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Social-ecological system approach relevant for modelling the ecological niche of a mangrove gastropod at small regional scale

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ABSTRACT

The gastropod *Terebralia palustris* is found in mangroves from the Indo-Pacific, where it plays important ecological roles and is fished by humans. As such, it reflects interactions occurring within the socio-ecosystem, although information regarding its regional distribution and ecological niche is uneven. The present study aimed at defining the relative importance of factors of the mangrove socio-ecological system (MSES) on the realized niche of *T. palustris* at the regional scale. We studied its distribution at the scale of Mayotte Island (France, Indian Ocean), including local ecological knowledge and environmental memory held by population. To this end, a survey campaign of the 29 mangroves of Mayotte allowed mapping its occurrence and correlating the spatial pattern to factors of the MSES related to three dimensions of the niche (accessibility, abiotic, and biotic) pertaining to both societal and ecological components. Questionnaire interviews revealed both past presence and current presence undetected by the survey campaign. At the scale of Mayotte, the gastropod is found on large and deep mangroves, distant from the sea by a deep central and external mangrove, where *Avicennia marina* is not the only mangrove tree species and the canopy is relatively opened, at the bottom of watersheds holding large urban areas. Our study showed that dealing with both ecosystemic and societal subsystems and their involvement in each dimension of the niche concept is a promising way of understanding the drivers of species distribution in anthropized systems.

1. Introduction

The realized niche of a species can be seen as the consequence of three dimensions (Soberón and Peterson, 2005): (1) abiotic variables, i.e. the presence of environmental conditions in which the species can persist; (2) the biotic environment with the presence of interactions between species and (3) accessibility for the species, i.e. the area must be accessible to the species thanks to its movement or dispersal capacities. Defining a species distribution, and understanding its drivers, are thus useful for quantifying the realized niche of a species (Guisan and Thuiller, 2005 and references therein).

Species distribution models (SDM) are commonly used to explain species distributions by relating field observations of species occurrences (presence, presence-absence or abundance) to environmental or spatial data or both used as predictor variables (Elith and Leathwick, 2009; Guisan and Zimmermann, 2000). These variables relate to the three dimensions of the niche defined above, affecting species distribution directly or indirectly at different spatial scales (Guisan and Thuiller, 2005). Abiotic factors alone are usually considered when modelling species distributions at a global scale (e.g. Sharifian et al., 2021), although worldwide species introductions can also increase the accessible area(s) available to species (Kraemer et al., 2015). Species interactions will exert their strongest influence on species distribution at small regional to local scales (Guisan and Thuiller, 2005).

Increasingly, the human species affects the distribution of other species both negatively through, for example, land use or exploitation and positively through conservation plans including restoration and reintroduction (Ren et al., 2014). Indeed, human societies are part of

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social-ecological systems (SES) (sensu Berkes and Folke, 1998) where ecological and societal compartments are inseparable and interdependent due to their interactions and feedbacks (Berkes and Folke, 1998). Changes in the societal or ecological subsystem often have impacts on the other subsystem (Walker and Salt, 2006), and both can affect, either individually or in interaction, the distribution of species. Relevant predictors aimed at explaining the distribution of species at small regional scale should thus relate to both dimensions of the SES.

Regional to local scale is also best suited to understanding the realized niche for conservation purposes (Elith and Leathwick, 2009; Fois et al., 2018). In marine systems, however, the use of SDM for conservation purposes falls behind that of understanding current patterns of distribution, the impacts of climate change, or methodological advancement in modelling (Melo-Merino et al., 2020). While most studies take place at a local scale, mostly focusing on fish, molluscs and marine mammals, few are carried out on the north-western Pacific Ocean and the Indian Ocean (Melo-Merino et al., 2020). SDM have only recently been used for conservation issues (e.g. Record et al., 2013). Instead, most studies on mangroves have focused on the distribution of mangrove tree species on a global (Quisthoudt et al., 2012; Record et al., 2013) or more regional (Samal et al., 2023) scale. More recently, a few studies have been conducted on SDM for mangrove animal species at various spatial scales, from the global distribution of mangrove crabs (Sharifian et al., 2021) to the Indo-West Pacific distribution of mangrove gastropods (Adamu et al., 2024) down to the distribution of gastropods along the Indian coast (Bharti and Shanker, 2021). Additional studies on the distribution of mangrove species other than trees is thus needed beyond the scale of single mangrove units in order to inform SES conservation.

The giant mangrove whelk, *Terebralia palustris* (Linnaeus, 1767; Potamididae, Gastropoda) is considered one of the major species in the assembly and functioning of mangrove ecosystems in the Indo-Pacific (Cannicci et al., 2008). This epigenous species plays an important role in the degradation, consumption and recycling of mangrove leaves, and thus in the fate of the carbon stock in mangroves (Cannicci et al., 2008). It is widely distributed over the Indian Ocean from South Africa (Raw et al., 2014) to Australia (Wells and Keasing, 2019). This species is harvested for food, as bait for fishing or for lime production (e.g. Scales et al., 2017), sometimes up to the point of impacting its population dynamics significantly (de Boer et al., 2000). *T. palustris* is also known to be absent from heavily polluted areas (Cannicci et al., 2009 and references therein).

Considering its important role in mangrove SES (MSES), understanding the drivers of *T. palustris* distribution is relevant for SES management and conservation perspectives. Yet, within its range, the distribution of *T. palustris* within mangroves, and its underlying factors, remains unclear and contradictory. Several studies report a diffuse presence of the species inside mangroves (Fratini et al., 2004; Nishihira et al., 2002) while others suggest higher abundances in the upper part of the mangroves (Australia: Wells and Keasing, 2019). Clear spatial segregation between juveniles and adults is also observed in some mangroves (e.g. Pape et al., 2008) but not in others (e.g. Fratini et al., 2004). Most studies on *T. palustris* focus on the scale of the mangrove unit and only one study focused on its temporal variation on a finer scale, although without investigating the factors underlying the observed pattern (Raw et al., 2014).

In Mayotte, a 374 km^2 island of the Indian ocean where one third of the coastline is bordered with mangroves, villages are close to the mangroves, leading to a diversity of societal components making up the MSES (Longépée et al., 2021). Yet, no comprehensive data of the current or past distribution can support our understanding of its realized niche within this complex MSES context. In such data-poor areas, the social memory (SM, Berkes et al., 2003) of inhabitants on local ecological knowledge (LEK, Olsson and Folke, 2001) can be a rich source of information to understand the past spatio-temporal dynamics of a species' distribution (Beaudreau and Levin, 2014).

The aim of this study was thus to identify underlying social-ecological factors explaining the distribution of *T. palustris* at the time of study in order to characterize its realized niche at a regional scale. For this purpose, metrics relating to both the ecological and social dimensions of the MSES were considered to identify the main drivers underlying the species distribution at the island scale. These metrics were used to identify SES factors characterizing mangroves where *T. palustris* was present or absent and to quantify the importance of individual factors pertaining to the three niche dimensions (abiotic, biotic and accessibility) constraining the realized niche. Finally, we surveyed the social memory of inhabitants in order to identify potential historical factors that might be responsible for current species distribution.

