Assessing Ghost crab distribution, abundance and habitat use along the Coromandel Coast, Tamil Nadu

By

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In

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Under the supervision of

Dr. G.V.Gopi, Scientist-F

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June 2025

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DECLARATION

I hereby declare that the work conducted under the thesis entitled **"Assessing Ghost crab distribution, abundance and habitat use along the Coromandel Coast, Tamil Nadu"**, is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Gopi G.V., Scientist-F** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding, and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Keerthi V** entitled **"Assessing Ghost crab distribution, abundance and habitat use along the Coromandel Coast, Tamil Nadu"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Keerthi V has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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EXECUTIVE SUMMARY

1. Sandy beach ecosystems around the world are facing numerous threats and tremendous pressure due to ever increasing human population. One such threat, relevant to the Indian coastline, is the large scale plantations of shelterbelts of the exotic pine, *Casuarina equisetifolia*, which alters beach geomorphology. The effects of such plantations on permanent shore-dwelling organisms are poorly studied. Hence Ocypode crabs, the most conspicuous macro-invertebrate on sandy beaches, has been used as a model taxon to study the effects of different kinds of inland vegetation (Casuarina plantations, Mangrove plantations, native dune vegetation) on beach geomorphology and consequently, shore dwelling ghost crabs. The present study aims to - (1) Assess the density, distribution and demography of ghost crabs across treatments (2) Understand variations in habitat use and burrow architecture across treatments (3) Understand the effects of inland vegetation on beach geomorphology
2. A total of 24 transects, temporally replicated thrice each month between January 2025 - April 2025, were walked to estimate densities of ghost crabs using burrow counts as a proxy. 87 burrows across the treatments were cast using a mixture of Plaster of Paris and water and traits such as depth, diameter, shape and branching patterns were studied. Coast characteristics like slope, compactness, beach width, moisture and temperature were recorded at each study site.
3. Mean burrow densities and across shore distribution of *Ocypode ceratophthalmus* differed across the treatment types, with lowest densities in beaches adjacent to Casuarina plantations. This however wasn't statistically significant. The burrow structures also differed in complexity across treatments with the major drivers for this

difference being the size of the crab and the type of inland vegetation. Environmental variables were not found to have significant effects on burrow architecture.

4. The results indicate that the type of inland vegetation affects the population of ghost crabs through changes in beach geomorphology. Ghost crabs were also found to modify the structure of their burrows with changes in the habitat quality and environmental conditions, which gives insights into their adaptive capacities. The study, thus raises questions on the effects of certain management interventions, like the planting of shelterbelts on habitat quality and on the ecology of the species dwelling in the said habitats.

1. INTRODUCTION

Accounting for 43% of India's coastline, sandy beaches are dynamic ecosystems at the land-sea interface (Mukhopadhyay & Karisiddaiah, 2014) .They provide essential habitats for a wide range of species, including nesting areas for sea turtles, feeding areas for shore birds and crucial breeding and foraging habitats for a variety of invertebrates which dwell and depend entirely upon this ecosystem. As a consequence of increasingly concentrated human populations at the coast, these vital ecosystems are under tremendous pressure which in turn reduces their resilience to climate change and other natural exogenous stressors. Out of these numerous threats, many traditional coastal management strategies such as the construction of seawalls and groynes for coastal armouring, large-scale plantation efforts inadvertently prove to be detrimental to the health of the ecosystem (Defeo et al., 2008).

In Tamil Nadu, a world bank project was initiated in 2007 to plant *Casuarina equisetifolia* in the sand dunes of the East Coast in the aftermath of the 2004 tsunami. Extensive plantations covered more than one-third of the Tamil Nadu Coast in the belief that these plantations would act as bioshields and blunt the impact of high-intensity sea waves and winds on the coast during calamities (Subramanean and Reddy, 2010). However, these plantations drastically affect beach geomorphology and consequently its inhabitants. Large-scale shelterbelt plantations drastically alter the processes of sand dune formation, which is an integral part of beach ecosystems. They also cause erosion and subduction of tracts of beaches and interfere in the dynamics of sand movement. Casuarina, which is an exotic, also does not support local biodiversity - the leaf litter in these plantations is thick, does not decompose easily and therefore it prevents the germination and growth of native vegetation (Chaudhari et al., 2009). Naturally, there is also a loss of habitat for fauna - documented in the Olive Ridley Sea Turtle (Chaudhari et al., 2009) and sand skinks (Subramanean and Reddy, 2010) in the Indian coast.

The impacts of such plantations on permanent coast-dwelling invertebrates such as Ocypode crabs, which perhaps are the most conspicuous and arguably the most charismatic denizens of sandy shores, are unknown. Ghost crabs (subfamily Ocypodinae) are semi-terrestrial crabs, distributed widely on sandy shores in tropical and subtropical regions (Sakai and Turkay, 2013). These crabs are critical components of food chains and food webs - they have been described as “vultures of coastal ecosystems”, they are crucial scavengers, predators as well deposit feeders (Souza, 2021) . Crabs are also commonly referred to as ecosystem engineers of the coast due to the bioturbation caused as a result of their burrowing activities (Holdredge et al., 2010). Ghost crabs are well-suited to be ecological indicators due to : (1) Widespread distribution (2) Conspicuous nature and the relative ease of identification (3) Ease of estimation of abundance through burrow counts (Schlacher et al., 2016) . A meta-analysis on the use of ghost crabs as eco-indicators reveal that only a narrow range of pressures, chiefly urbanisation, beach nourishment and recreation, have been assessed. There exists tremendous potential for the integration of ghost crabs as a model taxon to assess a wider range of impacts from various other human-induced as well as natural stressors. (Schlacher et al., 2016).

This study aims to assess the differences in ghost crab distribution, abundance and habitat-use between coastal beaches with varying types of inland vegetation (that potentially influence beach geomorphology). This study highlights broader implications for coastal biodiversity and management by evaluating the effects of casuarina plantations on ghost crab populations.

1.1 International and National status of Ghost Crabs :

Ghost Crabs as Bioindicators

Ghost crabs are widely recognised as ecological indicators of sandy beach health due to their sensitivity to human and environmental pressures. A large number of studies globally, have used ghost crabs as a model taxon to evaluate the impacts of certain anthropogenic pressures - chiefly urbanisation, on ghost crab populations. Their conspicuous burrowing behaviour, ease of sampling and widespread presence on tropical and subtropical beaches make them ideal eco-indicators. Studies show significant reductions in their abundance in areas subjected to stressors like vehicle traffic and habitat modification. Despite their utility, research predominantly relies on proxies, such as burrow counts, rather than direct biological measures, limiting mechanistic insights. Expanding their use to assess emerging threats, including climate change and pollution, offers potential to integrate ghost crabs as a model taxon in broader impact assessments (Schlacher et al., 2016).

Ghost crabs occur globally in the tropical and subtropical regions. At present, 22 species have been recognised, which belong to two genera - Ocypode, which contains 21 species and Hoplocypode, which is mono-generic (*H.occidentalis*). Out of twenty two, six species of ghost crabs (Genera : *Ocypode*) are found on the sandy beaches along the Indian coast. These are *O.brevicornis*, *O.ceratophthalmus*, *O.macrocera*, *O.cordimanus*, *O.pallidula*, *O.rotunda*. *O.ceratophthalmus* and *O. brevicornis* are found all along the coasts of Indian mainland while *O.macrocera* is only found on the East Coast of India. *O.cordimanus* is found all along the West Coast of India while *O. rotunda* is found in a small part of Gujarat’s coastline and not enough information is known about the distribution of *O.pallidula*. (Sakai and Türkay, 2013)

An inventory of crabs in Cuddalore yielded two species of ghost crabs - *O. ceratophthalmus* and *O. macrocera* (Soundarapandian P, 2013). Nagarajan et al., 2022 report *O.brevicornis* to be the most abundant intertidal crustacean. The authors also stress on the importance of these species to coastal ecosystems as scavengers in the otherwise microbe-deficient sandy systems.

1.2 Impacts of Casuarina Plantations on beach geomorphology and shore-dwelling organisms

Casuarina equisetifolia, native to Australia and parts of South-East Asia, was widely planted in coastal Tamil Nadu to act as shelterbelts post the tsunami which struck in 2004. A review on the adverse effects of Casuarina plantations on beach geomorphology by Awale and Phillott, 2014, brings notice to the mechanisms through which Casuarina outcompetes native species. Production of a large number of seedlings in a short time coupled with thick leaf litter that does not decompose easily and the production of phytotoxic allelopathic compounds prevent the germination of native understory vegetation. This process destabilises and disrupts the natural beach structure leading to flattened beaches more vulnerable or prone to erosion.

Chaudhary et al, 2009 investigated the impacts of Casuarina plantations on nesting beach selection by Olive Ridley turtles. It was found that nesting was significantly lower in beaches with Casuarina stretches when compared to open non-vegetated beaches and those with native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus*. The authors also observed steeper slopes and reduced beach width in areas with plantations.

Subramanean and Reddy, 2010 studied how Casuarina plantations impacted populations of sand skinks (*Eutropis bibronii*). The findings of the study revealed that the shade provided by *Casuarina equisetifolia* trees prevented the skinks from basking in their preferred habitats, thus displacing them. Sand skinks were found in lower abundances in areas with plantations. The authors also observed that the sand skink populations recovered in areas where the plantations had been removed up to 45m from the high tide line and the regeneration of natural vegetation occurred.

