



ECOLOGY OF THE FACULTATIVE PHYTOTELMIC CRAB
PLATYCHIRARMA BUETTIKOFERI (DE MAN, 1883) (DECAPODA,
BRACHYURA, SESARMIDAE)

BY

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ABSTRACT

The mangrove forests surrounding Douala, Cameroon, have a long history of human impact due to rapid urbanization, resulting in patches of true mangrove forest interspersed with areas dominated by the mangrove-associated *Pandanus* species. A survey carried out to assess the possible shift in crab fauna composition and dominance between mangrove and *Pandanus* dominated areas revealed an undescribed phytotelmic habitat for *Platyichirarma buettikoferi*. This species was found colonizing the natural reservoirs of fresh water represented by *Pandanus* spp. Our results show *P. buettikoferi* to be ecologically dependent upon *Pandanus* spp., and absent on the mangrove floor and trees, strongly indicating a phytotelmic adaptation. Our data suggest that this species is a facultative phytotelmic species well adapted to *Pandanus* spp. dominated areas. Further studies on the reproductive biology and feeding behaviour of *P. buettikoferi* may shed light on this unique phytotelmic lifestyle and its role in mangrove ecosystem functioning.

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RÉSUMÉ

Les forêts de mangroves entourant Douala, au Cameroun, ont une longue histoire d'impacts humains en raison de l'urbanisation rapide. Celle-ci résulte en des parcelles de forêt de mangrove entrecoupées de zones dominées par *Pandanus*, espèce associée à la mangrove. Une étude faite pour évaluer le changement dans la composition faunistique de crabes et la dominance entre les zones dominées par les mangroves et les *Pandanus* a révélé un habitat phytotelmique pour *Platychirama buettikoferi*, jamais décrit auparavant. Cette espèce a été trouvée en train de coloniser les réservoirs naturels d'eau douce représentés par *Pandanus* spp. Nos résultats montrent que *P. buettikoferi* est écologiquement dépendant de *Pandanus* spp., et absent du sol et des arbres de la mangrove, ce qui indique fortement une adaptation phytotelmique. Nos données suggèrent que cette espèce est une espèce phytotelmique facultative bien adaptée aux zones dominées par *Pandanus* spp. D'autres études sur la biologie reproductive et le comportement alimentaire de *P. buettikoferi* pourraient documenter ce mode de vie phytotelmique unique, ainsi que son rôle dans le fonctionnement de l'écosystème de la mangrove.

INTRODUCTION

Human activity is known to have detrimental impacts on the whole mangrove ecosystem (Ellison, 2008; Saenger, 2012), especially through deforestation (Hutchison et al., 2014), uncontrolled sewage discharge from urban areas (Mohamed et al., 2008; Cannicci et al., 2009; Bartolini et al., 2011; Penha-Lopes et al., 2011) and global warming (Ellison & Cannicci, 2016). These impacts can significantly transform the forests, triggering a negative cascade effect on the whole ecosystem assemblage leading to a reduction of biodiversity and functionality (Valiela et al., 2001; Worm et al., 2006; Duke et al., 2007; Halpern et al., 2008; Butchart et al., 2010; Fusi et al., 2016).

The Wouri River Estuary in Cameroon is one of the most thriving mangrove ecosystems in West Africa (UNEP, 2007); but, due to population growth and shipping activity in Douala harbour and to an oil platform close to the Gulf of Guinea, it is also one of the most impacted (Scheren, 2002; Alemagi, 2007). In particular, rapid population growth in Douala has led to large-scale deforestation due to a growing demand for housing and logging cultivation (Saenger et al., 2008; Nfotabong-Atheull et al., 2009, 2011, 2013).

