal distribution of burrow types. Together, the PERMANOVA and nMDS analyses reinforce the value of using burrow typology composition as a diagnostic tool for assessing ecological variability and disturbance in mangrove ecosystems.

These multiscale patterns are further synthesised in the heatmaps presented in Fig. 3, which visually integrate the effects of site, year, and climatic season on the abundance of *Ucides cordatus* burrow types. The observed progression of SGL and OPE burrows in Juréia, peaking in summer 2017 and declining thereafter, contrasts with the erratic patterns in Superagui, where harvesting pressure may contribute to greater variability. Seasonal increases in CLO burrows during winter, and the less consistent responses of MLT and ABD categories, reflect the functional heterogeneity of burrow types under varying environmental conditions. Collectively, these patterns highlight the potential of burrow typology as a cost-effective, non-invasive biomonitoring tool that can capture early ecological shifts across spatiotemporal scales.

(4) Ecological and conservation implications

Building on this visual and functional framework, burrow typologies emerge as powerful, non-invasive indicators for ecological monitoring. Their responsiveness to environmental gradients, spatiotemporal variation, and potential disturbance makes them particularly well-suited for detecting early signs of ecological stress in *U. cordatus* populations. The persistence and distribution of these structures across diverse habitat conditions further enhance their value in long-term conservation and management strategies.

As key bioturbators, *U. cordatus* individuals play a crucial role in sediment turnover, nutrient cycling, and the decomposition of organic matter. Studies by Aller et al. (2024) and Michaud et al. (2024) reinforce the functional importance of burrow structures in modulating sediment-water exchanges, redox conditions, and solute dynamics. Plugged burrows may act as temporary reservoirs of reduced compounds, while open burrows enhance hydrological connectivity and oxygenation. This dynamic is ecologically relevant and detectable through typological monitoring.

Recruitment zones of *U. cordatus* are typically located at the transitional boundary between arboreal and herbaceous mangroves (Schmidt et al., 2010). Maintaining the integrity of these zones, particularly under scenarios of sea level rise, is essential for ensuring population renewal. Physical disturbance or land-use changes that compromise these transitional habitats can have lasting impacts on recruitment and population resilience (Diele and Koch, 2010; Wunderlich and Pinheiro, 2013; Gomes et al., 2024).

Incorporating physiological and population-level indicators alongside typological data can strengthen the diagnostic power of monitoring protocols. For example, oxidative stress biomarkers (Santos et al., 2019) and reproductive metrics (João and Pinheiro, 2019) can complement burrow-based surveys to yield a multidimensional picture of population health. Moreover, as highlighted by community-based approaches (Machado et al., 2018; Côrtes et al., 2018), integrating local ecological knowledge (LEK) can improve compliance, relevance, and continuity of monitoring programmes in both protected and extractive contexts.

The presence of juvenile crabs in adult burrows (Schmidt and Diele, 2009; Kassuga and Masunari, 2015)highlights the ecological interdependence among life stages and underscores the relevance of burrow typologies in detecting recruitment events. This feature is especially useful in environments undergoing rapid change, where early-stage responses may signal broader ecosystem transformations.

Burrow typology provides a cost-effective and ecologically meaningful alternative to traditional monitoring methods such as trapping. Unlike capture-based approaches, which require extended field time, specialised equipment, and often produce behavioural bias, typological surveys allow for rapid, standardised, and non-destructive assessments across spatial and temporal scales. Table 5 compares both approaches, highlighting the operational and ecological advantages of burrow-based protocols.

Finally, Fig. 3 reinforces the integrative value of burrow typologies in monitoring: by capturing multiscale variation in time, space, and behaviour, this approach aligns with emerging conservation paradigms that prioritise early detection of ecological thresholds. As emphasised by Osland et al. (2025), identifying resilience tipping points before irreversible change occurs is essential for developing predictive and adaptive conservation strategies. In this context, *U. cordatus* burrows represent not only physical structures, but also ecological sentinels of mangrove integrity.

5. Conclusions

Recent global estimates have highlighted the central role of mangroves in supporting commercially important species, with densities of *Ucides cordatus* in Brazilian mangroves reaching nearly 2individuals per m^2 (Zu Ermgassen et al., 2025). These findings underscore the ecological and economic relevance of this species, reinforcing its value as an indicator of environmental quality and resilience in estuarine systems.

