#### 1 Modeling the ecological niche of an emblematic mangrove species: a social-2 ecological system approach

- 3 Brosse Rémi <sup>1,2\*</sup>, Golléty Claire <sup>2,3\*</sup>, Longépée Esméralda <sup>4</sup>, Dupont Lucie <sup>2</sup>, Lamure Tardieu
- 4 François-Xavier <sup>2,5</sup>, Mercky Yann <sup>2</sup>, Schaal Gauthier <sup>1</sup>
- 5 <sup>1</sup>Univ Brest, CNRS, IRD, Ifremer, UMR 6539, LEMAR, Plouzané, France
- 6 <sup>2</sup>Université de Mayotte, 97660 Dembéni, Mayotte, France
- 7 <sup>3</sup>MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Montpellier, France
- <sup>4</sup>UMR 8586 Prodig, université Paris 1 Panthéon-Sorbonne, CNRS, IRD, AgroParisTech, 5,
   cours des Humanités, F-93 322 Aubervilliers Cedex
- <sup>5</sup>Espace-Dev, IRD, Univ Montpellier, CUFR de Mayotte, Univ Guyane, Univ La Réunion,
   Univ Antilles, Univ Nouvelle Calédonie, Montpellier, France
- 12 \* Corresponding authors: <u>remi.brosse020@gmail.com</u> and <u>claire.gollety@univ-mayotte.fr</u>
- 13 Data are provided as private-for-peer review via the following link:
   14 <u>https://figshare.com/s/87fabf69b791003b8922</u>

### 15 Abstract

16 The gastropod *Terebralia palustris* is found in mangroves from the Indo-Pacific, where it plays important ecological roles and is exploited by humans. As such, it reflects interactions 17 occurring with the socio-ecosystem, yet our understanding of its distribution and ecological 18 niche are still scarce. Understanding the relative importance of factors of the mangrove socio-19 20 ecological system (MSES) on the realized niche of T. palustris may be used to better define the 21 three dimensions of the niche (abiotic, biotic and accessibility). We studied the distribution of T. palustris at the scale of Mayotte Island (France, Indian Ocean) through the prism of MSES, 22 23 including local ecological knowledge and environmental memory held by population. To this 24 end, a survey campaign of the 29 mangroves of Mayotte made it possible to finely map its occurrences and correlate the spatial patterns to a variety of factors of the MSES related to 25 three dimensions of the niche, including societal and ecological components. Questionnaire 26 27 interviews were conducted to highlight potential relationships between current and past 28 distribution of the species. Mangrove characteristics constrain the realized niche of T. palustris 29 at the scale of the island. The gastropod is found on large and wide mangroves where the habitat is heterogeneous. Instead, societal variables had little influence on the distribution of the 30 31 species. Our study showed that dealing with both ecosystem and societal subsystems and their 32 involvement in each dimension of the niche concept therefore is a promising way of 33 understanding the distribution of a species in anthropized systems.

## 34 Key-words

ecological niche; Indian Ocean; mangrove; social-ecological system; social memory; speciesdistribution

## 37 Highlights

- Terebralia palustris is found within 13 of the 29 landward mangrove units in Mayotte
- Realized niche of *T. palustris* is mostly explained by the abiotic dimension
- Little influence of society features on the presence of *T. palustris*
- Interdependencies between large, heterogeneous mangroves and animal populations
- Contribution of local ecological knowledge to understand distribution of *T. palustris*

## 43 Introduction

Understanding the drivers of realized ecological niches requires the joint study of 44 45 environmental and geographic processes (Elith and Leathwick 2009). Fundamental niches 46 (sensu Hutchinson 1957) can be opposed to realized niches, the latter including the influence of biotic interactions such as competition and predation (Silvertown 2004). The relationship 47 48 between species distribution and the niche concept is not always straightforward (Pulliam 49 2000), as fundamental niches can also be restricted by dispersal ability (see Cain et al. 1998) 50 or historical reasons (recurrent extinction events for example) (Holt 2003). On the contrary, species can be present in suboptimal habitats (where reproduction is lower to mortality) but 51 52 persist thanks to constant supply of individuals from source habitats (see Pulliam 1988). The 53 niche concept can therefore be seen as the consequence of three dimensions (Soberón and 54 Peterson 2005): (i) abiotic variables, i.e. the presence of environmental conditions in which the 55 species can persist; (ii) the biotic environment with the presence of interactions between species and (iii) accessibility for the species, i.e. the area must be accessible to the species thanks to its 56 57 movement or dispersal capacities.

58 The boundaries of fundamental niches can be assessed experimentally in the absence of biotic 59 interactions (see Kearney and Porter 2004). Niche definition based on field observational studies thus refer to realized niches (Colwell and Rangel 2009). Species distribution models 60 61 (SDM) are commonly used to explain species distributions by relating field observations to predictor variables that directly or indirectly affect species (Guisan and Zimmermann 2000). 62 63 These variables can be linked to limiting factors, to any type of disturbance (natural or humaninduced) and to resources (Guisan and Thuiller 2005). Human society can affect the distribution 64 65 of species through, for example, land use or climate change (Guisan and Thuiller 2005), but also positively through conservation plans or the reintroduction of species (e.g. Pearce and 66 Lindenmayer 1998). In this context, the concept of social-ecological systems (SES) (sensu 67 Berkes and Folke 1998) considers that ecological and societal compartments are inseparable 68 and interdependent due to their interactions and feedbacks (Berkes and Folke 1998). Changes 69 70 in the societal or ecological subsystem often have impacts on the other subsystem (Walker and 71 Salt 2006), and both can affect, either individually or in interaction, the distribution of species.