1.3 Importance of the proposed study in the context of current knowledge status:

Estimating ghost crab abundance, demography and distribution along the Coromandel Coast, Tamil Nadu, establishes baseline data on populations of these crabs and helps infer the influence of inland vegetation on the population dynamics of ghost crabs. Ghost crabs have tremendous potential to be used as bioindicators of ecosystem health. This however, has not been adequately explored and only a narrow range of stressors, such as urbanisation and recreational uses of beaches have been assessed. There is wide scope to evaluate the impact of other stressors such as pollution, climate change, introduction of exotic flora and fauna on ghost crab populations. Further, in the Indian scenario, very few studies have gone beyond taxonomy and making area-wise inventories to explore the ecology of ghost crabs. Studying their distribution, habitat use and burrow characteristics across treatments would help further the knowledge on ghost crab ecology and any differences observed would provide insights into how inland vegetation affects their daily and spatial needs, and how they adapt to changes in habitat structure. The present study, therefore, aims to :

To assess the influence of different kinds of inland vegetation - *Casuarina equisetifolia* plantations, Mangrove plantations, patches with native dune vegetation (*Ipomoea pes-caprae and Spinifex littoreus*) on ghost crab abundance, distribution and habitat-use.

1.4 Objectives:

1. To assess ghost crab populations - Density, demography (inferred from burrow counts and size classes) and distribution across different treatments.
2. To understand differences in habitat use and burrow architecture across treatments
3. To evaluate the differences in coast characteristics - beach width , slope, sand temperature, compactness and moisture across treatments

1.5 Research Questions & Hypothesis & predictions with justification(s):

1. Does inland vegetation affect crab densities, demography and distribution?

   Ghost crab populations will be affected by coast health and environmental characteristics and will therefore, differ across the treatments.

   Inland vegetation type (Casuarina/ Native vegetation/ no vegetation) affects beach geomorphology (Chaudhari et al., 2009), which may consequently have an effect on ghost crab population. Casuarina plantations are dense monocultures with thick root systems which result in the stabilisation and compaction of soil. The natural sand dynamics - movement of sand due to wind and waves are disrupted (Chaudhari et al., 2009). Ghost crabs rely on loose, well aerated sand to construct their burrows (Stelling-Wood et al., 2016) - limiting this critical resource would affect their spatial distribution and abundance negatively. Vegetated beaches would harbour highest crab densities followed by areas with no vegetation and Casuarina plantations.

2. Does inland vegetation affect habitat-use by ghost crabs? Does burrow structure (complexity and depth) vary across treatments?

Casuarina plantations reduce the availability of suitable burrowing substrate, forcing crabs to relocate to suboptimal areas or to cluster in whatever space remains. Therefore, I predict that a greater number of burrows will be found closer to the sea.

2. METHODS

2.1 STUDY AREA

The study was conducted in the sandy beaches along the Coromandel Coast, Tamil Nadu in Chennai and Cuddalore districts. The differences in the abundance, habitat-use and burrow structure of ghost crabs will be assessed in the following different treatment types - ***Casuarina equisetifolia*** **plantations, Mangrove plantations and patches with native dune vegetation (*Ipomoea pes-caprae and Spinifex littoreus*)**. Attempts were made to include open non-vegetated stretches of beaches as a treatment type. However, such potential sites differed from the others in factors like extremely high human foot fall (for recreational use as well as the presence of fishing hamlets), which would have affected ghost crab populations in ways other than what was being tested in the present study.

Study sites include :

1. **Chidambaram** - Pichavaram range from Kodiyampalayam to MGR thittu with mangrove plantations as inland vegetation (from 11.38°N, 79.81°E to 11.40°N, 79.81°E).
2. **Cuddalore** - Silver Beach to Sonakuppam (from 11.73°N, 79.78°E to 11.72°N, 79.78°E) and Sothikuppam Beach (from 11.69°N, 79.77°E to 11.70°N, 79.78°E) with Casuarina plantations as inland vegetation.
3. **Chennai** - Neelankarai (from 12.94°N, 80.26°E to 12.94°N, 80.26°E) and Injambakkam (from 12.92°N, 80.25°E to 12.93°N, 80.25°E) with native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus* as inland vegetation.

The study area has been chosen due to the ongoing plantation drive that is being carried out by the Tamil Nadu Government under the Green Tamil Nadu Mission under the scheme "Rehabilitation of Coastal habitats through the formation of Bio- shields with Casuarina, Palmyrah, Cashew, Mangrove, restoration of seagrass and coral reefs" from the year 2023-24 to 2025-26 in all coastal Districts of the State. This study aims in assessing the effects of such large-scale plantations on beach geomorphology and consequently, its inhabitants.

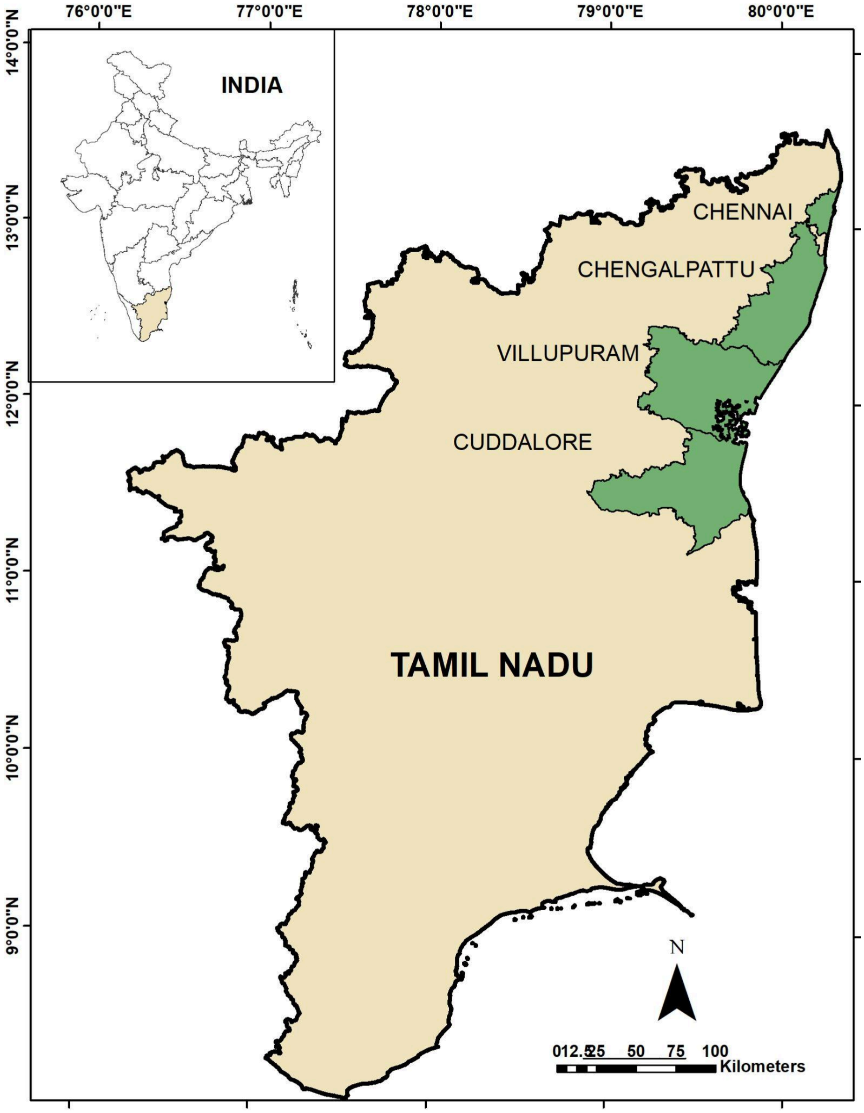


Fig 1: Map depicting study area - coasts of Chennai and Cuddalore

2.2 FIELD METHODS

The study is designed to investigate the influence of inland vegetation type on ghost crab abundance, habitat-use and burrow architecture across multiple treatments in two coastal districts of Tamil Nadu. The treatments include *Casuarina equisetifolia* plantations, Mangrove plantations and patches with native dune vegetation (*Ipomoea pes-caprae and Spinifex littoreus*) .An initial reconnaissance survey was used to check the availability of each treatment based on which it was proportionally, thus ensuring robust representation across the landscape. The field methods that were carried out to achieve each objective are detailed in the following subsections.

1. To assess ghost crab populations -density, demography and distribution across different treatments.

From review of existing literature on crab biodiversity along the south-east coast of India (Soundarapandian, 2013), it is known that three species of ghost crabs - *Ocypode ceratophthalma*, *O. macrocera* and *O. brevicornis* co-occur in the study area. To enumerate the abundance, surveys for all the three species will be carried out using the following two methods:

Belt transects to count ghost crab burrows

Belt transects of 5m width will be laid out perpendicular to the coast, starting from the low tide line up to the inland vegetation. The length of the transects would, therefore, be the same as the width of the beach where the ghost crabs are being sampled. The transect would be divided into three zones - (1) Intertidal zone (between the high tide line and the low tide line) (2) Supralittoral zone (beyond the high tide line) (3) Inland vegetation zone. These zones were further divided into 5*5m sub-plots to collect data at a much finer scale. Burrow counts were carried out in these zones in every subplot , along the transect to estimate crab abundance. Burrow counts are a reliable proxy for ghost crab abundance as each individual occupies only one burrow (Brook et al., 2009). Tidal regimes are a major determinant of crab activity along with the time of the day, therefore sampling will be carried out at low tide in the early mornings, preferably during spring tides (Brook et al., 2009). This would also ensure the counting of burrows in the intertidal zone.