This urbanization has transformed hectares of forest dominated by mature mangrove trees, such as *Rhizophora* spp. and *Avicennia germinans* (L.) Stearn, 1764, into highly degraded areas with a dramatic change in botanical assemblages (Din & Baltzer, 2008; Nfotabong-Atheull et al., 2011). In many of the affected areas, the mangrove-associated screw-pines of the genus *Pandanus* (Tomlinson, 1986) rapidly took over and are now the dominant species to appear in the

vegetation secondary succession. *Pandanus* spp. (Pandanaeae) are known to shelter animals from predators, such as the micro-mammal *Sminthopsis virginiae* de Tarragon, 1847 (Braithwaite & Lonsdale, 1987), and to provide a suitable habitat for many birds (Verbeek et al., 1993). They also have an important role in the feeding ecology of terrestrial decapods such as *Cardisoma carnifex* Herbst, 1796, and *Birgus latro* Linnaeus, 1767 (Grubb, 1971; Lee, 1985).

Screw-pines, similarly to the New World bromeliads, are phytotelms (i.e., with structures that retain rainwater), providing micro-aquatic environments in their leaf axils for a wide variety of animals, including some reptiles and amphibians (Laessle, 1961; Fish, 1983). Crabs are also known to inhabit phytotelmata. In Madagascar, *Malagasya goodmani* Cumberlidge, Boyko & Harvey, 2002, and *Labuanium gracilipes* H. Milne Edwards, 1854, were found to be associated with *Pandanus* (Cumberlidge et al., 2002). Likewise, in the West Pacific the genus *Scandarma* Schubart, Liu & Cuesta, 2003 has been described thriving in *Pandanus*, e.g., *S. lintou* Schubart, Liu & Cuesta, 2003 in Taiwan. These species disclose biological traits similar to *Metapaulias depressus* Rathbun, 1896 and *Geosesarma* spp. that are known to live as phytotelmic species (see review in Cumberlidge et al., 2005).

A recent survey of Cameroonian mangroves described a high biodiversity of macrobenthonic brachyuran crabs belonging to the family Sesarmidae (see Fusi et al., 2016). Of the eight species found to inhabit the mangroves and adjacent habitats, *Platyichirarma buettikoferi* (De Man, 1883) appeared to be frequently associated with *Pandanus* trees. The present study was designed to investigate the possible phytotelmic association of *P. buettikoferi* with *Pandanus* trees of the Wouri estuary and the changes in population dynamics resulting from the ecological shift from mangrove to screw-pine dominated forests.

MATERIAL AND METHODS

Species studied

Platyichirarma buettikoferi (Sesarmidae Dana, 1851) has been recorded along the West African coast from Liberia to Angola (Manning & Holthuis, 1981). The species is easily recognized by its characteristic purplish blue flat chelipeds with red tips (in live animals). Brightly coloured male chelipeds, in particular, are important for signalling females (Manning & Holthuis, 1981). The species is usually found in the landward part of true mangrove forests, beyond the area reached by the highest high tides (see Rathbun, 1921: 450). Ovigerous females were reported in March, June, July-August, and October-December (Rathbun, 1921; Rossignol, 1957; Manning & Holthuis, 1981). In Cameroon, *P. buettikoferi*

has been recorded under the humid leaf litter found on the banks of a riverine forest close to the sea in Kribi and in the Wouri estuary mangrove forests (Fusi et al., 2016).

Study area

This study was carried out in and around the mangrove forests of the Wouri River estuary, one of the largest estuaries in West Africa, surrounding the city of Douala, Cameroon (fig. 1). The climate is equatorial, and the area receives high rainfall, on average about 4000 mm per year. Most of the rain falls between March–November (rainy season), with a short dry season often punctuated by showers in December–February. The humidity is high year-round (approximately 100%).

The survey was performed in September and October 2009 in two forests: Wouri Bridge, hereafter abbreviated to WB (4°4'19"N 9°42'58"E), and Essengue, hereafter abbreviated to ES (4°53'N 9°40'39"E). WB is located north of Douala, close to the bridge crossing the Wouri River. Part of this forest was cleared 20 years ago for construction of the bridge and currently the whole forest has regrown with extended patches of *Pandanus candelabrum* P. Beauv. associated with mature forest dominated by *Avicennia* sp. and *Rhizophora* spp. (Din & Baltzer, 2008).

ES forest, located south of Douala at the edge of the harbour, was recently affected by clearing due to rapid development of the commercial port. This forest is colonized by several species of mangrove-associated flora (Nfotabong–Atheull et al., 2013), including *Nypa fruticans* (Thunb.) Wurmb., *Guibourtia demensei* Harms, and *P. candelabrum*.