72 SDM relate species occurrences (presence, presence-absence or abundance) to environmental 73 or spatial data or both to understand or predict species distribution (Elith and Leathwick 2009). They are also used to locate unknown populations of poorly known and rare species for 74 conservation purposes (Fois et al. 2018). Although SDM are used less frequently in marine 75 76 systems, their application has become increasingly popular in recent decades (Melo-Merino et 77 al. 2020). However, their use is uneven: (i) from a taxonomic point of view, research has 78 focused more on fish or molluscs; (ii) from a geographical point of view, it has concentrated 79 very little on the northwestern Pacific Ocean and the Indian Ocean; (iii) from a scale point of 80 view, the majority of studies have adopted a rather local approach (Melo-Merino et al. 2020). SDM have been only recently used in mangrove research for climate change and conservation 81 issues (e.g. Record et al. 2013). Most of these studies, however, have focused on the 82 distribution of mangrove tree species on a global (Quisthoudt et al. 2012; Record et al. 2013) 83 or more regional (Quisthoudt et al. 2013) scale. A few studies have been conducted on SDM 84 85 for mangrove animal species (e.g. global distribution of mangrove crabs in Sharifian et al. 86 2021).

87 The giant mangrove whelk, *Terebralia palustris* (Linnaeus, 1767; Potamididae, Gastropoda) is 88 considered one of the major species in the assembly and functioning of mangrove ecosystems 89 in the Indo-Pacific (Cannicci et al. 2008). This epigenous species plays an important role in the 90 degradation, consumption and recycling of mangrove leaves, and thus in the fate of the carbon stock in mangroves (Fratini et al. 2004; Slim et al. 1997). It is widely distributed from the 91 92 Western Indian Ocean to the Western Pacific Ocean (Oostingh 1925; from South Africa see Raw et al. 2014; to Australia see Wells 1980). This species is harvested for food, as bait for 93 fishing or for lime production (e.g. Scales et al. 2017), sometimes up to the point of impacting 94 95 its population dynamics significantly (De Boer et al. 2000). T. palustris is also known to be absent from the most polluted areas (Cannicci et al. 2009; Machiwa and Hallberg 1995). 96

97 Within its range, the distribution of T. palustris within mangroves remains unclear and contradictory. Several studies report a diffuse presence of the species inside mangroves 98 99 (Kenya: Fratini et al. 2004; Japan: Nishihira et al. 2002) while others suggest higher 100 abundances in the upper part of the mangroves (Australia: Wells 1980). Clear spatial 101 segregation between juveniles and adults is also observed in some mangroves (e.g. Pape et al. 102 2008) but not in others (e.g. Fratini et al. 2004). Most studies on *T. palustris* focus on the scale 103 of the mangrove studied while only one study focused on its temporal distribution on a finer 104 scale without investigating factors underlying this distribution pattern (Raw et al. 2014). 105 Considering its ecological importance as well as interactions with human activities in SES, understanding the drivers of T. palustris distribution in mangroves could be important for 106 107 management and conservation perspectives.

108 The aim of this study is to test whether the presence/absence of T. palustris can be explained 109 by a combination of variables in the mangrove socio-ecological system (MSES) in relation to the three dimensions of the niche concept (abiotic, biotic and accessibility). Environment and 110 human activities-related metrics were characterized to identify the main drivers underlying its 111 112 distribution at the scale of Mayotte Island (Indian Ocean). Societal components of MSES in Mayotte are very diverse, villages are close to the mangroves, and may have a direct impact on 113 mangrove environment (Longépée et al. 2021). Beyond the contemporary assessment of the 114 MSES with regard to T. palustris, we also used local ecological knowledge (LEK, Olsson and 115 116 Folke 2001) held in the social memory (SM, Berkes et al. 2003) of inhabitants to obtain data on T. palustris distribution (see Dupont et al. in review). In data-poor areas, SM on LEK can 117 be a rich source of information to understand the past spatio-temporal dynamics of species' 118 119 distribution (e.g. Beaudreau and Levin 2014).

# 120 Methods

### 121 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

126 of 4 m in spring tide (Jeanson et al. 2019).

127 Mangroves cover 694 hectares of intertidal areas, which span along about 29% of the coastline 128 (Jeanson et al. 2019). In total, 29 mangrove units are listed, each stand covering between 0.8 129 ha and 180 ha  $(23 \pm 36$  ha). The mangroves of Mayotte are characterized by the presence of 130 eight mangrove tree species, which form three forest belts along the intertidal gradient (for 131 more detail see Longépée et al. 2021): (1) a seaward fringe, (2) the central mangrove, and (3) 132 the landward mangrove. Unlike in some other places in the south-western Indian Ocean (e.g.

- 133 Fratini et al. 2004; Cannicci et al. 2009), *T. palustris* is only located in the landward mangrove
- in Mayotte (Brosse 2019). This habitat is often represented by stands of large Avicennia marina
- 135 (Forssk.) Vierh. sometimes accompanied by small *Ceriops tagal* (Perr.) C.B.Rob. and shrubby
- 136 forms of *A. marina* bordering saltpans (Cremades 2010).