The number of transects in each treatment was decided based on the availability of each treatment, therefore the distance between each transect also depended on the same. The distance between the transects was 250m in Chidambaram, 200m in Chennai and 150m in Cuddalore because of the limited availability of Casuarina plantations in the study area. 150m was fixed as the minimum distance between transects because earlier studies have reported the home ranges of crabs to be up to 150m (Schlacher, 2010).

Attempts were made to ascertain the identity of species as well as collect data on the age and sex of the individual by burrow excavation or by luring out the occupant. This procedure, although invasive, does not drastically affect the life of the crabs because ghost crabs are known to rebuild burrows anywhere within 1-14 days (Lucrezi, 2014). However, this wasn’t possible due to the extremely labour and time-intensive nature of burrow excavations. Therefore, the above methodology was used to estimate only the populations of *Ocypode ceratophthalmus*, the Horn-eyed ghost crab, which was the only species of ghost crab found in all the proposed study sites. Burrows of *Ocypode macrocera*, the Red Ghost Crab possessed distinct patterns around the burrow opening, which along with direct opportunistic sightings were used to assess its populations at Kodiyampalayam, the only study site at which it was present.

2. To understand differences in habitat use and burrow architecture across the treatments

Casting using beeswax or gypsum (2:1 ratio of Plaster of Paris and water) can be done to understand burrow structure and depth (Lucrezi and Schlacher, 2014). The depth and the burrow diameter were measured using the excavated casts. The shape and patterns of the casts will be recorded through visual observations (Gul and Griffen, 2018). This procedure will be carried out after sunset to ensure that the crabs are out of their burrows.

Use of the available habitat by individuals belonging to different size and hence age classes as well as different species will be studied using data from the excavated casts as well from the belt transects.

3. To evaluate the differences in coast characteristics beach width , slope, sand temperature, compactness, moisture across treatments

The coast characteristics listed above may be potentially influenced by the type of inland vegetation. They may, in turn, affect ghost crab populations because of which they would also be considered as covariates. These parameters will be measured as follows:

Understanding how beach width changes with actions such as plantations, construction of sea walls, etc is essential for informing future management strategies. This is an important parameter for measuring the health of a beach and is usually defined as “the distance between dune crest and shoreline position at high tide” (Method for Coastal Management, Field Studies Council). However, since ghost crabs are also known to utilise the intertidal zone, the width of this region (distance between the high tide line and the low tide line) was also incorporated into beach width.

Slope was measured using methods suggested by Emery, 1961 and Chaudhary, 2009.

Soil penetrability or compactness was measured using the BJPS method of soil penetration (Jones and Reynolds, 1996). A calibrated pointed metal rod is dropped into the ground from a set height and the depth of penetration was then measured. (Brook S, 2009)

Soil moisture and sand temperature are other factors that could influence burrow morphology and size. Therefore, surface temperature and moisture was recorded using a moisture meter and digital thermometer, respectively. (Gul and Griffen, 2018).

2.3 ANALYTICAL METHODS

All the analysis listed below were performed using R version 4.5.0 and the packages contained within it.

1. **To assess ghost crab populations -density, demography and distribution across different treatments.**

Burrow densities were calculated across the treatments using the formula - Density = Total count of active burrows/(Width of the transect*Length of the transect for each transect, which was then averaged out to obtain mean densities of *O. ceratophthalmus* across different treatments. The significance of the results were tested using the Kruskal-Wallis Test as the data was not normally distributed.

Burrow size class distribution was used as a proxy to understand the age-structure of the population. Densities of burrows across different sizes were obtained and their distribution across the width of the shore was visualised using heatmaps, line plots and box-plots, plotted using the package ggplot2.

2. **To understand differences in habitat use and burrow architecture across the treatments.**

Differences in parameters such as depth, diameter, shape and the number of branches of ghost crab burrows were visualised using box plots, plotted using the package ggplot2. The mean values of these burrow depths and diameters were obtained and the significance of difference across treatments were tested using the nonparametric Kruskal-Wallis Test. If the differences were found to be significant, Dunn's Test was used post-hoc to identify the pairs of treatment which differed significantly. Fisher's exact test was used to compare the shape and branching pattern of burrows across treatments since these variables were categorical.

Before running linear models, the predictor variables were checked for multicollinearity. This was kept in mind while building linear models to understand the determinants of depth. Models were run using log-transformed values of depth to meet the assumptions of linear regression. A combination of the AIC scores, model fit and the ecological interpretation of the results was used to select the best model.

3. **To evaluate the differences in coast characteristics beach width , slope, sand temperature, compactness, moisture across treatments**

Kruskal-Wallis test and ANOVA were used according to the distribution of the variable to compare the values of the above mentioned parameters across treatments. These differences were also visualised using simple box plots, plotted using the package ggplot2.

3. RESULTS

3.1 Assessing ghost crab populations - density, demography and distribution across different treatments

The present study assessed the populations of the Horn-eyed ghost crab (*Ocypode ceratophthalmus*) across three treatment types, i.e. sandy beaches with different types of inland vegetation - (1) Casuarina plantations (2) Mangrove plantations along with native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus* and (3) only native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus* (17 casts). Literature review and observations during data collection revealed that other ghost crab species - *Ocypode macrocera* and *Ocypode brevicornis* were not present in all the study sites. Therefore, only *O.ceratophthalmus* populations were compared between the different treatments.

7.1.1 Density of Ghost Crab burrows across Treatments

Mean burrow density varied across the different treatment types as summarised in Table 1. The highest burrow densities were observed in sandy beaches with native dune vegetation (mean = 0.052 burrows/m² at Injambakkam and 0.06 burrows/m² at Neelankarai in Chennai), followed by sites with the inland vegetation being Mangrove plantations (mean = 0.05 burrows/m²) with the lowest densities being reported from beaches adjacent to Casuarina plantations (mean = 0.023 burrows/m² and 0.032 burrows/m² at two different plantation sites at Cuddalore). However, these differences in density were not statistically significant according to the results of Kruskal-Wallis Test (p= 0.16).

Table 1 : Mean burrow densities of *Ocypode ceratophthalmus* across Treatments

Location	Treatment Type	Mean_ Density/ sq. m	SD	Species Present
Chennai_Injambakkam	Native	0.052	0.058	*O.ceratophthalma*
Chennai_Neelankarai	Native	0.06	0.078	*O.ceratophthalma*
Cuddalore_OldCity	Casuarina	0.023	0.039	*O.ceratophthalma*
Cuddalore_SilverBeach	Casuarina	0.032	0.036	*O.ceratophthalma*
Chidambaram_Kodiyampalayam	Mangroves	0.05	0.066	*O.ceratophthalma* *O.macrocera*

Table 2 : Proportion of burrows of different size classes across treatments

		Proportion of burrows of different size classes			
Location	**Treatment Type**	**V small**	**Small**	**Med**	**Large**
Chennai_Injambakkam	Native	0.3377	0.3796	0.1911	0.0916
Chennai_Neelankarai	Native	0.3553	0.3684	0.1754	0.1009
Cuddalore_OldCity	Casuarina	0.1614	0.7228	0.1018	0.014
Cuddalore_SilverBeach	Casuarina	0.2766	0.3085	0.2553	0.1596
Kodiyampalayam	Mangroves	0.2692	0.4257	0.2183	0.0869

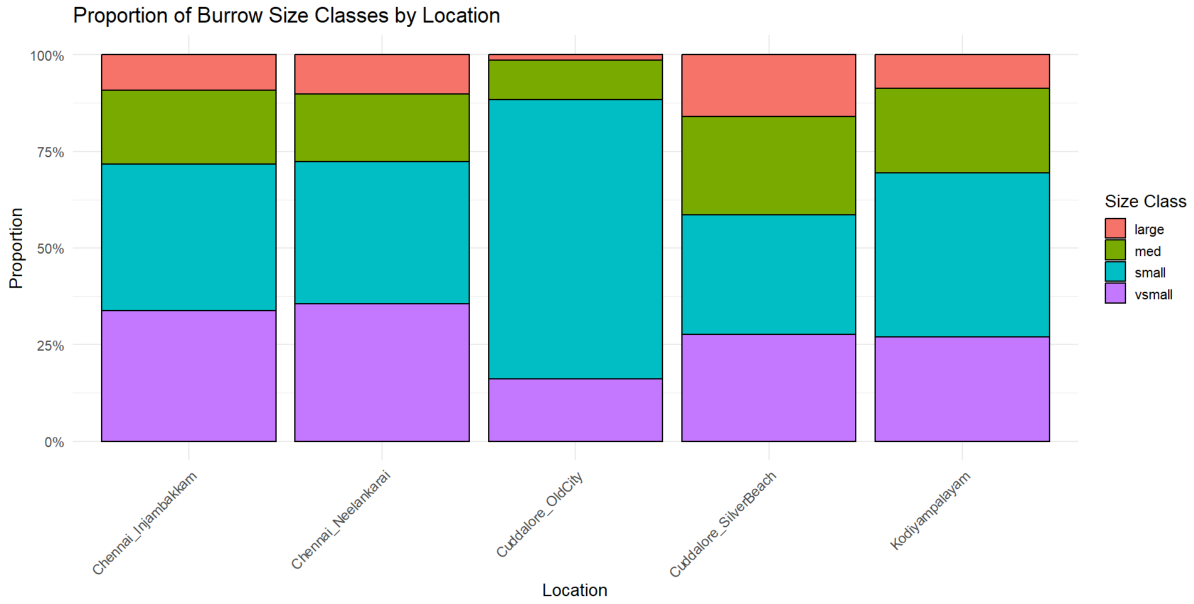


Fig 2: Proportion of burrows belonging to different size classes at different locations