The locality of Bois des Singes (4°0'49"N 9°40'28"E), hereafter BS, located southwest of Douala, was also considered since there no *Pandanus* spp. were found. Similarly to WB, BS is a mature forest mainly dominated by *Rhizophora racemosa* Meyer, 1818, *Rhizophora mangle* L., 1764, and *Rhizophora harrisonii* Leechman, 1918. We considered this forest as a control to verify the exclusive relationship between *P. buettikoferi* and *Pandanus candelabrum*.

Sampling

A total of 49 specimens of *Pandanus* spp. (39 in WB and 10 in ES; fig. 2) were randomly chosen along two transects in each forest. For every plant, we checked the phytotelmata present and recorded the number of crabs, the crabs' species, each crab's sex and the height above the ground of the inhabited phytotelmic microhabitat. In cases where specimens were small and it was not possible to determine their sex, they were classified as juveniles. We then categorized the phytotelmata into three categories: 0–100, all animals found within the first 100 cm

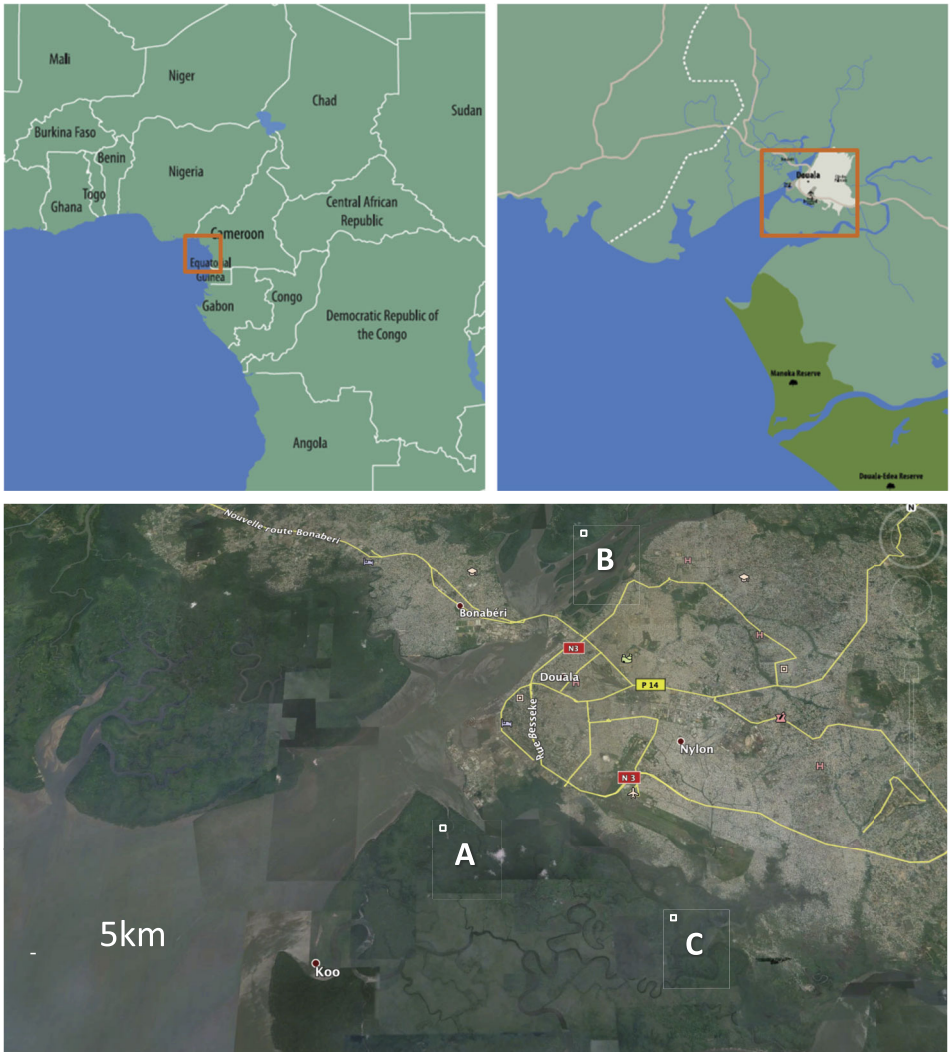


Fig. 1. The study site in Cameroon, showing the location of the survey in three steps of increasing detail, with indicated: A, Essengue mangrove forest; B, Wouri Bridge mangrove forest; C, Bois de Singes mangrove forest.

from the ground (the lowest leaf axils were recorded at 10 cm above ground); 101–200, all animals found between 101 cm and 200 cm; and >200 cm, all animals recorded at heights greater than 200 cm.