137 Mayotte is in the midst of a demographic boom (density of 690 inhabitants/km<sup>2</sup>) resulting in an expansion of urbanized areas in the coastal zone (Genay and Merceron 2017). As a 138 consequence, some landward mangroves are decreasing or being lost due to village expansion 139 140 (majority of slum houses), human exploitation (wood cutting, cattle grazing, salt production, 141 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 142 143 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 144 145 harvesting and use of the species was established in 2000 (decree n°347, DAF, 2000) but this 146 has not been prolonged beyond 2018 (decree n°2018/DMSOI/601).

### 147 MSES mapping analysis variables

148 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 analyzed presence/absence data

150 from mangrove field surveys against MSES characteristics from mapping metrics.

151 Sampling effort focused on *T. palustris* habitat within the 29 mangroves from Mayotte's two

main islands (Figure 1). Each unit was then explored in its entirety by two people prospecting

- the area about ten meters apart to avoid missing any presence of the species. The presence or
- absence of the species on each site was recorded between February and April 2021 during the
- 155 wet season.

Most of the data mapping was extracted by updating the polygons of mangrove habitats created 156 during the mapping of the natural habitats of the mangroves of Mayotte (Cremades 2010). The 157 158 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 159 160 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 161 aiming to explain the realized niche of *T. palustris* at the scale of the island. They are classified 162 into four categories in relation to the three dimensions of the niche concept ("connectivity", 163 164 which contributes to the accessibility dimension; "hydrodynamics exposure", which contributes also to the abiotic dimension; "mangrove features" and "society features" that 165 contribute both to the biotic and abiotic dimensions). 166

#### 167 **Connectivity**

The minimum distance to another mangrove (in m) reflects the potentially higher connectivity
(through larval dispersal) between neighboring mangroves than between distant ones.
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.

#### 172 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

180 centroid of each mangrove was calculated.

#### 181 Mangrove features

182 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 asproxies for size and three as proxies for quality were defined as follows.

185 Total mangrove and landward mangrove areas of each unit (in m<sup>2</sup>) have been calculated directly from the MANG-layer on QGIS. Vertices on the land and sea sides were extracted from the 186 MANG-layer and the minimum distances between these vertices were plotted using the « NN 187 188 Join » plugin of QGIS. Average distances for all these segments (land to sea and sea to land) correspond to the average width of each mangrove unit and each landward mangrove. Average 189 190 altitude of the landward mangrove (in m) has been computed from the BDALTI MNT (IGN, 191 2013; controlled accuracy of 1 m) on QGIS with the assumption that T. palustris avoids dry 192 environments landward, to avoid desiccation (Slim et al. 1997), and exposed environments seaward (Houbrick 1991). The percentage of surface area occupied by monospecific Avicennia 193 194 marina habitats within the landward mangrove (based on personal field observations suggesting presence of T. palustris mainly where A. marina stands dominate) was calculated 195 from the total surface area occupied by habitats dominated by A. marina on the basis of the 196 typology created by Cremades (2010). The percentage of landward mangrove that is covered 197 198 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 199 gastropod is present. It was calculated by remote sensing from a Random-forest classification 200 on Pléiades satellite imagery of 50 cm resolution (Pléiades© CNES 2018 Distribution Airbus 201 DS) on Orfeo ToolBox 8.0.1. 202

#### 203 Societal features

Human presence can affect the mangrove ecosystem in a number of different ways and it is difficult to measure these pressure links (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. The considered descriptors assume that urban areas are potentially associated with greater inputs of pollutants (number of waste and wastewater) and direct exploitation, and that agricultural areas (agricultural inputs and hydro-sedimentary inputs via soil erosion) are also potentially associated with greater inputs. Some impacts may be direct for *T. palustris*, such as harvesting or pollution.

such as harvesting or pollution. Other impacts may be indirect through habitat degradation.

Watershed population density (in hab.km<sup>-2</sup>) 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 200 216 m of the landward limit of each mangrove was calculated through the use of the modeling of

infrastructures on Mayotte (BD Topo®, IGN 2021) on QGIS. Residential occupation in the

218 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<sup>2</sup>) was

calculated on OGIS within the watershed from the RPG parcellaire 2.0 (IGN, 2019). Each

- agricultural parcel declared represents an area that together gives the agricultural area within
- 223 the watershed of the mangrove.

## **LEK and SM data collection**

A questionnaire survey campaign was conducted in 2022 (April-May) to call upon the social 225 226 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 227 228 the gastropod was found absent during the sampling effort of 2021 (see Methodology section 229 2). 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 230 disappeared because of direct (overharvesting: see Lebigre 1996) or indirect (pollution: see 231 Cannicci et al. 2009) human pressure. Based on village-mangrove proximity and a qualitative 232 233 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 234 polluted, less distant), Mounvambani (less polluted, more distant), Ironi Bé (more polluted, 235 236 more distant) and Mgombani-Baobab (more polluted, less distant).