Table 3 : Mean burrow densities of burrows of *O. ceratophthalmus* belonging to different size classes

	Burrow densities and Standard deviation				
Location	**Treatment Type**	**V. Small (<2cm)**	**Small (2-4 cm)**	**Medium (4-6 cm)**	**Large (>6cm)**
Chennai_Injambakkam	Native	0.43(±0.21)	0.483(±0.201)	0.243(±0.112)	0.116(±0.114)
Chennai_Neelankarai	Native	0.405(±0.188)	0.420(±0.146)	0.2(±0.124)	0.115(±0.094)
Cuddalore_OldCity	Casuarina	0.184(±0.133)	0.824(±0.421)	0.116(±0.09)	0.016(±0.02)
Cuddalore_SilverBeach	Casuarina	0.13(±0.108)	0.145(±0.087)	0.12(±0.042)	0.075(±0.091)
Chidambaram_Kodiyampalayam	Mangroves	0.688(±0.44)	1.088(±0.535)	0.558(±0.243)	0.222(±0.172)

3.1.2 Demography from Burrow Size Class Distribution

Studies on ghost crabs have demonstrated that there exists a strong collinearity between the diameter of burrow openings and the width of the carapace of the crab (Tiralongo et al., 2020). Therefore, burrow size classes here have been used as a proxy for crab size (and consequently age class). Sites with native dune vegetation and Mangrove plantations showed a wide spread of all size classes, including a higher proportion of medium and large sized burrows, probably constructed by adult males and females, which indicates a demographically balanced population. In contrast, Casuarina plantations had comparatively higher proportions of small and very small burrows, probably constructed by juveniles and sub-adults, suggesting limited recruitment into adulthood. Table 2 and Fig 2 summarise and provide a visual representation of the proportion of burrows of different size classes across treatments. The mean burrow densities and their standard deviations of burrows of different size classes are provided in Table 3 .

3.1.3 Demography from Burrow Size Class Distribution

Fig 3 is a heatmap that shows the distribution and densities of burrows of different size classes at varying distances from the low tide line (LTL) across different treatments. A line plot has also been given (Fig) to provide an easier visualisation of the overall burrow distribution across shore for all the different treatment types. From Fig. 4 it is evident that Casuarina plantations support the least burrow density overall and the burrows are limited to shorter distances from the LTL compared to the other two treatments. Mangrove plantations had the widest distribution of burrows across the beach width.

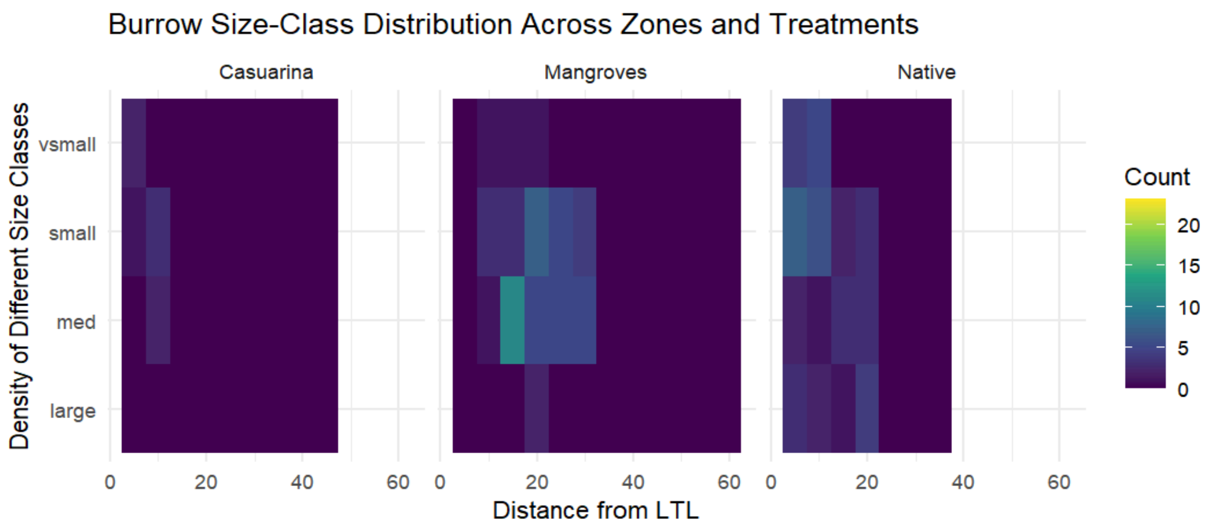


Fig 3: Heatmap depicting burrow size-class distribution across zones and treatments

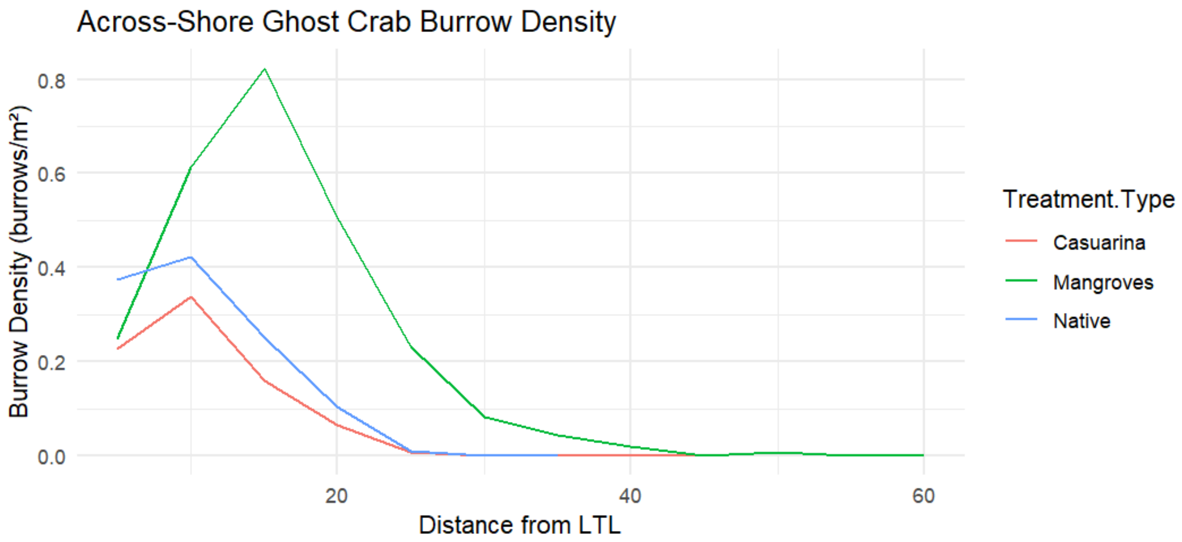


Figure 4: Across-shore ghost crab burrow density

3.2 Burrow Architecture

3.2.1 General Structure of burrows

A total of 87 intact burrows were excavated post casting out of which 77 were constructed by *Ocypode ceratophthalmus* and 10 by *Ocypode macrocera*. *O.macrocera* was found only in one of the five study sites, hence the number of casts excavated for this species is low. The process of casting burrows was carried out at sandy beaches with three different types of inland vegetation - (1) Casuarina plantations (22 casts) (2) Mangrove plantations along with native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus* (48 casts) and (3) only native dune vegetation like *Ipomea pes-caprae* and *Spinifex littoreus* (17 casts).

A total of 6 different burrow shapes were recorded. These included I shaped burrows, a single tubular structure (50 casts), J shaped burrows (32 casts), Y shaped burrows (1 cast), U shaped burrows (2 casts), S shaped burrows (1 cast) and a conical burrow (1 cast). These burrows were either unbranched or had 1 or 2 branches. All the burrows constructed by *O.macrocera* were found to be J shaped which ended at a bulb-like chamber which was occupied by the crab.

Burrows were found to range between a depth of 6 cm to 142 cm with diameters between 1.25 to 7 cm across treatments. The mean depth and diameter showed differences across treatments, which has been listed in Table 4 and visualised graphically in Fig. 5 (a) and (b). The box and whisker plots revealed differences in the mean depth and diameter of burrows across treatments and the statistical significance of these differences was tested by the Kruskal-Wallis test as the distribution of depths and diameters were found to be non-normal.

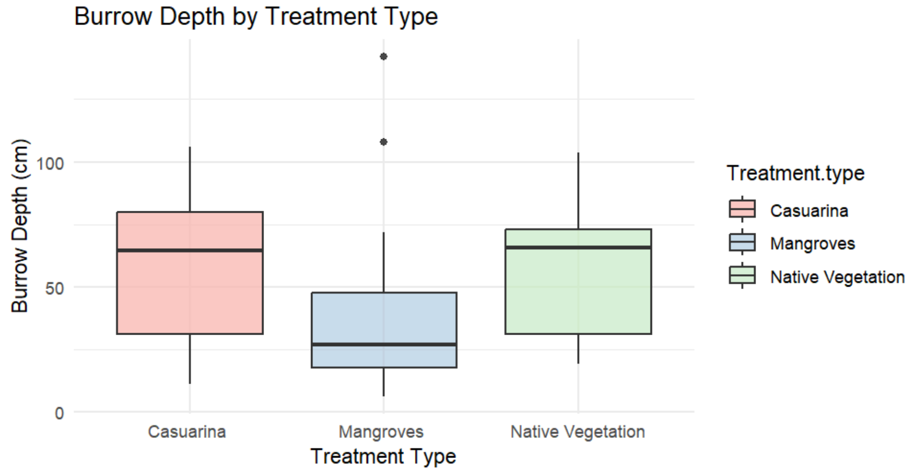
Burrow depths were found to differ significantly between treatments (p = 0.0005476) and Dunn’s post-hoc test revealed that burrow depths between Casuarina and Mangrove Plantations as well as Mangrove Plantations and native dune vegetation were significantly different (p = 0.0032 and p = 0.101 respectively) but not between Casuarina Plantations and native dune vegetation (p = 1).