To assess the overall composition of brachyuran fauna, and eventually verify the exclusive association of *P. buettikoferi* with *Pandanus candelabrum*, two random transects (100–500 m apart) were established in each vegetation belt (*Rhizophora*, *Pandanus* or *Avicennia* dominated) in each forest. Along each transect, three 2 ×

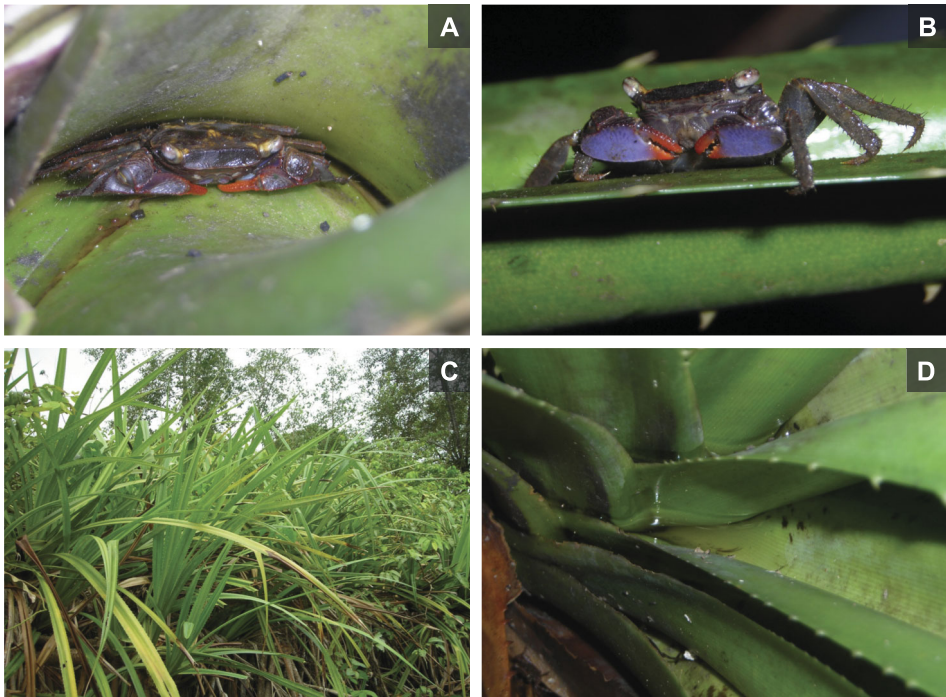


Fig. 2. A, *Platyichirarma buettikoferi* (De Man, 1883) (male) in a leaf axil; B, ditto, note the distinct, flat frontal part of the chelae; C, *Pandanus candelabrum* P. Beauv. leaf cluster complex, which typically dominates the first succession in cleared mangrove forests; D, ditto, leaf axil filled with water.

2 m² quadrats were randomly sampled to assess the abundance and density of the brachyuran populations. Based on the complexity of the habitat and the varied behaviour of the studied species, different sampling techniques were used to assess the abundance of the various groups of macrofauna (for more information about the sampling methodology see Skov et al., 2002; Fusi et al., 2016). For safety reasons, this survey could not be performed for the ES forest.