237 Inhabitants were randomly selected from cities or villages neighboring the considered mangroves. Some respondents were able to refer to other people who might have knowledge 238 on the gastropod. The choice of respondents was conditional on age and the length of time 239 240 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 241 lived near the mangroves of interest (Poroani and Tsimkoura for Bouéni Bay, Mgnambani and 242 243 Bambo-Est for Mounyambani, Mamoudzou and Mtsapéré for Mgombani-Baobab, and 244 Tsararano and Tsoundzou II for Ironi Bé – Figure 1). Questionnaires were made directly with people in the street or at their house by a researcher with help of a translator when necessary 245 246 (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 247 its activities in mangroves (Appendix A). A confidence score was calculated to identify 248 249 respondents who confused Cerithidae decollata and Terebralia palustris (see Dupont et al. in 250 review).

### 251 Data analysis

All data were analyzed 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 259 mangroves of presence and absence, a radar chart based on average MSES-related
260 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) (Breiman 2001) algorithm was used to estimate the importance of each 268 explanatory variable and the contribution of their categories in constraining the realized niche 269 270 of *T. palustris* at the scale of Mayotte. This machine learning approach was performed with the package "randomForest" (Liaw and Wiener 2002). At each node, a number of predictor 271 variables (mtry) were randomly selected and a number of trees (ntree) in a forest were drawn. 272 273 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 274 models was assessed by observing the increase of the OOB when each mtry is swapped while 275 276 all the others remain unchanged (Breiman 2001) using the method of the package "randomForest" (Liaw and Wiener 2002). Predictions for the 29 mangroves were carried out 277 from the 100 RF models in order to obtain a prediction percentage of the likely presence or 278 279 absence of T. palustris on these sites. Each model prediction was performed on the 20% of mangroves not used to train the model. 280
- Finally, the effect of age and gender on the ability to recognize *T. palustris* by the respondents was tested by a Chi<sup>2</sup> test of independence. Analyses were performed using the Sphinx IQ3 software.
- 284 **Results**

### **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 (Figure 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 (Figure 1).



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Figure 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.

### 297 Importance of variables

The importance of variables in the random-forest model was calculated from 100 RF (Figure 2). All the variables explaining more than 50% of the model are variables characterizing mangrove features. The surface of the landward mangrove ( $92.9 \pm 12.8\%$ ) and of the entire mangrove ( $87.1 \pm 16.8\%$ ) 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 ( $68.1 \pm 22.0\%$ ) followed by mangrove width ( $65.3 \pm 21.2\%$ ) and landward mangrove width  $(53.4 \pm 20.4\%)$ . All other variables were found to be irrelevant to explain the presence of *T. palustris* in mangroves.



306

307 Figure 2: Boxplot (rectangles) with median value (black line) showing the importance of variables 308 explaining the presence of Terebralia palustris in mangroves by machine learning modeling (Random-309 forest; n = 100, mtry = 4; ntree = 200). Only variables not significantly different from each other by 310 Wilcoxon test are displayed with the symbol "ns". All other comparisons are significantly positive. 311 Abbreviations: Mang dist = minimum distance to another mangrove unit; Mang area = mangrove area; 312 Land mang area = landward mangrove area; Mang width = average mangrove width; Land mang width = average landward mangrove width; Mono Av = percentage of area occupied by 313 314 monospecific habitat of Avicennia marina; Canopy closure = percentage of area covered by trees in 315 landward mangrove; Land mang alti = average altitude of the landward mangrove; Sea dist = average 316 distance to the sea of the landward mangrove; Fetch = fetch; Pop dens = watershed population density; 317 P build area = percentage of area occupied by buildings within 200 m of the mangrove; Urban area = 318 urban area; Agri area = agricultural area.

### 319 Realized niche

320 Variable-by-variable differences were tested between sites with and without T. palustris 321 (Figure 3). The landward mangrove area is significantly greater in stands with T. palustris (14.6 322  $\pm$  12.1 ha) than without (0.9  $\pm$  1.2 ha) (Wilcoxon test: W = 5, p-value < 0.001). The area of mangroves with T. palustris (43.7  $\pm$  47.4 ha) is also significantly greater than that without T. 323 *palustris*  $(6.6 \pm 4.9 \text{ ha})$  (W = 7, p-value < 0.001). The proportion of A. marina in the landward 324 325 mangroves of the presence sites  $(56.5 \pm 17.7\%)$  is significantly lower than in those of the absence sites  $(91.9 \pm 15.5\%)$  (W = 191, p-value < 0.001). The width of mangroves with T. 326 *palustris* (158.8  $\pm$  67.8 m) is also significantly larger than without (69.9  $\pm$  42.1 m) (W = 16, p-327 328 value < 0.001) and the landward mangrove width is also significantly larger in mangroves with T. palustris  $(72.1 \pm 42.2 \text{ m})$  than without  $(24.4 \pm 14.8 \text{ m})$  (W = 15, p-value < 0.001). Similarly, 329 the distance from the centroid of the landward mangrove to the sea is significantly longer in 330 mangroves with T. palustris  $(553.6 \pm 221.2 \text{ m})$  than without  $(353.3 \pm 146.4 \text{ m})$  (t test, t = -2.8, 331 332 df = 20.0, p-value < 0.05). Canopy closure in the landward mangrove of presence sites (59.4  $\pm$ 14.4%) is significantly reduced compared to that of absence sites  $(76.5 \pm 18.7\%)$  (t = 2.8, df = 333 27.0, p-value < 0.01). In addition, the urban area is significantly larger in mangroves with T. 334 *palustris*  $(84.4 \pm 70.5 \text{ ha})$  than without  $(38.1 \pm 68.8 \text{ ha})$  (W = 48, p-value < 0.05). None of the 335 336 other variables studied display significant differences between mangroves with and without T. 337 palustris.