Similarly, burrow diameters were also found to differ significantly between treatments (p = 0.007434) and Dunn’’s Test was used post-hoc to understand where the differences lie between the groups. The results showed that the difference in diameters was only statistically significant between Casuarina Plantations and native dune vegetation (p = 0.006), whereas Casuarina vs Mangrove Plantations and Mangrove Plantations vs native dune vegetation did not show much of a difference (p = 0.1043 and p = 0.3223, respectively).

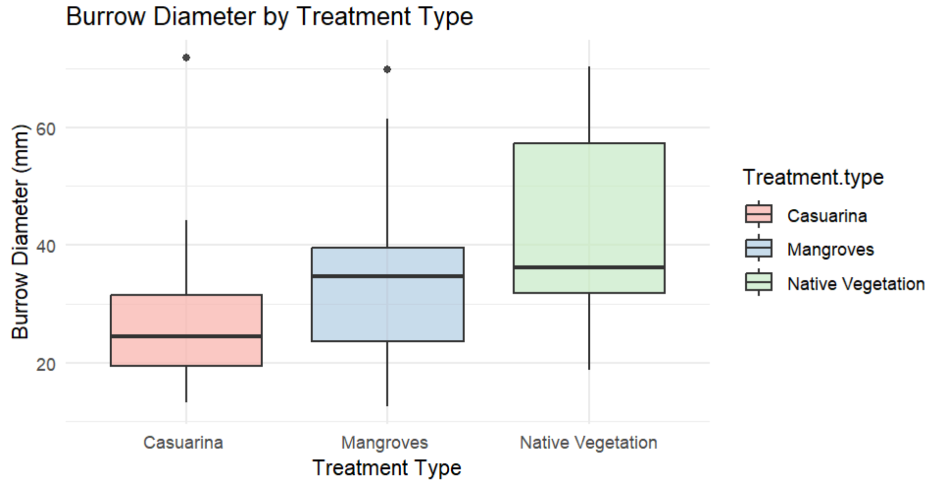
Fisher’s exact test was used to determine if the shape and branching of the burrows varied significantly between treatments. Significant differences were not found in the distribution of different-shaped burrows across treatments (p = 0.3028), while branching did vary significantly (p = 0.00001) between the three treatments. Figs. 5 (c) and (d) depict these variations graphically.

Table 4: Mean burrow depth and diameter

Parameter	Native Vegetation	Casuarina Plantation	Mangrove Plantation
Mean diameter	41.37	27.04	33.26
Std deviation	15.85	12.68	13.46
Mean depth	57.78	58.67	35.23
Std deviation	28.17	29.24	25.98



5(a)



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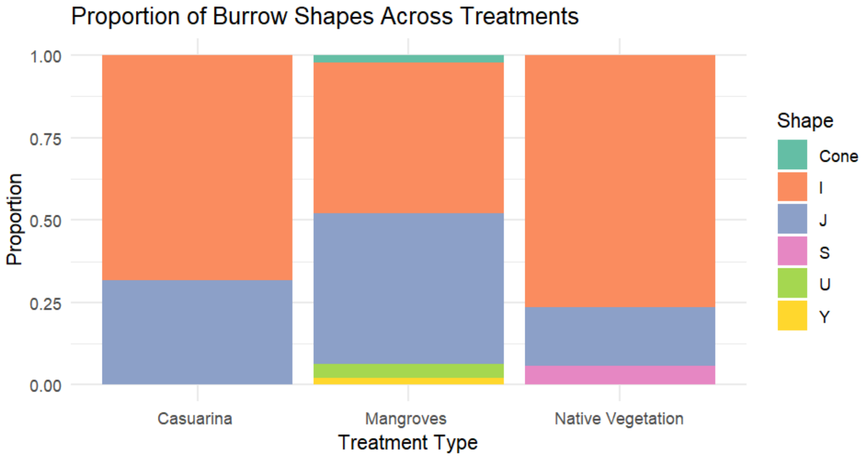
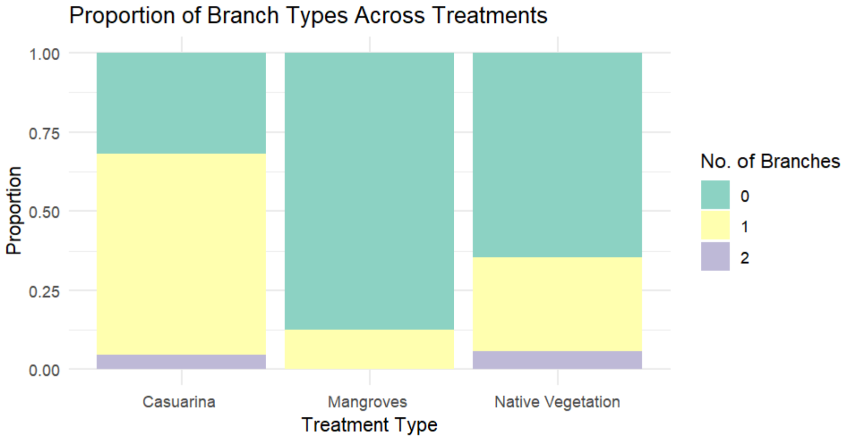


5(c)



5(d)

Figs. 5. (a) Burrow diameters across treatments (b) Burrow depths across treatments (c) Proportion of burrow shapes across treatments (d) Proportion of branch types across treatments

3.2.2 Determinants of Burrow Architecture

Multicollinearity between predictor variables

The covariates were tested for collinearity before running linear models to improve the reliability and interpretability of the results. Earlier studies (Tiralongo et al., 2020; Yılmaz,2020; Vachhrajani, 2016) have found strong correlations between burrow diameter and the width of the carapace of the crab. However, in the present study, crabs weren't captured during burrow excavation. Therefore, diameter is used as a covariate as a proxy for the size of the crab which in turn is an effect of the age of the crab. Fig 6 (a) and (b) depicts strong collinearities between burrow diameter and distance from the low tide line (LTL) (cor = 66%). Similarly moisture and sand temperature are also strongly correlated to the distance from the LTL (cor = -70% and cor = 73% respectively). This is intuitive, because as we move away from the water line the sand moisture content decreases while sand temperature increases. Sand moisture and temperature were also found to be collinear (cor = -50%).

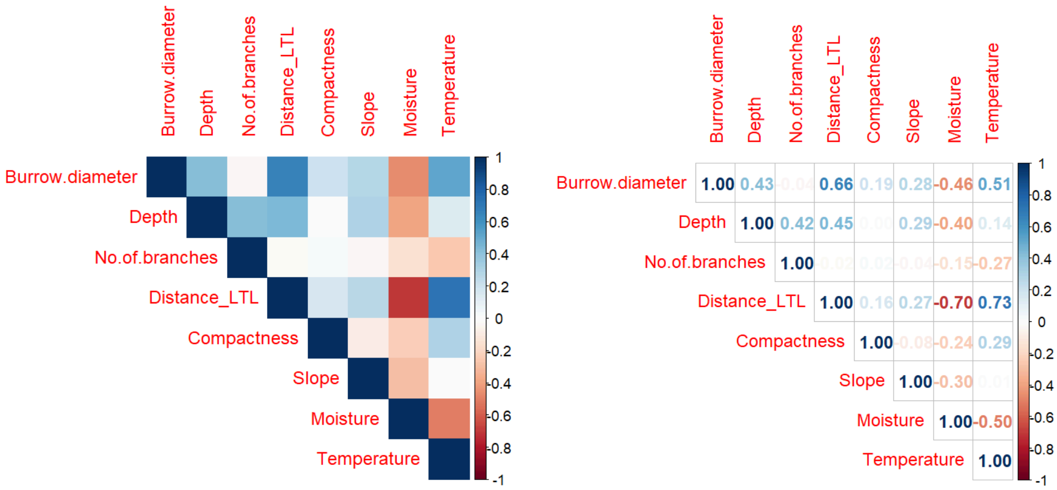


Fig. 6 (a) and (b) Heatmap and values of multi-collinearity between predictor and environmental variables