2. Methods

2.1. Study area

Located in the Mozambique Channel (Indian Ocean, Comoros Archipelago), Mayotte is surrounded by an almost continuous 157 km long reef. The archipelago is characterized by a humid tropical climate with two seasons: a hot season from November to April and a dry season from May to October. Mayotte is exposed to semi-diurnal tides with a maximum tide amplitude of 4 m in spring tide (Jeanson et al., 2019).

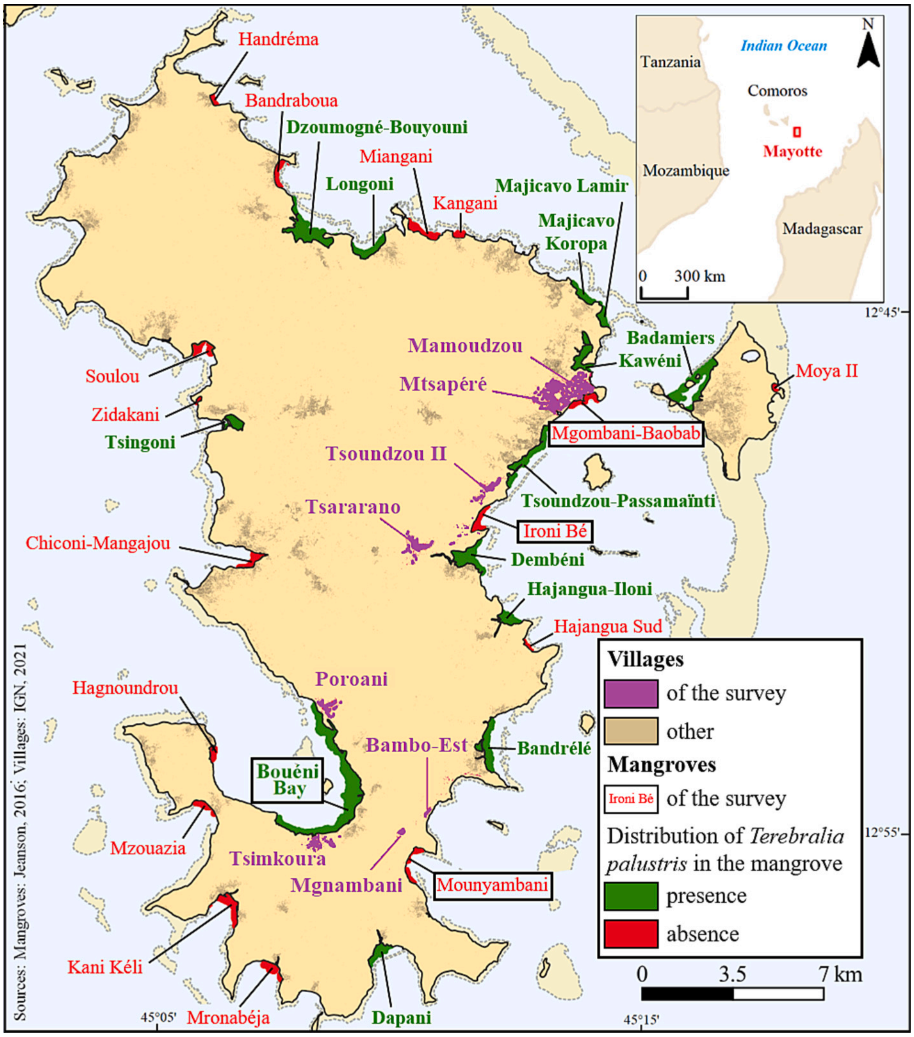
Mangroves cover 694 ha of intertidal areas in total, which span along about 29 % of the coastline (Jeanson et al., 2019). In total, 29 mangrove units are listed, each stand covering between 0.8 ha and 180 ha (23 ± 36 ha). The mangroves of Mayotte are characterized by the presence of eight mangrove tree species, which form three forest belts along the intertidal gradient (for more detail see Longépée et al., 2021): (1) a seaward fringe, (2) the central mangrove, and (3) the landward mangrove. Unlike in some other places in the south-western Indian Ocean (Cannicci et al., 2009; Fratini et al., 2004), *T. palustris* is only located in the landward mangrove in Mayotte (Brosse, 2019). This habitat is often represented by stands of large *Avicennia marina* (Forssk.) Vierh. sometimes accompanied by small *Ceriops tagal* (Perr.) C.B.Rob. and shrubby forms of *A. marina* bordering saltpans (Cremades, 2010).

Mayotte is in the midst of a demographic boom (density of 690 inhabitants/km^2) resulting in an expansion of urbanized areas in the coastal zone (Genay and Merceron, 2017). As a consequence, some landward mangroves are decreasing or being lost due to village expansion (majority of slum houses), human exploitation (wood cutting, cattle grazing, salt production, seafood or fishing activities) and agriculture encroachment (Jeanson et al., 2014; Longépée et al., 2021). In order to protect and manage these ecosystems, the first Mangrove Management Plan ("Plan d'aménagement forestier") was recently established (ONF, 2019). Yet, it remains to be effectively implemented. Regarding *T. palustris*, a prefectural decree prohibiting the fishing and use of the species was established in 2000 (decree n°347, DAF, 2000) but this has not been prolonged beyond 2018 (decree n°2018/DMSOI/601).

2.2. MSES mapping analysis variables

In order to study the distribution of *Terebralia palustris* over the territory of Mayotte and the relative importance of MSES factors on its realized niche, we analysed presence/absence data from mangrove field surveys against spatial metrics relating to MSES characteristics.

Sampling effort focused on *T. palustris* habitat within the 29 mangroves from Mayotte's two main islands (Fig. 1). The presence or absence of the species on each site was recorded between February and April 2021 during the wet season. For this purpose, the landward mangrove of each unit (average ± standard deviation of 7.08 ± 10.59 ha over the island, Appendix B, supplementary material) was explored in its entirety by two people prospecting the area about ten meters apart to avoid missing any presence of the species. The first 5 to 10 m of the landward portion of the central mangrove were also explored in order to rule out any presence on this part of the ecosystem.



Sources: Mangroves: Jeanson, 2016; Villages: IGN, 2021

Fig. 1. Location of the 29 mangroves explored and the 8 villages (in purple) bordering the mangroves of interest (surrounded text) for the collection of LEK data by questionnaire survey, in the context of the island of Mayotte (France, Indian Ocean). The presence (in green) and absence (in red) of *Terebralia palustris* within the mangroves are represented following field sampling in the 29 mangroves of Mayotte. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Most of the data mapping was extracted by updating the polygons of mangrove habitats created during the mapping of the natural habitats of the mangroves of Mayotte (Cremades, 2010). The update (named MANG-layer) was performed using QGIS 3.10 LTR (QGIS Development Team, 2020), based on the overlay of Cremades' layers with aerial photographs entirely processed by France's Institut Géographique National (IGN) dating from 2016 and knowledge acquired from the field sampling of 2021. Eventually, 14 variables were used in the model aiming to explain the realized niche of *T. palustris* at the scale of the island. They are classified into four categories in relation to the three dimensions of the niche concept: “connectivity”, which contributes to the accessibility dimension; “hydrodynamic exposure” and most mangrove and society features, which contribute to the abiotic dimension; tree-related mangrove features and the proxy for fishing pressure, which contribute to the biotic dimensions.