#### 338

339Figure 3: Modeling of realized niche of *Terebralia palustris* at the scale of Mayotte based on average340MSES-related characteristics. Average values taken by sites of presence (green) or absence (red) of *T*.341*palustris*. A significant difference ( $\alpha < 0.05$ ) via a Wilcoxon test or a t-test between the presence and342absence mangroves is represented by an asterisk (\*).

#### Discrimination of mangroves with and without Terebralia 343 palustris 344

The 14 different considered variables significantly discriminate sites with and without T. 345

346 *palustris* (PERMANOVA,  $F_{1,27} = 10.8$ ,  $R^2 = 0.3$ , p-value < 0.001). Axis 1 of PCA (Figure 4),

347 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 (Figure 4), explaining 17.4% 348 of the variance, is mostly explained by societal components of the MSES and hydrodynamics

- 349 350
- variables. This axis displays most of the intra-group dispersion.



351

352 Figure 4: Principal component analysis of the characteristics of the 29 mangroves of the island of 353 Mayotte. Ellipse containing 60% of sites of presence (green) or absence (red) of Terebralia palustris. 354 Abbreviations: Mang dist = minimum distance to another mangrove unit; Mang area = mangrove area; 355 Land mang area = landward mangrove area; Mang width = average mangrove width; 356 Land mang width = average landward mangrove width; Mono Av = percentage of area occupied by 357 monospecific habitat of Avicennia marina; Canopy closure = percentage of area covered by trees in 358 landward mangrove; Land mang alti = average altitude of the landward mangrove; Sea dist = average distance to the sea of the landward mangrove; Fetch = fetch; Pop dens = watershed population density; 359 360 P build area = percentage of area occupied by buildings within 200 m of the mangrove; Urban area = 361 urban area; Agri area = agricultural area.

#### **Results on past presence from the questionnaire survey** 362

363 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). 364 Most respondents were between 30 and 49 years old (53.2%) with a majority of women 365 (57.6%). People over 50 years old were significantly overrepresented among those with 366 knowledge of *T. palustris* (53.7%) (Chi<sup>2</sup> test,  $\chi^2 = 10.64$ , df = 2, p-value < 0.005). A large part 367 of the respondents frequenting the targeted mangroves recognize T. palustris (50.8%) (Figure 368 369 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 370 371 not explore specific areas of presence, or because they do not pay attention to the species. Thus, 372 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 373 374 from those who could not.

- 375 More respondents reported having seen *T. palustris* in the mangroves of Bouéni Bay (14 versus
- 5) and Ironi Bé (14 versus 11) than not (Figure 5). Finally, more respondents reported the
- absence of *T. palustris* in the mangroves of Mounyambani (4 versus 7) and Mgombani-Baobab
- 378 (8 versus 14). It should be noted here that for Mounyambani, we had difficulty finding people
- 379 who had lived in the village for more than 5-10 years.

380



Figure 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?"

# 383 **Discussion**

Before the present study, the presence of *Terebralia palustris* in Mayotte remained very little documented and its detailed distribution at the scale of all the mangrove units was not known. This survey of the 29 mangroves of Mayotte showed that this species was present in 13 of them, all but two presence sites being on the northern and eastern coasts.

Surprisingly, throughout the distribution range of *T. palustris*, there is a lack of information 388 389 regarding factors explaining its presence or absence on a larger scale than a mangrove unit. Previous studies have described the habitat of T. palustris in terms of environmental factors 390 within a mangrove (e.g. Fratini et al. 2004; Pape et al. 2008). Instead, our study is the first one 391 to assess the realized niche of the species on a larger scale (several neighboring mangrove 392 393 units) by considering broader factors based on socio-ecological systems. Our results indicate a 394 contrasting response between the different dimensions of the niche, with the four selected components (mangrove, societal, connectivity and hydrodynamics features) not influencing the 395 396 niche with the same force, and possibly affecting several dimensions at the same time.

## 397 Little difference in accessibility between sites

398 Connectivity features did not have much influence in our T. palustris distribution model. The distribution of the species observed in the field revealed an apparent opposition between the 399 400 two sides of the island, with only a few small, isolated areas of presence of T. palustris on the 401 west coast (Figure 1). T. palustris has a free-swimming larval stage (Rao 1938) but its duration is still unknown. According to the phylogeographic study of T. palustris populations in the 402 403 western Indian Ocean, connections exist between populations in western Madagascar, Kenya and Tanzania (Ratsimbazafy and Kochzius 2018), suggesting that larval lifespan is not limiting 404 for the colonization of nearby mangroves in Mayotte. The mangroves characterized by the 405 406 presence of the species on the western coast of the island (Figure 1), however, are relatively isolated from the other mangroves of presence, which could be explained by (1) oceanographic 407 barriers within the lagoon or by (2) the inability of these mangroves to act as sources for 408 neighboring mangroves or both. The lack of detailed knowledge of the circulation within the 409 410 lagoon and the potential presence of oceanographic barriers does not allow us to conclude on this point. The recent modeling of the hydrodynamics of the lagoon of Mayotte (Parc Naturel 411 412 Marin de Mayotte, pers. comm.) should help unravel connectivity between mangroves around 413 the island. Either or both of these hypotheses could explain the case of the two mangroves of 414 absence predicted by the simulation as favorable habitat zones on the western and southern part of the island (Figure 1). Moreover, the presence of the species can be missed during the field 415 416 survey within the mangroves where the species is confined to very small areas with only a few 417 individuals. This happened in Tsingoni, where a small population was only found during a second site visit, and Bouéni Bay, where scattered patches were found thanks to the local 418 ecological knowledge held in the social memory (LEK/SM) survey. In both cases, these 419 populations are extremely narrowly distributed ( $\sim 0.1$  ha) compared to the landward mangrove 420 421 surface area (6.4 and 33.7 ha respectively). This low presence can be explained either by the 422 fact that these mangroves are no longer supplied by old sources or that they are no longer 423 capable of containing larger populations due to other abiotic or biotic factors. The hypotheses 424 raised here need to be clarified by studying the genetic diversity of the species at the island 425 scale.