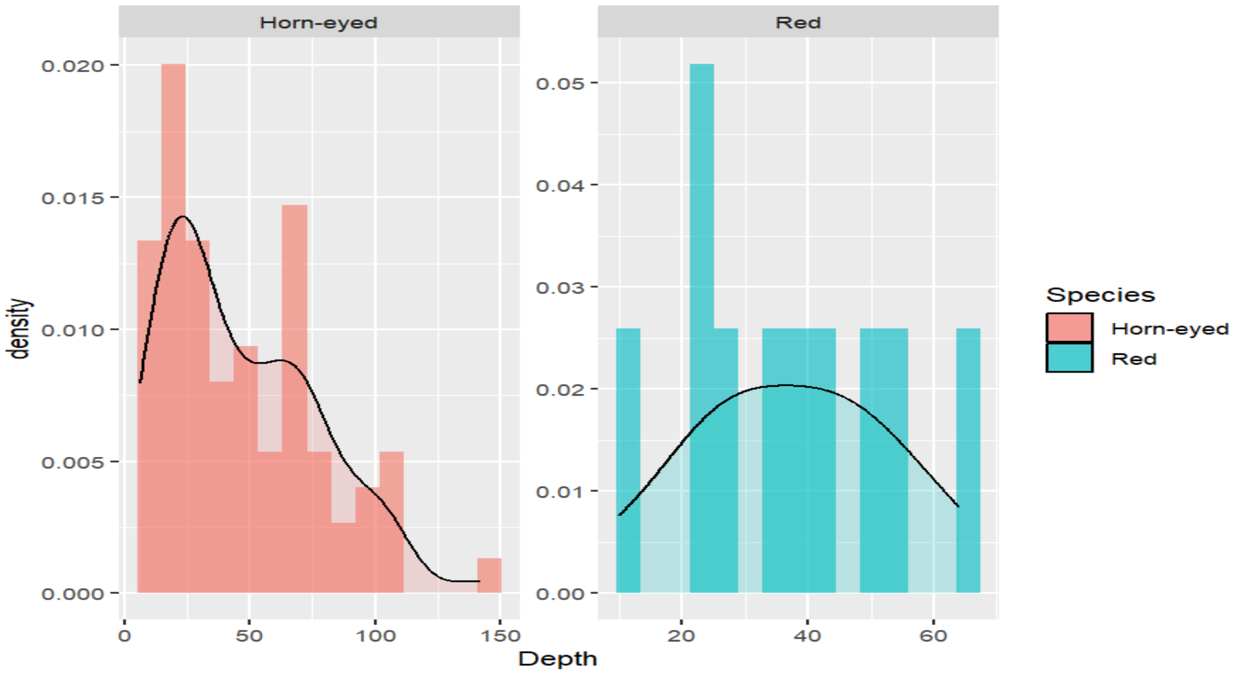


Fig 7 : Distribution of burrow depth in burrows constructed by *O.ceratophthalmus* (Horn-eyed ghost crab) and *O.macrocera* (Red Ghost crab)

3.2.3 Burrow Depth

Burrow depth is a function of the burrow diameter, which is a proxy to the size and hence the age of the crab constructing the burrow. To check if the treatment type has an effect on the depth-diameter relationship, linear models were run after log transforming the values of burrow diameter, since the values of diameter were not normally distributed as shown in Fig.7. Keeping in mind the values of collinearity between the predictor variables, several linear models were run to determine what influenced burrow depth. Burrow depth was the response variable and the predictors were - (1) Burrow diameter (proxy for age of the crab) (2) Distance from the LTL (3) Treatment type (4) Compactness (5) Moisture. Tables 5 and 6 show all the models used and how they are arranged based on AIC values.

Two models with the lowest AIC values (delta<2) were compared and the model which made better sense ecologically was chosen according to the principle of parsimony. The results of the selected model are presented in Table 7 . The major predictors of burrow depth were found to be the burrow diameter (size and hence age of the crab) and the treatment type. An adjusted R-squared value of 0.3807 indicated that the model was a good fit.

Table 5 : Models used to explain the variation in Depth

Model no.	Metrics
1	log_Depth~ Burrow.diameter
2	log_Depth ~ Distance_LTL
3	log_Depth ~ Treatment.type
4	log_Depth ~ Burrow.diameter*Distance_LTL
5	log_Depth ~ Burrow.diameter+Treatment.type
6	log_Depth ~ Treatment.type+Compactness+Moisture
7	log_Depth ~ Burrow.diameter*Distance_LTL+Treatment.type

Table 6 : Model selection table ranked by AIC

Model no.	Intercept	BD	LTL	Treatment	BD:LTL	C	M	df	logLIk	AIC	AICc	delta	Weight
7	3.099	0.018	0.03	+	-4.28e-05			7	-69.769	153.53	155	0	0.677
5	3.197	0.026		+				5	-72.845	155.68	156.4	1.48	0.323
1	2.808	0.023						3	-84.65	175.3	175.6	20.64	0
4	2.752	0.016	0.01		2.44e-05			5	-83.505	177.01	177.8	22.8	0
6	4.317			+		0.021	-0.013	6	-82.702	177.4	178.5	23.5	0
2	2.978		0.04					3	-87.045	180.08	180.4	25.43	0
3	3.904			+				4	-87.513	183.02	183.5	28.56	0

Table 7 : Results of Model 5

	Estimate	Std. Error	p Value	Significance
(Intercept)	3.196621	0.172975	< 2e-16	***
Burrow diameter	0.02616	0.004534	1.33E-07	***
Treatment type Mangrove Plantations	-0.741689	0.150024	3.93E-06	***
Treatment type Native Vegetation	-0.357969	0.195905	0.0713	.

Significant. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

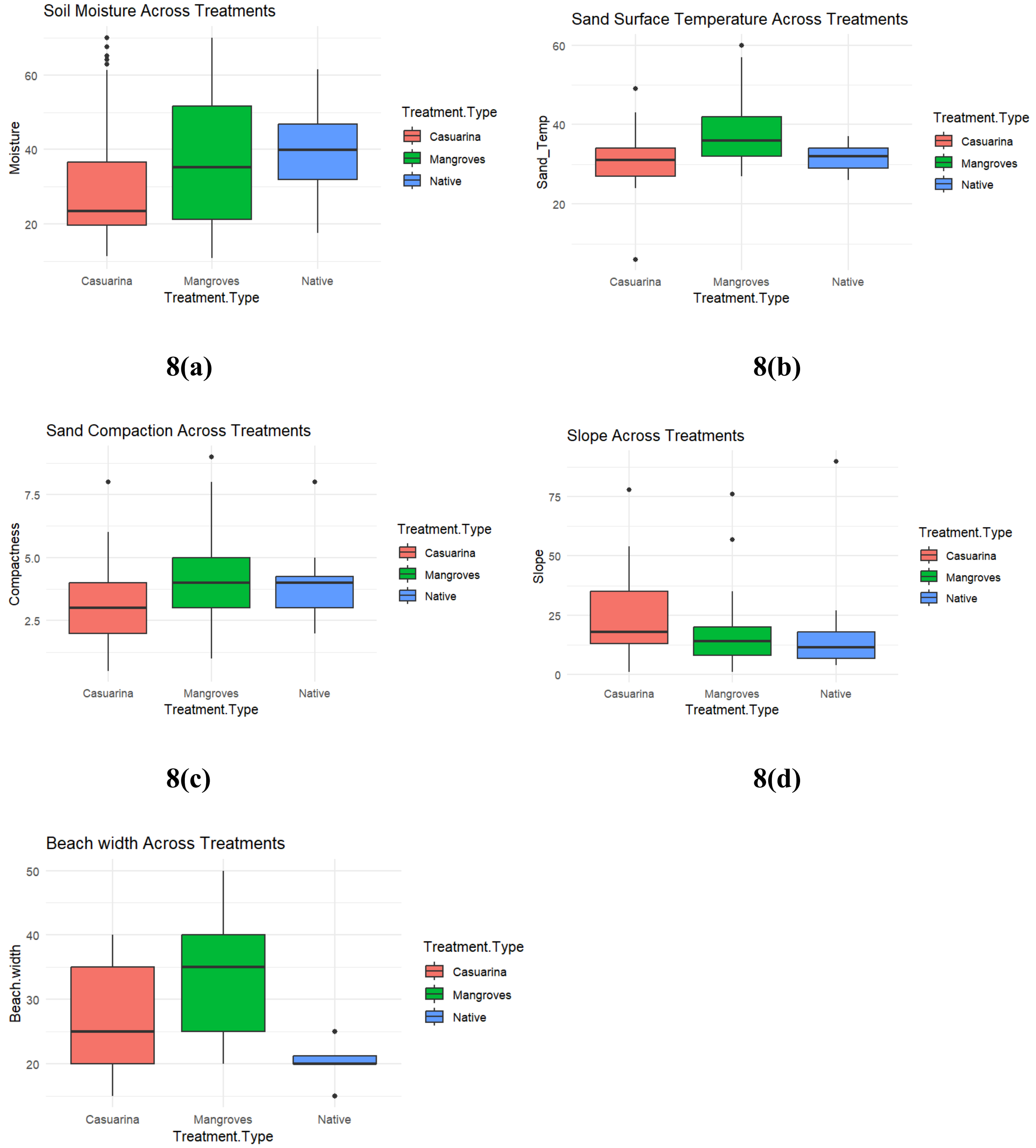
Residual standard error: 0.5723 on 83 degrees of freedom

Multiple R-squared: 0.4023, Adjusted R-squared: 0.3807

F-statistic: 18.63 on 3 and 83 DF, p-value: 2.499e-09

3.3 Visualising differences in coast characteristics across treatments

The environmental variables - moisture, temperature, compaction, slope and beach width were compared between treatments and the differences were tested for statistical significance (Table 8). Visual representations are provided in Fig.8.