2.3. Connectivity

The minimum distance to another mangrove (in m) reflects the potentially higher connectivity (through larval dispersal) between neighbouring mangroves than between distant ones. Indeed, in the context of an island alternating small bays and rocky headlands, most mangrove units are isolated from distant ones (Fig. 1). We thus hypothesized that mangroves of presence are more likely to form clusters of neighbouring mangroves separating from mangroves of absence due to oceanographic barriers within the lagoon. Minimum distances between the mangrove centroids across the sea were extracted on QGIS with the « Least-Cost Path 1.0 » plugin after a rasterization treatment.

2.4. Hydrodynamics exposure

Hydrodynamics characteristics relate to the preference of *T. palustris* for sheltered landward environments (Houbrick, 1991). The wave fetch, average of the maximum distances (in km) that waves can travel without landfall to the points of interest (Burrows et al., 2008), is calculated in R (R Core Team, 2022) using the package « windfetch » (Seers, 2021). The average distance to the sea of the landward mangrove (in m), a proxy for swell and wave protection, is a variable calculated from the MANG-layer data. The distance between each patch centroid to the lowest tidal sea (chart datum) was extracted on QGIS and then the average distance of the centroid of each mangrove was calculated.

2.5. Mangrove features

This category assumes that, in order to thrive, viable *T. palustris* populations require a minimal suitable habitat area both in size and quality (Griffen and Drake, 2008). Four variables as proxies for size and three as proxies for quality were defined as follows.

Total mangrove and landward mangrove areas of each unit (in m^2) have been calculated directly from the MANG-layer on QGIS. Vertices on the land and sea sides were extracted from the MANG-layer and the minimum distances between these vertices were plotted using the « NN Join » plugin of QGIS. Average distances for all these segments (land to sea and sea to land) correspond to the average depth of each mangrove unit and each landward mangrove. Average elevation of the landward mangrove (in m) has been computed from the BDALTI MNT (IGN, 2013; controlled accuracy of 1 m) on QGIS with the assumption that *T. palustris* avoids dry environments landward, to avoid desiccation (Slim et al., 1997), and exposed environments seaward (Houbrick, 1991). The percentage of landward mangrove that is covered by trees is a proxy for canopy closure; as *T. palustris* is known to be present in shaded environments (Crowe, 1997), the higher the tree cover, the higher the probability that the gastropod is present. It was calculated by remote sensing from a Random-forest classification on Pléiades satellite imagery of 50 cm resolution (Pléiades© CNES 2018 Distribution Airbus DS) on Orfeo ToolBox 8.0.1. The percentage of surface area occupied by monospecific *Avicennia marina* habitats within the landward mangrove (based on personal field observations suggesting presence of *T. palustris* mainly where *A. marina* stands dominate) was calculated from the total surface area occupied by habitats dominated by *A. marina* on the basis of the typology created by Cremades (2010).

2.6. *Societal features*

Human presence can affect the mangrove ecosystem in a number of different ways and it is difficult to measure these pressure effects separately (Branoff, 2018). This is why we use here an indirect and varied approach to characterize land use. The societal indicators relate to exploitation, uses, and pollution, thus contributing both to the biotic and abiotic dimension of the niche. The following descriptors assume that urban areas are potentially associated with greater inputs of pollutants (macroscopic waste and wastewater, abiotic interaction) and direct exploitation (biotic interaction), and that agricultural areas are a source of agricultural inputs and hydro-sedimentary inputs via soil erosion (abiotic dimension). Fishing or pollution may impact *T. palustris* directly, while habitat degradation may be an indirect impact.

Watershed population density (in $hab.km^{-2}$) was calculated by multiplying the number of dwellings per watershed (IGN, 2021) extracted on QGIS, by the mean number of inhabitants per dwelling in Mayotte (Genay and Merceron, 2017). In order to account for direct runoff from dwellings surrounding the mangrove, the percentage of area occupied by buildings within 200 m of the landward limit of each mangrove was calculated through the use of the modelling of infrastructures on Mayotte (BD Topo®, IGN 2021) on QGIS. Residential occupation in the watershed (in m^2) is based on the continuity of the buildings between them to form an envelope comprising all buildings within 20 m of each other (Cuniberti et al., 2005). This urban area was constructed from the BD Topo® layer (IGN, 2021) on QGIS. The agricultural area (in m^2) was calculated on QGIS within the watershed from the RPG parcellaire 2.0 (IGN, 2019). Each agricultural parcel declared forms the agricultural surface area within the watershed of the mangrove.

2.7. *LEK and SM data collection*

A questionnaire survey campaign was conducted in 2022 (April–May) to call upon the social memory of the inhabitants on their LEK of *T. palustris* in order to better understand the current distribution of the species. This survey was carried out in villages near the mangroves where the gastropod was found absent during the sampling effort of 2021 (see Fig. 1). The choice of mangroves for this survey was carried out using criteria of anthropogenic impact, based on the assumption that *T. palustris* was present before in these mangroves but disappeared because of direct (Lebigre, 1996) or indirect (pollution: see Cannicci et al., 2009) human pressure. Based on village-mangrove proximity and a qualitative index of water mass eutrophication (Biotope, 2022), four mangroves were chosen for the LEK study. One mangrove for each combination of the two effects was selected: Bouéni Bay (less polluted, less distant), Mounyambani (less polluted, more distant), Ironi Bé (more polluted, more distant) and Mgombani-Baobab (more polluted, less distant).

Inhabitants were randomly selected from cities or villages neighbouring the considered mangroves. Some respondents were able to refer to other people who might have knowledge on the gastropod. The choice of respondents was conditional on age and the length of time inhabiting the village: only adults living or having frequented the city or village for more than 5 years were questioned. The short questionnaires were conducted with 203 inhabitants who lived near the mangroves of interest (Poroani and Tsimkoura for Bouéni Bay, Mgnambani and Bambo-Est for Mounyambani, Mamoudzou and Mtsapéré for Mgombani-Baobab, and Tsararano and Tsoundzou II for Ironi Bé – Fig. 1). Questionnaires were passed to people in the street or at their house by a researcher with help of a translator when necessary (French, *Shimaore*, and *Kibushi*). The questionnaire was divided into two parts: one on LEK based on SM regarding *T. palustris* occurrence and another one on the respondents' profile and its activities in mangroves (Appendix A, supplementary material). A confidence score was calculated to identify respondents who confused *Cerithidae decollata* and *Terebralia palustris* (see Dupont, 2022).

2.8. *Data analysis*

All data were analysed in R (R Core Team, 2022). The conditions of use of each parametric test presented below was first verified through the normality of the variable tested with the Shapiro-Wilk test and the homogeneity of variance using the Levene's test. If these conditions are not verified, the corresponding non-parametric test is performed.

To test the null hypothesis that there is no difference between mangroves with and without *T. palustris* for each explanatory variable, a *t*-test or a Wilcoxon test were conducted depending on the previously tested conditions. To visualize the values taken by each variable for mangroves of presence and absence, a radar chart based on average MSES-related characteristics was performed with the "radarchart" package (Ashton et al., 2016).