### 426 **The abiotic dimension of the niche**

The abiotic dimension of the niche concept is based on the environmental conditions that enable the species to persist in a given location thanks to its physiological abilities (Soberón and Peterson 2005). These conditions can be impacted by factors of various origins. In our study, we have targeted variables specific (1) to the physical environment, (2) hydrodynamics, and (3) the society through its use of space and its resulting pollution. These three categories do not respond in the same way in our model to explain the presence of the species.

- 433 The structural environment through mangrove variables indicates a higher influence in our T. 434 palustris niche modeling. The probability of encountering populations of T. palustris in a mangrove appears to be linked to the size and the quality (defined below) of the suitable habitat. 435 436 Indeed, T. palustris is found in larger (2 to 1 ratio), wider (4 to 1 ratio) mangroves where the 437 landward mangrove is also more developed (size and width of the landward mangrove being 438 correlated with those of the total mangrove). Numerous studies have shown that small habitat 439 size influences extinction risk by reducing the carrying capacity (Griffen and Drake 2008). Yet, 440 it is difficult to explain the precise impact of these factors on species presence, as area may also indirectly correlate with other factors that directly affect species richness like habitat diversity, 441
- 442 which is often assumed to increase in direct relation to area (Kohn and Walsh 1994).
- In most cases, habitat heterogeneity increases with the size of the ecosystem, due to a greater variety of microhabitats (Connor and McCoy 1979). Although mangroves are floristically homogeneous, they often display considerable structural and biogeochemical heterogeneity along intertidal gradients (Lugo and Snedaker 1974; Alongi et al. 1992). So the larger the mangrove, the more likely the complexity of the mangrove forest resulting from a higher variability in tree and canopy density, ground topography, or abiotic conditions.

Desiccation is one of the most stressful processes for marine gastropods through longer 449 450 exposure to the air and light. Shade has been shown to play an essential role in helping T. palustris avoid desiccation (Crowe 1997; Slim et al. 1997; Wells and Lalli 2003). Although 451 452 exposure to the air is longer higher on the shore, in our model, differences in altitude of the 453 landward mangrove cannot be used to explain the exclusive presence of the species in the upper part of the shore in Mayotte to further characterize the species' niche. Surprisingly, canopy 454 closure was found to explain the absence of the species in the mangroves of Mayotte according 455 456 to our model. We would, however, expect a closed canopy to provide the shade the species needs to avoid desiccation. This contrast leads us to believe that other parameters, notably 457 biotic ones (discussed below), are involved in explaining this negative relationship between 458 canopy closure and the presence of the species. 459

Hydrodynamic variables had small (sea distance, which correlates with mangrove width) or no 460 (fetch) influence on the presence of T. palustris in mangroves. The species is found in 461 mangroves with the greatest distance between landward mangrove and the sea. The energy of 462 463 waves arriving in landward mangrove is thus more attenuated, through the friction of the sedimentary bottom and the resistance generated by the mangrove trees, favoring the deposition 464 and accumulation of fine sediments (Mazda et al. 1997). Finer mud particles have a greater 465 capacity to adsorb organic matter, enabling the species to find more food resources (Penha-466 Lopes et al. 2009). Furthermore, the species requires a low-hydrodynamic environment for its 467 continued movement and feeding at high tide (Fratini et al. 2001). Finally, low hydrodynamics 468 are needed to limit the resuspension of microalgae and avoid strong leaching of the litter on 469 470 which T. palustris feeds.

On the contrary, it is interesting to note that *T. palustris* is relatively absent from mangroves on the west and south coasts of the island, which are undergoing significant surface erosion, especially due to the joint effect of hydrological conditions and exposure to swell and waves (Jeanson et al. 2014). These surface losses under the influence of local hydrodynamics could also explain the distribution of the species on the island. Yet, *T. palustris* is only found in the landward parts of mangroves in Mayotte, not subjected to the negative influence of this local hydrodynamic. Further studies should thus focus on the contribution of the landward mangrove

478 surface dynamics for the presence of the species.

Humans can affect the mangrove ecosystem in a number of ways, changing physical, edaphic or chemical conditions, in other words the abiotic dimension. In our study, land use variables had little role in explaining the distribution of the species. In fact, *T. palustris* was found to be present both on sites where urban influence is considered the highest (e.g. Tsoundzou-Passamaïnti or Badamiers) and the lowest (e.g. Dapani or Hajangua-Iloni), illustrating the low influence of the degree of urbanization and soil permeabilization of the watershed through the considered human occupation-related variables.