8(a) **8(b)**

8(c) **8(d)**

8(e)

Fig.8 Variation of environmental variables characterising beach geomorphology across Treatments (a) Soil Moisture (b) Sand Surface Temperature (c) Sand Compaction (d) Slope (e) Beach Width

Table 8: Statistical significance of difference in environmental variables across treatments

Test	**Parameters considered**	**p value**	**Significance**
Kruskal-Wallis	Soil Moisture by Treatment Type	0.078	
Kruskal-Wallis	Sand Temperature by Treatment Type	0.0003	***
Anova	Compactness by Treatment Type	0.0181	*
Kruskal-Wallis	Slope by Treatment Type	0.06	
Kruskal-Wallis	Beach width by Treatment Type	2.23E-07	***

4. DISCUSSION

4.1 Density, Distribution and Demography

4.1.1 Density of Ghost Crab burrows across Treatments

The results of the study clearly illustrate how ghost crab population structure and distribution across sandy beach habitats is influenced by the presence of inland vegetation. The horn-eyed ghost crab, *O.ceratophthalmus,* densities were highest in sites with native dune vegetation, followed by mangrove-associated areas with the least densities being found in beaches adjacent to Casuarina plantations. Sandy beaches with native dune vegetation are the closest to the natural, ideal habitat conditions of ghost crabs, i.e native dune systems. Such systems are the results of several natural processes, both short- and long-term such as severe episodes of storm, sand accretion due to the action of winds and tides, etc. Native dune vegetation aids these processes by reducing erosions and by trapping sediments which in turn contributes towards dune growth (Sigren, 2014). *Casuarina equisetifolia*, Australian pine, native to Australia and South-east Asia, modifies the beach geomorphology (Zoysa, M. (2008); Chaudhari, 2009; Miah,2013) , thereby creating suboptimal conditions which limit ghost crab populations. These ecological implications persist even though the density differences weren't statistically significant (p=0.16). Further studies, across seasons, and greater number of transects could be carried out to verify the findings.

4.1.2 Demography and Size-Class Structure

Size-class distribution patterns of *O.ceratophthalmus* revealed interesting insights into the demographic structure of populations across different treatments. Beaches with native dune vegetation and mangrove plantations supported populations that were demographically balanced, with substantial densities of medium and large sized burrows - a proxy for adult crabs. Such demographically balanced populations indicate the optimal nature of these habitats because of their ability to support viable and reproductively active populations.

On the other hand, Casuarina plantations had a greater proportion of small and very small burrows, which are indicative of poor survival beyond juvenile phase or dispersion of adult crabs to other optimal areas. Such skewed demographic structures could be an early warning sign of population decline. However, it is important to note here that age structures within ghost crab populations are very poorly understood due to absence of intensive research, leading to a lack of baseline information to compare the results obtained in the present study.

4.1.3 Burrow Distribution Across Shoreline

The distribution of burrows was also analysed as a function of the distance of the burrow from the low tide line. Across all the three treatments, a greatest number of burrows were found at distances less than 20 m from the low tide line. Burrow densities in the lower intertidal region as well as in supralittoral regions over 20 m from the low tide line were lesser with burrows ceasing to exist beyond 45m in mangrove plantations and 25m in beaches with native dune vegetation and Casuarina plantations.

Beaches adjacent to Casuarina plantations harboured the lowest densities of burrows at all distances across the shore. A narrow band of distribution concentrated closer to the shore could be due to effects of soil compaction, altered temperature and moisture gradients, reduced beach width or increased human disturbance in the altered habitats. The effects of these variations in these variables across treatment types is tested statistically in later sections.

Densities across the stretches with native dune vegetation was only slightly better, while beaches adjacent to mangrove plantations performed significantly better compared to Casuarina plantations. This could be due to the effects of several other factors - Kodiyampalayam beach was remote and had lesser human footfall, therefore much lesser disturbance compared to the other two treatment types. Efforts were made to select study sites that were similar to each other in most aspects other than the treatment type, however, the limited presence of sandy beaches adjacent to Mangrove plantations was a limiting factor. The heatmaps and the line plots reinforce these patterns visually.

4.2 Burrow Architecture

4.2.1 General Structure of burrows

The present study revealed that the burrow morphology of Ocypode ceratophthalmus varied considerably in shape, size and branching pattern and hence in the overall complexity of burrow structure. Burrows ranged between depths of 6 cm to 142 cm with simple single tubed structures to curved structures with multiple branches. The architectural complexity and size of ghost crab burrows provide indirect evidence of behavioural and physiological responses to environmental conditions. Variations in the patterns of burrow construction (depth-diameter relationship, shapes and branching) indicate that ghost crabs modify their burrowing behaviour in response to habitat quality.

Studies have previously shown that crab carapace width shows a strong correlation with burrow opening diameter and that larger crabs constructed burrows with wider diameters and deeper depths (Tiralongo, 2020). Juvenile ghost crabs, which are smaller in size, construct shallower burrows for a few reasons - Smaller gill areas necessitate frequent exposure to the sea to renew their respiratory water. Therefore these crabs are found closer to the waterline (also shown in Fig.3) which leads to inundation of burrows with sea water with the tidal regime. This coupled with the fact that these individuals spend a lesser proportion of time inside their burrows due requiring near-constant exposure to seawater, explains the simple, shallow burrow structures (Chakrabarti, 1981). Larger crabs, with bigger gill surfaces, can tolerate prolonged periods of exposure to air. Therefore, during the day, these crabs plug the entrances to their burrows and stay put inside, resulting in deeper burrows. Deeper burrows also help maintain a required level of moisture in the chamber to prevent desiccation and to meet respiratory requirements(Chan, 2006).

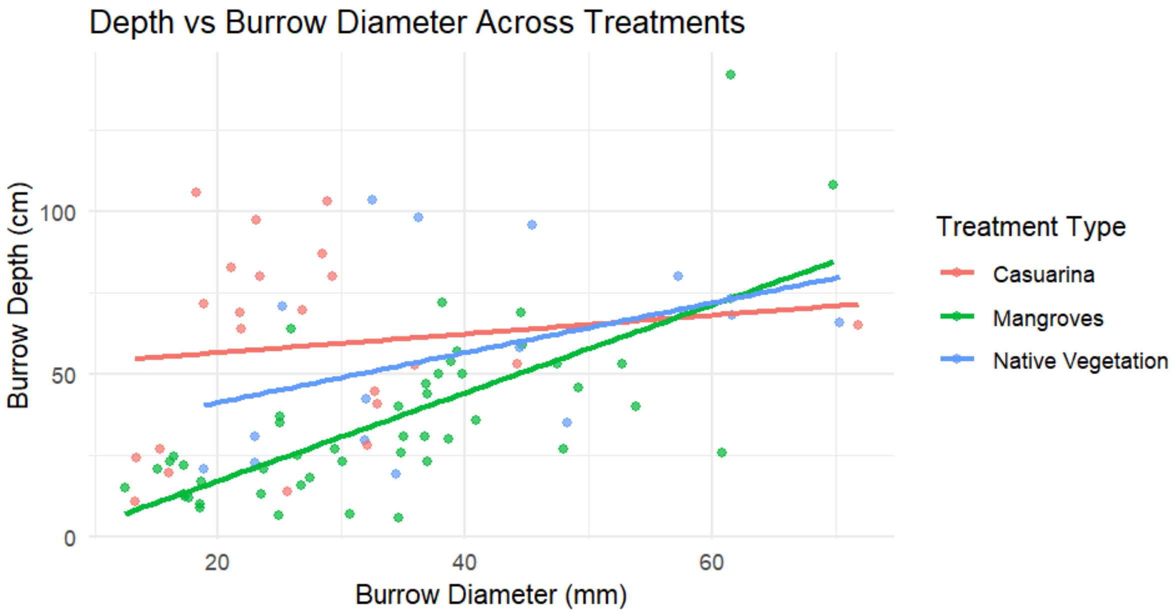


Fig. 9 : Depth vs Diameter relationship across treatments

Fig.9 gives the burrow diameter vs depth relationship across various treatments. A simple correlation analysis between depth and diameter across treatments reveals that a strong correlation exists in the beaches adjacent to the mangrove plantations (cor = 0.701), followed by native dune vegetation (cor = 0.432). In beaches adjacent to Casuarina plantations the depth-diameter correlation is very weak (cor = 0.125), indicating a disruption in the functional relationship between these two aspects of burrow structure. This suggests that, in these sites larger burrow openings are not consistently associated with deeper burrows. The Casuarina patches at the two different locations differed in the distance of the plantation from the high tide line. The plantation at Silver beach, Cuddalore, started within the swash zone of the beach, severely limiting the available space for the burrowing crabs as well leading to the inundation of all the burrows present in the beach. This ecological stress could limit burrowing behaviour coupled with unfavourable substrate conditions due to compacted soil and high root density of *Casuarina equisetifolia*. On the other hand, at the second plantation site, which was about 200m from the high tide line, at the Cuddalore Old Town, smaller burrow diameters also led to deeper but narrow burrows. This could possibly be because of altered micro-climatic conditions (variations in temperature, moisture gradients) that force crabs to dig deeper burrows to meet their needs. Therefore, it is evident that natural and semi-natural conditions permit consistent, predictable burrow structures, which reflect healthier populations.

The shape of the burrows, though not significantly different across treatments, could be influenced by crab species and species-specific behaviour and adaptations. In the present study, all the burrows constructed by *O. macrocera* were J shaped though other studies have reported a variety of other shapes as well (Dubey, 2013)

The significant variation in the branching frequency of burrows suggests influence of habitat complexity and substrate type. Complex burrows may aid in thermoregulation, predator avoidance or other reasons that are yet to be well studied and understood.