The variability of the sites with and without *T. palustris* was evaluated with a Principal Component Analysis (PCA) using the "FactoMineR" package (Lê et al., 2008) on the basis of the characteristics of the MSES. Dissimilarities on the basis of MSES-specific variables between sites with and without *T. palustris* were compared by a permutational multivariate analysis of variance (PERMANOVA) using the "adonis2" function of the "vegan" package (Oksanen et al., 2022). The null hypothesis behind this analysis is that the two groups do not differ in terms of position in the multivariate space.

A random forest (RF) algorithm (Breiman, 2001) was used to estimate the importance of each explanatory variable and the contribution of their categories in constraining the realized niche of *T. palustris* at the scale of Mayotte. Although our small sample size ($n < 30$) would not be adequate for prediction purposes (Wisz et al., 2008), it does allow identifying the relative importance of our variables. This machine learning approach was performed with the package "randomForest" (Liaw and Wiener, 2002). At each node, a number of predictor variables (mtry) were randomly selected and a number of trees (ntree) in a forest were drawn. These parameters were chosen to minimize the prediction error of the model: the "out of bag" (OOB) error. In order to minimize noise, the importance of explanatory variables in 100 RF models was assessed by observing the increase of the OOB when each mtry is swapped while all the others remain unchanged (Breiman, 2001) using the method of the package "randomForest" (Liaw and Wiener, 2002).

Finally, the effect of age and gender on the ability to recognize *T. palustris* by the questionnaire respondents was tested by a Chi^2 test of independence. Analyses were performed using the Sphinx IQ3 software.

3. Results

3.1. Distribution on the island of Mayotte

The mapping campaign of the presence of *Terebralia palustris* at the scale of the island revealed that the species was present within 12 of the 29 mangroves in 2021 (Fig. 1). Nevertheless, during the questionnaire survey in 2022, an inhabitant of Poroani mentioned a very small patch of current *T. palustris* presence in the Bouéni Bay mangrove. After field verifications, the count of mangroves of presence was raised to 13 (Fig. 1).

3.2. Realized niche

Variable-by-variable differences were tested between sites with and without *T. palustris* (Fig. 2). The landward mangrove surface area is significantly greater in stands with *T. palustris* (14.6 ± 12.1 ha) than without (0.9 ± 1.2 ha) (Wilcoxon test: W = 5, *p*-value <0.001). The surface area of mangroves with *T. palustris* (43.7 ± 47.4 ha) is also significantly greater than that without *T. palustris* (6.6 ± 4.9 ha) (W = 7, p-value <0.001). The proportion of *A. marina* in the landward mangroves of the presence sites (56.5 ± 17.7 %) is significantly lower than in those of the absence sites (91.9 ± 15.5 %) (W = 191, p-value <0.001). The width of mangroves with *T. palustris* (158.8 ± 67.8 m) is also significantly larger than without (69.9 ± 42.1 m) (W = 16, p-value <0.001) and the landward mangrove width is also significantly larger in mangroves with *T. palustris* (72.1 ± 42.2 m) than without (24.4 ± 14.8 m) (W = 15, p-value <0.001). Similarly, the distance from the centroid of the landward mangrove to the sea is significantly longer in mangroves with *T. palustris* (553.6 ± 221.2 m) than without (353.3 ± 146.4 m) (*t*-test, $t = -2.8$, df = 20.0, p-value <0.05). Canopy closure in the landward mangrove of presence sites (59.4 ± 14.4 %) is significantly reduced compared to that of absence sites (76.5 ± 18.7 %) ($t = 2.8$, df = 27.0, p-value <0.01). In addition, the urban surface area is significantly greater in mangroves with *T. palustris* (84.4 ± 70.5 ha) than without (38.1 ± 68.8 ha) (W = 48, p-value <0.05). None of the other variables studied display significant differences between mangroves with and without *T. palustris*.

3.3. Discrimination of mangroves with and without *Terebralia palustris*

The 14 different considered variables significantly discriminate sites with and without *T. palustris* (PERMANOVA, $F_{1,27} = 10.8$, $R^2 = 0.3$, p-value <0.001). Axis 1 of PCA (Fig. 3), explaining 35.1 % of the variance, discriminates the sites with and without *T. palustris* on the basis of the ecological components of the MSES. Axis 2 of PCA (Fig. 3), explaining 17.4 % of the variance, is mostly explained by societal components of the MSES and hydrodynamics variables. This axis displays most of the intra-group dispersion.

3.4. Importance of variables

The importance of variables in the random-forest model was calculated from 100 RF (Fig. 4). All the variables explaining more than 50 % of the model are variables characterizing mangrove features. The surface of the landward mangrove (92.9 ± 12.8 %) and of the entire mangrove (87.1 ± 16.8 %) are the most important criteria in explaining the presence/absence of *T. palustris*. Percentage of surface occupied by monospecific habitats of *Avicennia marina* comes next (68.1 ± 22.0 %) followed by mangrove depth (65.3 ± 21.2 %) and landward mangrove depth (53.4 ± 20.4 %). All other variables were found to be irrelevant to explain the presence of *T. palustris* in mangroves.

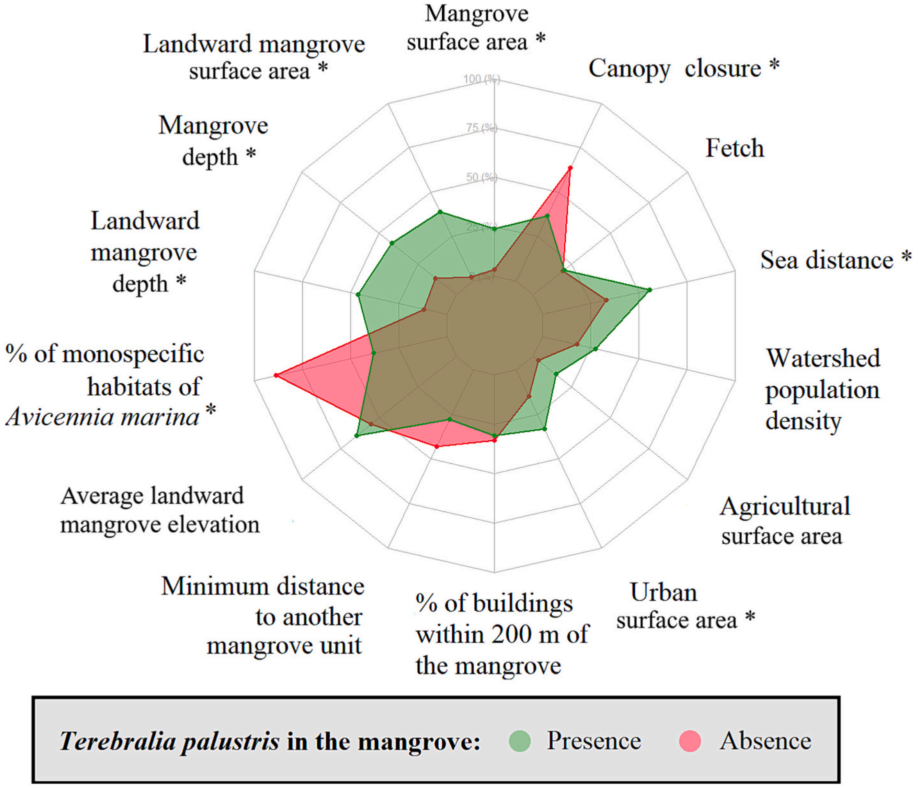


Fig. 2. Modelling of realized niche of *Terebralia palustris* at the scale of Mayotte based on average MSES-related characteristics. Average values taken by sites of presence (green) or absence (red) of *T. palustris*. A significant difference ($\alpha < 0.05$) via a Wilcoxon test or a t-test between the presence and absence mangroves is represented by an asterisk (*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