486 Across its range, responses of *T. palustris* to the effects of urbanization vary according to the context. T. palustris is known to disappear when human sewage pollution is too high (Cannicci 487 488 et al. 2009; Machiwa and Hallberg 1995). Studies in mesocosms revealed that T. palustris has 489 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 behavioral changes (Penha-490 491 Lopes et al. 2010). Over time, the hypoxic conditions created by this anthropogenic pollution lead to a reduction in reproductive capacities (Cheung et al. 2008) and a potential decline in 492 populations. Considering the aforementioned literature background, the lack of influence of 493 494 our indicators of urbanization is not surprising. Contaminations from effluents vary both as a function of the system and of the properties of the effluents (Branoff 2018). Mayotte 495 watersheds are relatively small, with little to no industries, subsistence farming for the most 496 part, and urbanization mostly localized along the coastline (Figure 1). Agricultural pollution is 497 498 mainly due to the uncontrolled use of pesticides in Mayotte. In addition, the wastewater treatment system in Mayotte is dysfunctional, which leads to the discharge of wastewater 499 directly into the mangroves, resulting in excess nutrients and eutrophication (De Grandcourt 500 501 2016). Large sewage inflows tend to be restricted to specific areas and problems of excessive nutrient inputs are therefore more likely to explain localized distributions within mangroves. 502 Indeed, T. palustris is generally not observed at the vicinity of wastewater outlets (R.B., 503 504 personal observation).

505 Human influence on mangroves can also induce destruction or fragmentation of all or part of T. palustris favorable habitat. Felling is an important threat to mangrove ecosystems, creating 506 forest fragments too small to sustain viable populations and increasing "edge effects" (Harris 507 508 1984). This process does not emerge in our study through societal proxies. Nevertheless, residents living near mangroves have reported the destruction or degradation of habitat of T. 509 *palustris* in the past, which has been linked to the disappearance of the species from these 510 mangroves (Dupont et al. in review). Despite the Random-forest model assigning the mangrove 511 of Ironi Bé as non-favorable habitat, most people being familiar with T. palustris reported the 512 presence of the species in the past. The construction of a road on a bush track through the 513 mangrove in the 1980s increased habitat fragmentation and pollution from road traffic, which 514 has potentially negatively impacted this population over the years. The disappearance of T. 515 *palustris* within a mangrove is complex and requires a site-specific examination including a 516 517 deeper questioning of SM on the evolution of *T. palustris* and the evolution of the mangrove.

518 LEK provides valuable information to understand species occurrence and habitat use for 519 elusive or hard to observe species (e.g. Beaudreau and Levin, 2014). LEK are held by regular and frequent environmental observers who, unlike a one-time scientific survey, are integrated 520 521 in terms of space and time (Thornton and Maciejewski Scheer 2012). The study of LEK on 522 past distribution by the SM provides a more complete understanding of biogeographic changes 523 and evolution of species over time, especially in poorly studied zones (Azzurro et al. 2019). In 524 our case, future studies could rely on LEK retained within the SM from all the mangroves of the island to ensure a comprehensive report of very small areas of current presence. Additional 525 526 evidence of past presence of the species would further refine the modeling of its past niche, 527 thus improving predictions of its future distribution under various management and 528 conservation scenarios. In particular, questioning the LEK of the inhabitants living in the 529 vicinity of the mangroves discussed above for which there is a disagreement between the 530 presence/absence observed and predicted could serve three purposes. On the one hand, in mangroves of absence identified by the model as favorable, LEK could help verify the current 531 532 absence and potential past presence thus improving our understanding of the factors limiting the dynamics of the species' distribution. On the other hand, it could evaluate the temporal 533 534 evolution of the distribution in the "model-unfavorable but presence" mangroves in order to understand whether the species' abundance has decreased following a loss of habitat. Finally, 535 it would also be interesting to conduct participatory mapping workshops with local residents 536 537 to establish the link between the species' distribution and the state of the habitat, based on old 538 aerial images of the evolution of the landward mangrove over the last few decades.

### 539 The biotic dimension of the niche

540 When considering the biotic dimension of the niche, it is important to emphasize that this refers 541 to all the positive or negative interactions with other species that modify the species' ability to 542 maintain populations (Soberón and Peterson 2005). In our case, these relationships could be 543 linked to facilitation (role played by mangrove trees), competition (with crabs) and predation 544 (especially by humans).

545 As we have already seen, canopy closure has a negative influence on the presence of T. 546 *palustris* within the mangroves of Mayotte according to our model as does the percentage of surface occupied by monospecific habitats of Avicennia marina. In fact, stands of A. marina 547 548 that are too dense and have canopies particularly closed must limit the penetration of light necessary for biofilm development, but also for the development of other tree species like 549 Ceriops tagal or Rhizophora mucronata. T. palustris is known to feed on leaves of these 550 species, occasionally on propagules or root bark (Fratini et al. 2004), but also on organic matter 551 and biofilm that can be found in more topographically diverse areas (Gontharet et al. 2014). 552 The species thus seems to benefit from having a diversity of food sources provided by a 553 554 heterogeneous habitat, enabling it to limit the competition with crabs.