4.2.2 Determinants of Burrow Architecture

Collinearity among environmental variables such as moisture, sand temperature and distance from the low tide line, is intuitive and expected from beach ecosystems. This was evident in the study, moisture content of the sand at the surface decreased as the distance from the low tide line increased (cor = -70), while temperature increased with distance (cor = 0.73), consistent with existing literature. Similarly moisture and temperature were also highly correlated. This validates the utility of using distance from the low tide line as a proxy variable to explain the effects of moisture and sand surface temperature in ecological models if the availability of measurements of these abiotic factors is constrained.

Keeping these collinearities in mind, linear models were run to understand the factors influencing the depth of ghost crab burrows across different treatment types. The selected model (Model 5, log(Depth) ~ Burrow.diameter + Treatment.type, Table 7) explained about 38% (Adjusted R-square = 0.3807) variation in burrow depth (after log transformation) as being due to the effects of the burrow diameter and the treatment type. $p<0.001$ associated with the F-statistic also indicates that the model is highly statistically significant. The results show that as burrow diameter increases, depth increases, which supports the idea that older or larger crabs dig deeper. Surprisingly, after controlling for burrow diameter (crab size), sites with mangrove plantations and native dune vegetation have shallower burrows (as given by the β = -0.74 and -0.35 for mangroves and native vegetation respectively). Burrows built in mangrove-associated beaches have significantly shallower burrows compared to areas with casuarina plantations ($p<0.001$), while the ones in native dune vegetation are marginally shallower ($p=0.07$). Crabs may need to dig deeper burrows in Casuarina plantations to escape heat or desiccation, possibly due to higher temperatures and lower moisture, which could be a behavioural adaptation for suboptimal surface conditions.

In contrast, mangrove and native vegetation sites may offer better microhabitat quality which are likely to reduce the energetic cost and the ecological necessity of digging deep. This allows crabs to invest less in burrow construction. Consequently, shallower burrows in these habitats may not reflect a deficit, but an efficient allocation of energy in optimal conditions.

Table 9: Comparison between Model 7 and Model 5

Metric	**lm7 (Depth ~ Diameter * Distance_LTL + Treatment)**	**lm5 (Depth ~ Diameter + Treatment)**
Interaction term?	Yes (Burrow.diameter * Distance_LTL)	No
Adjusted R²	0.4088	0.3807
Residual Std. Error	0.5592	0.5723
F-statistic (p-value)	12.89 (p = 3.15e-09)	18.63 (p = 2.5e-09)
Significant predictors	Treatment.type, marginal effect of Diameter	Diameter, Treatment.type
Interaction significance	Not significant (p = 0.932)	—

Although Model 7 (compared to Model 5 in Table 9) had a slightly higher R^2 and a lower AIC, the interaction term (Burrow diameter*Distance from the low tide line) is not significant, thus making the model unnecessarily complex. Therefore, Model 5 is chosen under the principle of parsimony, it is simpler and is still ecologically meaningful.

These results indicate that the burrow depth is influenced by both the size of the crab (burrow diameter) and the type of inland vegetation., while other environmental variables do not contribute significantly to explaining the depth variability. The findings indicate that ghost crabs respond behaviorally to local environmental circumstances, particularly in the way they build burrows. In damaged or changed environments, such as Casuarina plantations, increasing burrow depth may act as a compensatory mechanism to reduce surface-level stress. This lends support to the theory that burrow characteristics are determined not only by crab size, but also by habitat quality and environmentalparameters.

Importantly, this shows that burrow architecture, specifically burrow depth relative to crab size, may function as a bioindicator of habitat stress. Crabs digging deeper burrows for their size may be exposed to environmental stressors such as heat, dryness, or substrate compaction.

4.3 Differences in coast characteristics across treatments

Beaches with different types of inland vegetation showed different mean values of environmental and geomorphological variables. Sandy beaches with Casuarina plantations as the inland vegetation type showed the least amount of soil moisture, highest level of sand compaction (Compaction was measured by the depth that a pointed metal rod penetrated up to. Lesser the penetration depth, greater is the sand compaction) and the steepest slopes. These trends are consistent with those observed by Chaudhary, 2009. The trends observed in these parameters provide an ecological explanation to the variations observed in burrow depth across treatments. Lesser soil moisture would necessitate the digging of deeper burrows by individuals of all size classes. Further due to the compact nature of the substrate, greater amounts of energy would have to be spent on burrowing. Steeper slopes and reduced beach width could be early signs of beach erosion.

4.4 Management Implications

These patterns highlight the importance of preserving and restoring native beach vegetation for sustaining healthy ghost crab populations. Ocypode crabs, as the major macro-invertebrate, play a crucial role in beach ecosystems and can be a potential bio-indicator of coast health. This study attempted to further our knowledge of the ecology of these crabs, which is much needed given the sparse literature on ghost crab ecology. The findings also highlight the negative effects of casuarina shelterbelts on ghost crab populations and burrowing behaviour. Modifications in burrowing behaviour to suit microclimatic and habitat qualities suggest that ghost crabs are highly resilient species, which can tolerate and adapt to environmental stressors.

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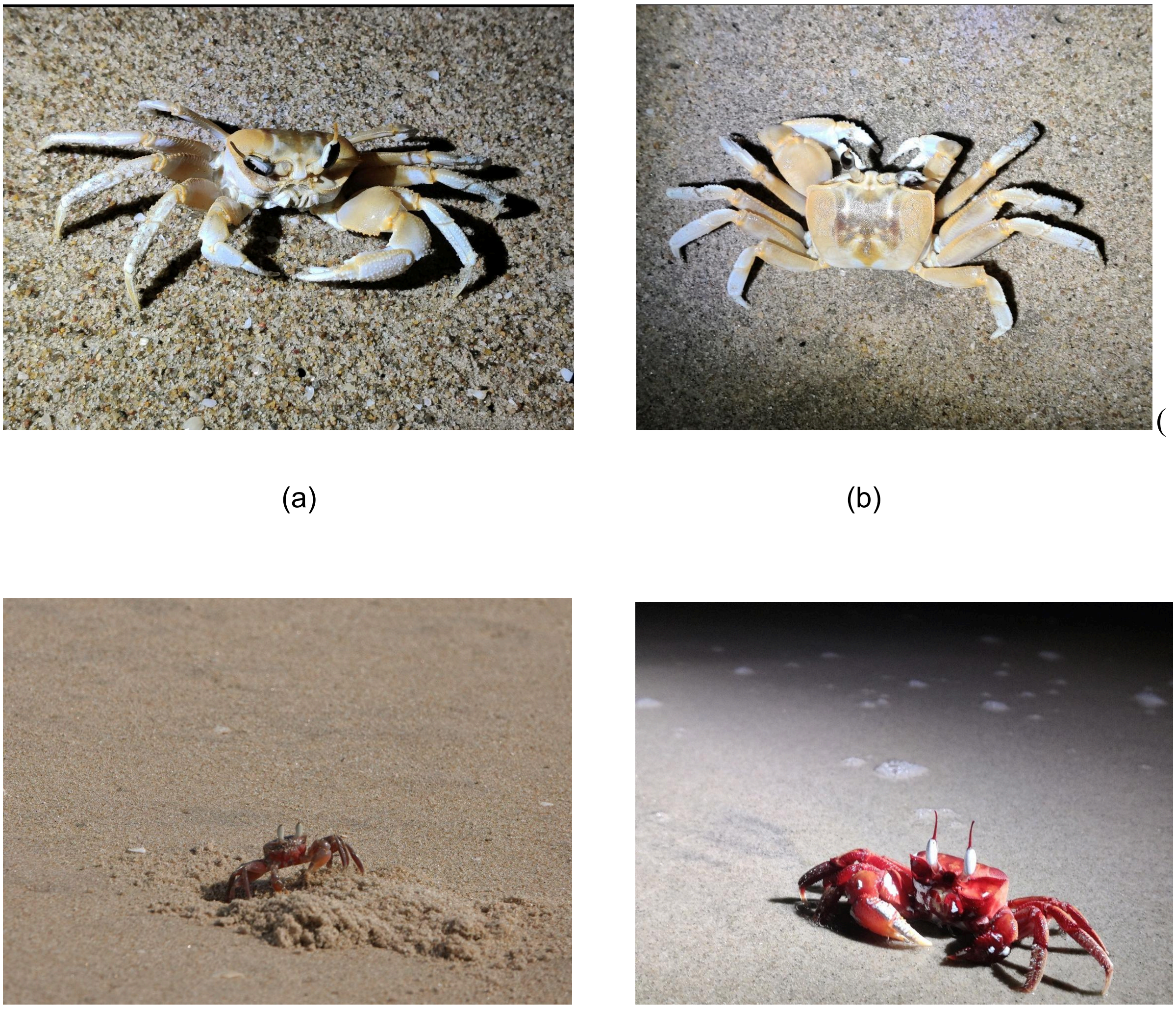
APPENDICES

Appendix 1 : Pictures of the study species - (a) and (b) *Ocypode ceratophthalmus* (c) and (d) *Ocypode macrocera*



(

(a) (b)

(c) (d)

Appendix 2 : An active ghost crab burrow

Appendix 3 : A select few casts of excavated burrows of varying structures - (a) multi-branched J shaped burrow (b) U shaped burrow (c) unbranched J shaped burrow (d) I shaped burrow (e) burrow constructed by *O.macrocera*

(a)

(b)

(c) (d)

(e)