Sediment water and leaf axil water temperature, conductivity, and pH were recorded by performing in situ measurements with measuring sensors (Acorn pH 6 meter Oakton Instruments®, Vernon Hills, IL, U.S.A.). These three variables are important because they affect the physiology of the animals. Temperature is one of the most important variables defining the metabolism of animals and is crucial for ectotherms whose body temperature matches the environmental temperature, and therefore it governs the biochemical processes of the animals. Conductivity indicates the presence of solutes in the water. Finally, pH is very important for crabs because it can affect their exoskeleton by dissolving the calcium carbonate structures. The amount of leaf axil water retrieved was 10-

20 ml. Crab specimens collected from phytotelmata were identified using Monod (1956) and the nomenclature reviewed following Shahdadi et al. (2019); sex and reproductive stage (ovigerous or non-ovigerous) were recorded and photographed. Ten specimens were stored in alcohol (70%) and deposited in the Zoological Collection of the Museum of Zoology of the University of Florence.

PERMANOVA (Anderson et al., 2008) was used to test the null hypothesis of no differences in *P. buettikoferi* population characteristics, pH and conductivity across the factors Site (fixed, orthogonal, two levels: WB – Wouri Bridge and ES – Essengue) and Transect (random, nested in Site, 2 levels). Statistical analyses were performed using the software PRIMER 6 (Anderson et al., 2008).

RESULTS

We recorded a significantly different assemblage of *Platyichirarma buettikoferi* in the two sites (PERMANOVA: $F = 7.41$; $df = 1.46$; $p < 0.01$), but no significant differences among the three categories of leaf axil height where the species was found. *P. buettikoferi* was persistently present in all the 49 leaf axils of *Pandanus candelabrum* examined.

A similar number of males, females and ovigerous females were found in every leaf cluster analysed from WB forest (average 4.7 ± 0.7 individuals), evenly distributed among sexes, and no statistical differences were detected among different height classes (table I; fig. 3). In ES forest, an average of 9.6 ± 1.37 individuals was recorded evenly distributed among the height classes, with a more pronounced variability of sex ratio distribution. No other species were found in the leaf axils, except for one individual sesarmid *Armases elegans* (Herklots, 1851) (0-100 cm height in WB) and one individual of a centipede (Scolopendridae, 0-100 cm height in ES). Despite the presence of other crab species, no specimens of *P. buettikoferi* were found on the forest floor, in either the *Pandanus* vegetated belt, or in the *Rhizophora* and/or *Avicennia* belts (figs. 3, 4).

All water temperatures recorded were around $27.3 \pm 0.9^\circ\text{C}$, with no differences between ground and axil water. Conductivity was significantly higher in phytotelmic water than in sediment water (fig. 5) (PERMANOVA, Conductivity: $F = 10.638$; $df = 2.65$; $p < 0.05$), but pH was significantly lower in phytotelmic water than in sediment water (PERMANOVA, pH: $F = 22.503$; $df = 2.65$; $p < 0.01$) both for the WB and ES forests.

DISCUSSION

Among the resident mangrove fauna, crabs and molluscs are undoubtedly the most important components in terms of abundance, biomass and their ecological

TABLE I

Characteristics of the phytotelmic microhabitats occupied by the mangrove crab *Platyichirarma buettikoferi* (De Man, 1863) (Sesarmidae) from the mangrove forests surrounding the city of Douala, Cameroon