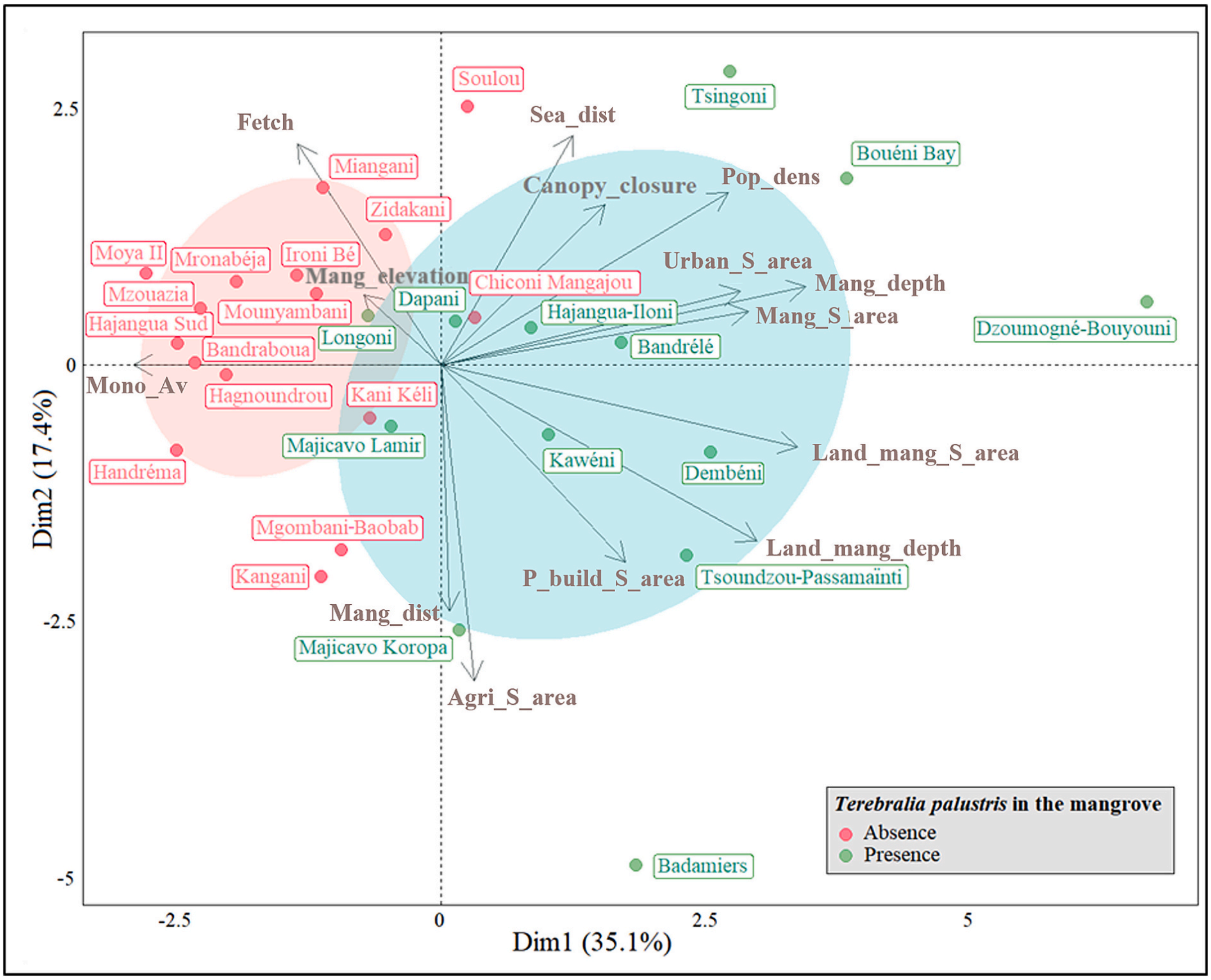


Fig. 3. Principal component analysis of the characteristics of the 29 mangroves of the island of Mayotte. Ellipse containing 60 % of sites of presence (green) or absence (red) of *Terebralia palustris*. Abbreviations: Mang_dist = minimum distance to another mangrove unit; Mang_area = mangrove area; Land_mang_area = landward mangrove area; Mang_depth = average mangrove depth; Land_mang_depth = average landward mangrove depth; Mono_Av = percentage of area occupied by monospecific habitat of *Avicennia marina*; Canopy_closure = percentage of area covered by trees in landward mangrove; Mang_elevation = average elevation of the landward mangrove; Sea_dist = average distance to the sea of the landward mangrove; Fetch = fetch; Pop_dens = watershed population density; P_build_area = percentage of area occupied by buildings within 200 m of the mangrove; Urban_area = urban area; Agri_area = agricultural area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. *Results on past presence from the questionnaire survey*

The questionnaire was completed by 203 inhabitants living near the four targeted mangroves (77 for Mgombani-Baobab, 60 for Ironi Bé, 39 for Bouéni Bay and 27 for Mounyambani). Most respondents were between 30 and 49 years old (53.2 %) with a majority of women (57.6 %). People over 50 years old were significantly overrepresented among those with knowledge of *T. palustris* (53.7 %) (Chi^2 test, $\chi^2 = 10.64$, df = 2, *p*-value <0.005). A large part of the respondents frequenting the targeted mangroves recognize *T. palustris* (50.8 %) (Fig. 5). It is impossible here to identify whether surveyed people who do not recognize *T. palustris* do so because the species is really absent from the mangrove they frequented, because users do not explore specific areas of presence, or because they do not pay attention to the species. Thus, to evaluate the presence or not of *T. palustris* in the targeted mangrove, within respondents who recognize *T. palustris*, we compared those who could locate it in the targeted mangrove from those who could not.

More respondents reported having seen *T. palustris* in the mangroves of Bouéni Bay (14 versus 5) and Ironi Bé (14 versus 11) than not (Fig. 5). Finally, more respondents reported the absence of *T. palustris* in the mangroves of Mounyambani (4 versus 7) and Mgombani-Baobab (8 versus 14). It should be noted here that for Mounyambani, we had difficulty finding people who had lived in the village for more than 5–10 years.

4. Discussion

Before the present study, the presence of *Terebralia palustris* in Mayotte remained very little documented and its detailed distribution at the scale of the island was not known. A partial survey of four mangrove units had suggested it was not present on all mangrove units (Brosse, 2019). The present survey of the 29 mangroves of Mayotte greater than 0.8 ha found the species on 13 of them, only one being on the south and two on the western coasts of the island.