Our study demonstrates that the abundance and typology of *U. cordatus* burrows respond significantly to multiscale temporal and spatial factors. Different burrow types reflect specific ecological phases and environmental conditions, making them effective indicators of both population dynamics and ecosystem functioning.

Temporal patterns reveal strong sensitivity to climate variability, especially interannual shifts, while spatial variability is primarily driven by microhabitat heterogeneity across fringe and apicum zones. Burrow typologies mirror behavioural plasticity, recruitment dynamics, and the impact of environmental disturbance, including anthropogenic pressure.

These findings underscore the importance of incorporating burrow typology into non-invasive, cost-effective monitoring programs. Incorporating local ecological knowledge and participatory science can further enhance the effectiveness of conservation efforts, particularly in data-poor or remote regions.

Considering recent advances in threshold ecology, especially those outlined by Osland et al. (2025), the typological plasticity observed in

Table 5

Comparative overview of methodological features between traditional and burrow typology methods for monitoring *Ucides cordatus* populations in Atlantic mangroves. This qualitative comparison highlights differences in invasiveness, field effort, logistical complexity, time per sampling unit, environmental constraints, behavioural bias, biological data obtained, applicability in protected areas, temporal replicability, and integration with habitat characteristics. The synthesis is based on previous studies (Diele and Koch, 2010; Glaser and Diele, 2004; Piou et al., 2007, 2009; Nordhaus et al., 2006, 2009; Duarte et al., 2014; Pinheiro and Almeida, 2015; Pinheiro et al., 2018; Masuda et al., 2023; Pinheiro, 2025) and on empirical field experience from the present study.

Criteria	Traditional method ('Redinha' trap)	Burrow typology method(Present study)
Invasiveness	Moderate to high (physical capture of crabs)	Non-invasive
Effort and logistics	High (requires multiple visits, bait preparation, and specialised gear)	Low to moderate (visual/manual inspection and categorisation of burrows)
Field time persampling unit (5 × 5 m)	>2 h per plot	<30 min per plot
Sampling efficiency	Moderate (dependent on crab activity and trap performance)	High (all visible and closed burrows can be assessed and counted)
Environmentalconstraints	High (influenced by tide, weather, and sediment conditions)	Moderate (visibility may drop at high tide, but method remains applicable across habitats)
Behavioural bias	Present (selects only active individuals)	Minimal or absent (includes inactive and active individuals)
Biological dataretrieved	Direct data on size, sex, and reproductive status	Estimated size (from entrance diameter); indirect indicators of activity level or presence; ecological and behavioural phase
Suitability forprotected areas	Limited (conflict with conservation regulationsand require permits)	High (non-destructive, rapid, and easily implemented in protected areas)
Temporal replicability	Variable (affected by crab activity cycles and seasonal constraints)	Consistent (based on standardised criteria, independent of crab emergence)
Data integration with habitat features	Limited (requires independent habitat data collection)	High (directly linked to spatial gradients, vegetation, and flooding patterns)

U. cordatus burrows should be recognised as a potential early indicator of transformative stress in mangrove ecosystems. Proactive monitoring of such traits may support the development of more predictive and adaptive conservation frameworks that can respond to changes in ecological regimes.

Ultimately, preserving the ecological integrity of mangrove zones, with particular emphasis on transitional habitats essential for recruitment, is crucial to ensure the long-term viability of *U. cordatus* populations in the face of accelerating climate change and growing anthropogenic pressure.

CRediT authorship contribution statement

Marcelo A.A. Pinheiro: Writing – original draft, Validation, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alison C. Wunderlich:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Sérgio S. Rocha:** Writing – original draft, Supervision, Project administration, Conceptualization. **Marcio C.A. João:** Validation, Investigation, Formal analysis, Data curation. **Esli E.D. Mosna:** Visualization, Investigation, Formal analysis, Data curation. **Salise B. Martins:** Visualization, Investigation, Formal analysis. **Setuko Masunari:** Writing – review & editing, Visualization, Validation, Funding acquisition, Formal analysis, Data curation.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The data supporting the findings of this study will be available in the UNESP Institutional Repository upon publication. Until then, the datasets are available from the corresponding senior author (MAAP) upon reasonable request.

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