555 Beyond anthropogenic inputs, humans can also affect coastal ecosystems through direct exploitation. Although shell middens were observed in Mayotte (field survey observations), 556 the current use of T. palustris remains restricted to a small number of people in Mayotte 557 558 (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. 559 Firstly, the species may have disappeared some time ago in the studied mangroves, not allowing 560 561 the younger generations interviewed to recognize it. Secondly, younger generations may be less likely to frequent the mangrove than older generations. Indeed, harvesting of T. palustris 562 for food or as bait for fishing is a decreasing practice in Mayotte (Dupont 2022) and is thus 563

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, harvesting was more important in some mangroves (Dupont et al. *in review*), which could explain, in combination with other processes, the current distribution of the species via the past disappearance of certain populations, later unable to be recolonized from other source populations.

## 570 The relative contributions of each dimension of the niche

571 The study of the niche of *Terebralia palustris* within the SES framework has shown that each 572 sub-system, societal and ecosystemic, can be involved in different ways on the three 573 dimensions of the niche. The study of the niche thus seems to be better approached by dealing 574 with both the ecosystemic and societal subsystems and their implication in each dimension of 575 the niche concept.

The selected variables seem to have more influence on the abiotic dimension of the niche of T. 576 *palustris* through mangrove variables, especially structural ones, while society variables have 577 578 little or no influence on the presence of the species. The gastropod is mainly found on large 579 and wide mangroves where the landward part of the mangrove is relatively well developed, where Avicennia marina is not the only species of mangrove tree. This stresses the 580 581 interdependencies between large, heterogeneous mangrove forests and animal populations inhabiting mangroves in Mayotte. Beyond the specific case of T. palustris, complex and 582 heterogeneous habitats are known to host higher biodiversity and more resistant and resilient 583 assemblages, and should be considered as conservation targets in mangrove conservation and 584 restoration (Leung 2015). 585

In addition, mangrove trees play a facilitating role (sensu Bulleri et al. 2016) for T. palustris 586 by providing both shelter from desiccation (abiotic dimension) and a food source with its leaves 587 and fruits (biotic dimension). As mentioned earlier, too much shade, good for reducing 588 desiccation, is not necessarily good for the development of the diverse food sources of T. 589 *palustris*. The facilitating role of mangrove trees thus seems limited to the degree of canopy 590 closure, with a compromise between the advantage of shade to avoid desiccation and the 591 disadvantage for food diversity. At the scale of several relatively small mangroves that share a 592 common socio-ecological context, the niche of T. palustris remains complicated to define when 593 594 based on parameters that interact at different spatial scales such as canopy closure or altitude. Further characterization implies studying the effects of these factors at the scale of the habitat. 595

596 Even though societal features were not found to significantly affect the presence/absence of T. palustris at the scale of the island, this result is likely scale-specific. Human influence is diverse 597 and can be localized within mangroves, and induce small-scale consequences on the 598 599 populations of T. palustris. Such small scale effects were not assessed in the present study. Ecological patterns result from the interaction of various drivers, each one operating at a 600 specific spatial and temporal scale, and generating a pattern that can be expressed at another 601 scale (Levin 1992). Consequently, although environmental variables considered here explained 602 significantly the distribution of *T. palustris* at the island scale, inferring human influence might 603 have involved addressing this topic at a finer spatial scale. It therefore seems necessary to study 604 its distribution within individual mangroves, and thus to change the scale of study within the 605 SES, to gain a complete understanding of its realized niche. 606

# 607 Conclusion

In this study, we intended to implement a comprehensive approach to SDM by considering the question of *T. palustris* distribution at the scale of Mayotte Island through the prism of the social-ecological system. Since the mangrove ecosystem and society are interdependent and as humans can influence species' distribution through means that are not reflected by environmental variables and involved in all three dimensions of the niche concept, we believe that this approach is promising to understand the distribution of species in anthropized systems.

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 (e.g. Fratini et al. 2004 or Nishihira et al. 2002). At the scale of the island, the realized niche of *T. palustris* in Mayotte appeared to be mostly explained by environmental variables, and little by human-related drivers.

Finally, it was shown that the contribution of LEK retained within the SM was essential in 619 620 determining the presence of the species on sites of low presence. The presence being well known to some experts indicates that the presence is not anecdotal. In addition, relying on 621 622 social memory has made it possible to access information on the temporal dynamics of a species' distribution in an area and period with scarce and missing data respectively. The 623 624 combined approach of scientific survey and inhabitant observation of the species and 625 knowledge of the sites is relevant and complementary to understand the changes in distribution 626 over time.

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# 637 Author Contributions

CG, GS and EL were responsible for the development, conceptualization and supervision of the project, with a higher focus of GS on the ecology, EL on both the social sciences and the interdisciplinary framework, and CG for the ecology and interdisciplinary framework. Material preparation and ecology fieldwork were carried out by RB with YM and CG. Mapping analysis was carried out by RB with support from FXLT. The survey protocol was drawn up and implemented in the field by LD with the help of EL and RB. All statistical analyses were performed by RB. The first version of the manuscript was written by RB, and all the authors 645 corrected earlier versions of the manuscript. All authors read and approved the final 646 manuscript.

# 647 **Conflict of Interest Statement**

- 648 The authors have no known conflicts of interest to declare.
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