4.1. *Accessibility between sites*

The question of the accessibility of the different sites seemed to have a weak effect on the distribution of *T. palustris* around the island. Average values of fetch and minimum distance to another mangrove were not significantly different between mangroves of presence and absence. These connectivity features did not have much influence either in our *T. palustris* distribution model. Yet, the connectivity of isolated populations on the western coast raises questions on the dispersal of

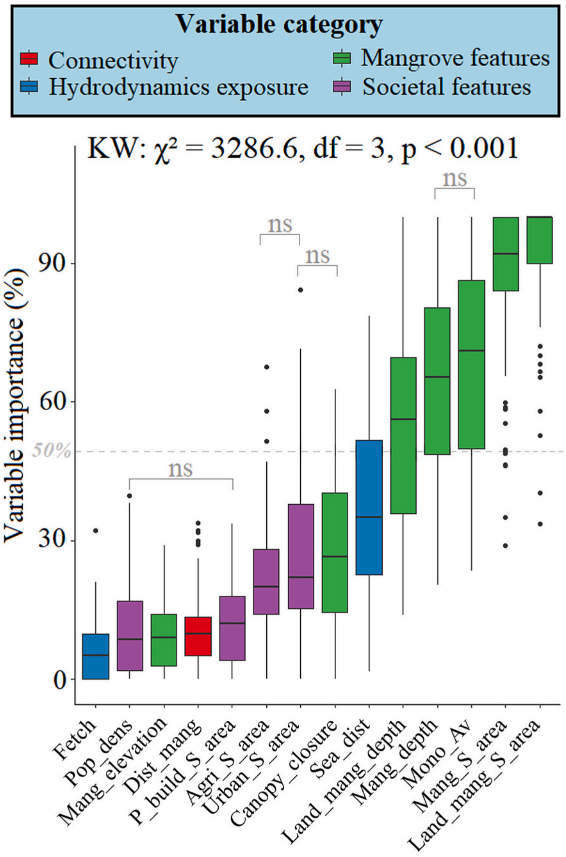


Fig. 4. Boxplot (rectangles) with median value (black line) showing the importance of variables explaining the presence of *Terebralia palustris* in mangroves by machine learning modelling (Random-forest; $n = 100$, mtry = 4; ntree = 200). Only variables not significantly different from each other by Wilcoxon test are displayed with the symbol “ns”. All other comparisons are significantly positive. Abbreviations: Mang_dist = minimum distance to another mangrove unit; Mang_area = mangrove area; Land_mang_area = landward mangrove area; Mang_depth = average mangrove depth; Land_mang_depth = average landward mangrove depth; Mono_Av = percentage of area occupied by monospecific habitat of *Avicennia marina*; Canopy_closure = percentage of area covered by trees in landward mangrove; Mang_elevation = average elevation of the landward mangrove; Sea_dist = average distance to the sea of the landward mangrove; Fetch = fetch; Pop_dens = watershed population density; P_build_area = percentage of area occupied by buildings within 200 m of the mangrove; Urban_area = urban area; Agri_area = agricultural area.

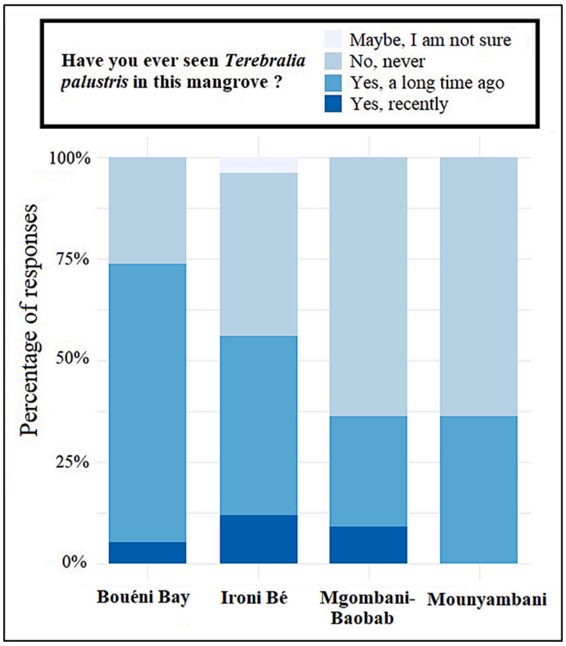


Fig. 5. Percentage of response ($n = 77$, response rate = 100 %) of respondents who recognize *Terebralia palustris* to the question “Have you ever seen *T. palustris* in this mangrove?”

intertidal species with planktonic larvae within the lagoon. *T. palustris* has a free-swimming larval stage (Rao, 1938) whose duration is still unknown. The phylogeographic study of *T. palustris* populations and of its close relative *Cerithidea decollata*, shows long distance connections between mangroves of the western Indian Ocean (Madeira et al., 2012; Ratsimbazafy and Kochzius, 2018), suggesting that larval duration might not be limiting for the colonization of neighbouring mangroves in Mayotte (Scheltema et al., 1996) or across small islands of the region (Gamoyo et al., 2019). Yet, only two sites of presence were observed on the western coast of the island (Fig. 1), with very small surface areas containing only a few individuals. In Tsingoni, the small population was only found during a second site visit, and in Bouéni Bay, scattered patches were found thanks to the local ecological knowledge of a surveyed inhabitant. Both of these populations are extremely narrowly distributed (~ 0.1 ha) over larger landward mangrove surface areas (6.4 and 33.7 ha respectively). This relative isolation could be explained by oceanographic barriers within the lagoon or by the inability of these mangroves to act as sources for neighbouring mangroves or both (Salinas-de-León et al., 2012). The lack of detailed knowledge regarding the circulation within the lagoon and potential oceanographic barriers does not allow us to favour either of these hypotheses. The recent modelling of the hydrodynamics of the lagoon of Mayotte (Parc Naturel Marin de Mayotte, *pers. comm.*), however, should help unravel connectivity between mangroves around the island in the future. The role of connectivity on the maintenance of these isolated populations is not clear and still remains to be explored within the particular context of lagoons, considering the contribution of patch spacing and location on dispersal (Pinsky et al., 2012).

4.2. *The abiotic dimension of the niche*

There was a significant contribution of several variables to the abiotic dimension of the niche, that is the environmental conditions that enable the species to persist in a given location (Soberón and Peterson, 2005). These conditions can be impacted by factors relating to both the quality and quantity of suitable habitat, under natural and anthropogenic influence. The presence of *T. palustris* seemed to be highly dependent on the amount of suitable habitat while fewer factors assessing the quality of the habitat explained differences in the species distribution.

T. palustris was found in significantly larger (2 to 1 ratio) and deeper (4 to 1 ratio) mangroves where the landward mangrove is also more developed (size and width of the landward mangrove being correlated with those of the total mangrove). These structural variables were four of the five most influential variables in our *T. palustris* niche modelling. Recent studies have shown that small habitat size influences extinction risk of species by reducing both their carrying capacity and population growth rate (Griffen and Drake, 2008). The precise impact of habitat size on species persistence is difficult to identify, as carrying capacity and population growth rate have also been linked to habitat quality (Griffen and Drake, 2008). Much research also aims to unravel the relative contribution of and interactions between patch size and fragmentation on species persistence (Fahrig, 2017; Heinrichs et al., 2016). Empirical studies contributing to this debate rarely use marine species (Fahrig, 2003). In our study, people familiar with *T. palustris* reported the past presence of the species in the mangrove of Ironi Bé, where construction of a road on a bush track through the mangrove in the 1980s increased habitat fragmentation. Furthermore, within the mangroves of Mayotte, *T. palustris* populations display different numbers and sizes of patches (Brosse et al. *in review*). *T. palustris* and the small mangroves of Mayotte would thus make for a relevant case study to further disentangle the effects of habitat size and fragmentation on population persistence and their respective mechanisms at play (Fahrig, 2017).

Beyond the size of the habitat, presence or absence of a species is also related to the quality of available habitat, especially in fragmented habitats (Mortelliti et al., 2010). The vertical distribution of many intertidal gastropods is influenced by their tolerance to emersion temperature and desiccation (Stickle et al., 2017). In our study, there were no differences in elevation of the landward mangrove between mangroves of presence and absence of *T. palustris* and elevation had a small influence in explaining the species distribution at the scale of the island. Intertidal gastropods also display escape behaviours to reduce thermal stress or desiccation (Chapperon and Seuront, 2011) suggesting that areas with more shade available should be more suitable to the species. Indeed, the presence of shade has been shown to play an essential role in helping *T. palustris* avoid desiccation (Crowe and McMahon, 1997; Slim et al., 1997; Wells and Lalli, 2003). Surprisingly, average canopy closure was found to be significantly higher in mangroves of absence and did not contribute much in explaining the opposition between sites of presence or absence in the PCA, but rather some of the between site variability within each of the two groups (Fig. 3). While shade is clearly more available in sites with higher canopy closure, these results suggest that other parameters, notably biotic ones (discussed below), might negatively affect the presence of the species in relation to canopy closure.

The differences in hydrodynamics across sites contributed little in explaining differences in the distribution of *T. palustris* across the island. Indeed, average fetch was not significantly different between sites of presence and absence and had extremely little influence on the presence of *T. palustris* in the mangroves (Fig. 4). In Mayotte, *Terebralia palustris* is only located in the landward mangrove, i.e. high on the shore, contrary to other places in its range where it is present in the mangrove in its entirety (Fratini et al., 2004; Nishihira et al., 2002) Yet, average sea distance, which correlates with mangrove depth, had a small influence on the presence of *T. palustris* in mangroves. Yet, the species is found in mangroves whose landward mangrove is significantly further away from the sea (Fig. 2). The energy of waves arriving in landward mangrove is thus more attenuated, through the friction of the sedimentary bottom and the resistance generated by the mangrove trees, favouring the deposition and accumulation of fine sediments (Mazda et al., 1997). Finer mud particles have a greater capacity to adsorb organic matter, enabling the species to find more food resources (Penha-Lopes et al., 2009). Furthermore, the species requires a low-hydrodynamic environment for its continued movement and feeding at high tide (Fratini et al., 2001). Considering the small depth of most of the mangroves of Mayotte, these conditions of low hydrodynamics might only take place in the landward mangroves, thus explaining the particular restriction of the species in this area in Mayotte compared to other locations. This hypothesis is backed by the fact that *T. palustris* is absent from most mangroves on the west and south coasts of the island, which are undergoing significant surface erosion, under the joint effect of hydrological conditions and exposure to swell and waves (Jeanson et al., 2014). In these mangroves, surface losses of most of the external mangrove and portions of the central mangrove might increase the local hydrodynamics of the landward mangrove beyond the levels required for the presence of *T. palustris*. Further studies should thus evaluate how different hydrodynamic conditions might constrain the location of the species over the intertidal gradient as a function of mangrove surface area.

The quality of the habitat can also be influenced by human activities, in particular through chemical impacts. Mangroves of presence were associated with watersheds of significantly larger average urbanized surface areas: if urban surface area indeed reflects the amount of direct runoff, it seems to be beneficial to *T. palustris*, although it contributes little to the overall niche model. For mangroves present at the bottom of small watersheds such as those in Mayotte, where substantial freshwater inputs are limited to the rainy season, it has been shown that the increased supply of freshwater can benefit mangrove vegetation (Herteman et al., 2011).

In addition to freshwater inputs, urbanization increases the amount of wastewater discharge. In Mayotte, the wastewater treatment system is either dysfunctional or non-existent, which leads to the discharge of wastewater directly into mangroves (Thongo, 2016). Inputs of these pretreated domestic waters modify the compositions of the crab and meiofauna communities found in the central mangrove (Capdeville et al., 2018). *T. palustris* is also known to disappear when human sewage pollution is too high (Cannicci et al., 2009). Studies in mesocosms, however, revealed that *T. palustris* has a high tolerance to severe sewage inputs but showed that the species is still stressed by low sewage concentrations (~ 20 %), resulting in reduced growth and behavioural changes (Penha-Lopes et al., 2010). Over time, the resulting hypoxic conditions lead to a reduction in reproductive capacities (Cheung et al., 2008) and a potential decline in populations. The lack of influence of our indicators of urbanization on the presence of the species over entire mangroves is likely due to the fact that large sewage inflows tend to be restricted to specific areas so that excessive nutrient inputs are more likely to explain localized distributions of *T. palustris* within mangroves than its overall presence or absence. Indeed, *T. palustris* is generally not observed at the vicinity of wastewater outlets (R.B., personal observation). Similarly, the absence of significant contribution of agricultural surface area in explaining the distribution of *T. palustris* might be due to the fact that subsistence farming is still dominant in Mayotte, despite pollution being generated due to the uncontrolled use of pesticides (Foucher et al., 2024), and that the number of declared parcels is still scarce (IGN, 2019).

4.3. The biotic dimension of the niche

Last but not least, the biotic dimension of the niche considers variables relating to both positive and negative interactions with other species likely to modify the species' ability to maintain populations (Soberón and Peterson, 2005). In our case, these interactions were related to resource availability and predation from humans.

A significant contribution of mangrove trees on *T. palustris* was revealed through their effect on food source diversity. First, the significantly negative influence of canopy closure on the presence of *T. palustris* suggests a threshold beyond which the facilitating effect of trees for shade provisioning must be outweighed by its negative effect on light penetration needed to sustain the microphytobenthos *T. palustris* feeds on (Fratini et al., 2004; Pape et al., 2008). This is contrary to what has been found in Thailand mangroves dominated by *Rhizophora apiculata* for various crab species and the Potamidid gastropod *Cerithidea decollata* (Kon et al., 2010). Second, the significantly negative effect of the average percentage of monospecific habitats of *A. marina* also suggests the need for a diversity of tree species such as *Ceriops tagal* that can also be present in the landward mangroves of Mayotte (UICN France, 2017). This species is expected to have a higher attraction and palatability than *A. marina* for *T. palustris* (Fratini et al., 2004). The species thus seems to require a diversity of food sources provided by a heterogeneous habitat to maintain its populations. Further studies should thus explore in more detail both the degree of heterogeneity needed and the factors driving this response for *T. palustris* at various spatial scales. Indeed, interference competition between various mangrove crab species has been shown to explain the exclusion of various species from shaded areas otherwise preferred for food accessibility (Cannicci et al., 2018).

Humans also interact with *T. palustris* through fishing. Although shell middens were observed in Mayotte (field survey observations), the current use of *T. palustris* remains restricted to a few people in Mayotte (Dupont et al. *in review*). During our inhabitant survey on mangroves of current absence, the species was mostly recognized by people over 50 years old, which may reflect several aspects. Firstly, the species may have disappeared some time ago in the studied mangroves, not allowing the younger generations interviewed to recognize it. Secondly, younger generations may be less likely than older generations to frequent the mangrove. Indeed, fishing of *T. palustris* for food or as bait for fishing is a decreasing practice in Mayotte (Biotope, 2022) and is thus diluted in the total population, which invalidates the use of inhabitant density as a proxy for the degree of exploitation in our model. This current state of practice is unlikely to cause overexploitation currently. In the past, fishing was more important in some mangroves (Dupont et al. *in review*), which might have contributed to the past disappearance of certain populations, later unable to be recolonized from other source populations.

4.4. Relevance of the SES approach for the evaluation of the niche

Previous studies described the habitat of *T. palustris* in terms of “environmental factors”, mostly referring to natural abiotic factors, within single mangroves (e.g. Fratini et al., 2004; Pape et al., 2008). These approaches are relevant at fine resolution, where micro-topographic variations or habitat fragmentation drive a patchy distribution of resources (Guisan and Thuiller, 2005). Studies of mangrove animal species distributions using SDM have also focused on abiotic factors only, ranging from global distribution (Sharifian et al., 2021) to subcontinental distribution (Bharti and Shanker, 2021). As such, the distribution of *T. palustris* over the entire Indian ocean might be driven by climatic or oceanographic factors acting mostly on the accessibility dimension of the niche (Adamu et al., 2024). This hypothesis remains to be tested for *T. palustris* as much as other ecologically relevant mangrove species, such as crabs, gastropods or molluscs, likely limited by the availability of occurrence datasets.

Instead, comprehensive presence and absence data of species distribution over several ecosystem units, such as the present one, are missing for mangroves and underrepresented in the tropics in general (Cayuela et al., 2009). Such datasets are needed to improve our understanding of the effects of mangrove loss or degradation on species distributions at the scale relevant for mangrove conservation (Elith and Leathwick, 2009). Understanding the distribution of species within a SES context is thus needed for mangroves that are increasingly subjected to negative anthropogenic activities at the scale of one to ten kilometres (Yando et al., 2021). Our study is the first one throughout the distribution range of the species to assess its realized niche over several neighbouring mangrove units within social-ecological systems by considering factors from both subsystems.

Our results indicate that ecosystemic and societal features are both at play, although in different strengths, in constraining the niche of *T. palustris*, mostly through its abiotic dimension at the scale of the island of Mayotte. Obviously, this result is partially resulting from the choice of variables that were confronted to the measured distribution of the species. In particular, few variables characterizing the accessibility were selected, as a consequence of the lack of knowledge on the larval stage of the species and the oceanographic barriers within the lagoon of Mayotte. Data on the likely connectivity between sites based on currents at the time of recruitment would help improve understanding the importance of accessibility for the distribution of the species. Similarly, the biotic dimension did not consider differences in distribution that might result from interactions with other species than humans. For example, competitive interference with mangrove crabs (Cannicci et al., 2018) might contribute to reducing the available niche of *T. palustris* in sites where the other dimensions might already limit the presence of the species to small populations.

The fact that societal features had a weak influence on the distribution of *T. palustris* at the scale of the island might be the result of these variables being imperfect proxies of the intended pressures. Despite the island being relatively small, little data exists on the amounts of natural let alone anthropogenic outputs from watersheds (Foucher et al., 2024). Characterizing indirect pressures such as pollution through agricultural inputs is further challenged by the fact that most agriculture is not declared and there is no data on illegal pesticide use (Foucher et al., 2024). Direct impacts to the habitat (construction, land inputs) were not considered in the present study, although they have also been identified by fishers to cause local disappearance of past patches (Dupont et al. In review).

At the time of study, the gastropod was mainly found on large and deep mangroves where the landward part of the mangrove is relatively well developed and separated from the sea by a wide central and external mangrove, where *A. marina* is not the only species of mangrove tree and the canopy is relatively open, at the bottom of watersheds holding large urban areas. Admittedly, this result from a single survey does not guarantee that all the surveyed populations are stable through time (Soberón and Peterson, 2005). The smallest populations (Bouéni Bay or Tsingoni in particular) might happen on sites formerly unfavourable or currently degraded. In this respect, knowledge of distribution from the social memory was crucial since LEK is held by regular and frequent environmental observers who, unlike a one-time scientific survey, is integrated in terms of space and time (Thornton and Maciejewski Scheer, 2012). The presence of the species being well known to some experts indicated that the presence was not anecdotal or new. The study of LEK on past distribution through the social memory has already been shown to provide a more complete understanding of change of species distribution over time in poorly studied zones (Azzurro et al., 2019). Further investigation of the past distribution of the species through social memory will help disentangle sites of absence due to unfavourable habitat from those due to habitat degradation or loss. Accessing the SM from all the mangroves of the island would also ensure a comprehensive report of past areas of current presence. Such data would further refine the modelling of the past niche of *T. palustris*, thus improving predictions of its future distribution under various management and conservation scenarios. Our study thus adds to the growing body of evidence showing the benefits of the combined approach of ecological and LEK surveys when studying species distribution in regions lacking information (Beaudreau and Levin, 2014).

5. Conclusion

In this study, we implemented an integrated approach to SDM by identifying underlying social-ecological factors driving the distribution of *T. palustris* at the scale of Mayotte Island. This approach was also relevant for identifying an important attribute of SES, namely the question of scale. Both ecological (shade and elevation) and societal (pollution) factors seem to be acting on species distribution within mangroves differently at different spatial scales. From the point of view of our model species, there might also be thresholds beyond which there might be system changes. The interaction between hydrodynamics and the mangrove dimension and the facilitating role of mangrove trees both deserve further investigation.

At the scale of the island, the realized niche of *T. palustris* in Mayotte appeared to be mostly explained by variables from the ecological subsystem. Further studies of the distribution of the species should nonetheless question the influence of biotic and abiotic variables from both subsystems whether at the scale of several or single mangrove units that are in close dependency with society. In the particular context of islands surrounded by lagoons, understanding of the role of oceanographic barriers on larval connectivity is needed to further characterize the accessibility of mangrove species to various sites. There also remains much to be clarified on the effects of habitat size, fragmentation and heterogeneity on mangrove species persistence.

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CRediT authorship contribution statement

Brosse Rémi: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Golléty Claire:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Longépée Esméralda:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Dupont Lucie:** Writing – review & editing, Methodology, Investigation, Data curation. **Lamure Tardieu François-Xavier:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Mercky Yann:** Writing – review & editing, Methodology, Investigation, Data curation. **Schaal Gauthier:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors have no known conflicts of interest to declare.

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Data are provided as private-for-peer review via the following link: https://figshare.com/s/87fabf69b791003b8922

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Supplementary data

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Data availability

Data is available at the following link :
data_MSES_Terebralia (Original data) (Figshare)

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