Site	pH	Conductivity (mV)	Height (cm)	Total number of specimens	Male	Non-ovigerous female	Ovigerous female	Juvenile
Wouri Bridge	–	–	106	3	2		1	
Wouri Bridge	–	–	80	4	2	2		
Wouri Bridge	–	–	110	2	1	1		
Wouri Bridge	–	–	204	3	1	1	1	
Wouri Bridge	–	–	270	2			2	
Wouri Bridge	–	–	290	3	1	2		
Wouri Bridge	–	–	100	3	1	1	1	
Wouri Bridge	–	–	85	0				
Wouri Bridge	–	–	165	4	3	1		
Wouri Bridge	–	–	190	3	1	2		
Wouri Bridge	–	–	140	4	2	1	1	
Wouri Bridge	–	–	120	3	1	1	1	
Wouri Bridge	–	–	125	4	3	1		
Wouri Bridge	–	–	85	6	4		2	
Wouri Bridge	–	–	130	9	5	3	1	
Wouri Bridge	6.34	–	120	7	3	1	3	
Wouri Bridge	6.1	–	130	9	3	5	1	1
Wouri Bridge	–	–	120	7	4	2	1	
Wouri Bridge	–	–	90	4	2	2		2
Wouri Bridge	–	–	90	5	2	3		
Wouri Bridge	–	–	75	5	3	2		
Wouri Bridge	–	–	130	4	1	3		1
Wouri Bridge	–	–	110	7	4	2	1	
Wouri Bridge	–	–	150	4	2	2		
Wouri Bridge	–	–	190	3	2	1		
Wouri Bridge	5.78	46	140	7	3		4	
Wouri Bridge	6.12	25	130	12	1	8	3	2
Wouri Bridge	6.16	23	80	2		2		
Wouri Bridge	6.25	18	120	3	1	2		
Wouri Bridge	6.47	5	230	6	4	1	1	
Wouri Bridge	6.33	13	110	2	1	1		
Wouri Bridge	5.82	43	150	3	3			
Wouri Bridge	6.06	29	160	9	4	3	2	
Wouri Bridge	5.9	39	140	6	1	3	2	
Wouri Bridge	5.76	49	150	9	4	4	1	
Wouri Bridge	6.09	25	130	3	1	1	1	
Wouri Bridge	6.18	22	40	5	4	1		1
Essengue	6.04	27	30	8	3	1	4	
Essengue	5.85	36	20	7	2	4	1	
Essengue	5.66	36	20	8	5	2	1	
Essengue	5.72	45	10	3	3			1

TABLE I
(Continued)

Site	pH	Conductivity (mV)	Height (cm)	Total number of specimens	Male	Non-ovigerous female	Ovigerous female	Juvenile
Essengue	6.07	25	120	13	8	5		
Essengue	6.08	23	80	8	5	3		
Essengue	5.46	60	100	9	5	4		
Essengue	6.1	23	100	9	8	1		
Essengue	6.06	25	110	15	11	3	1	
Essengue	6.14	20	120	18	10	8		

Axil water pH and conductivity, height (= height from the ground), total number of specimens, and sexual assemblage are presented.

role (Fusi et al., 2016). Crabs, in particular, have a wide range of adaptations that allow them to colonize niches created by the complex interaction of vegetation structure and tidal regime (Kristensen, 2008; Nagelkerken et al., 2008; Sousa & Dangremond, 2011; Simoni et al., 2013). Furthermore, they play a pivotal role in mangrove ecosystem resilience (Cannicci et al., 2008; Kristensen, 2008; Lee, 2008, 2015; Dahdouh-Guebas et al., 2011; Ng et al., 2015).

Our data described the presence of *Platyichirarma buettikoferi* in all leaf axils of *Pandanus candelabrum* examined. Although this species has already been recorded in Cameroon (Manning & Holthuis, 1981 and ref. of Mr. Powell within, on p. 351; Ngo-Massou et al., 2012; Fusi et al., 2016), its close association with *P. candelabrum* described here in detail, and therefore its phytotelmic habit, has not previously been reported. Many animals use *P. candelabrum* for various purposes, for example shelter and food (Grubb, 1971; Lounibos, 1979; Lee, 1985; Braithwaite & Lonsdale, 1987; Verbeek et al., 1993; Cumberlidge et al., 2005), but *P. buettikoferi* seems to exclusively exploit the microhabitat formed by the complex leaf clusters. A similar adaptation has been described for another sesamid species, *Scandarma lintou*, found to strictly co-occur with *Pandanus odoratissimus* L. f., 1782, in southern Taiwan, in close proximity to streams or freshwater pools sheltered from strong winds (Schubart et al., 2003).

P. candelabrum leaves provide *P. buettikoferi* with a freshwater habitat that is physico-chemically different from the pore water of the sediment. Although pH was variable, the leaf axil water had a higher conductivity than the ground water, indicating the presence of more solutes. This reinforces that this aquatic microhabitat can be more stable (i.e., more able to buffer change in pH) than ground water, thereby avoiding potential stress for *P. buettikoferi*. *P. candelabrum* leaf axils were also found to collect potentially important food sources for this sesamid, such as propagules of the taller *Avicennia* sp. trees as well as leaves and

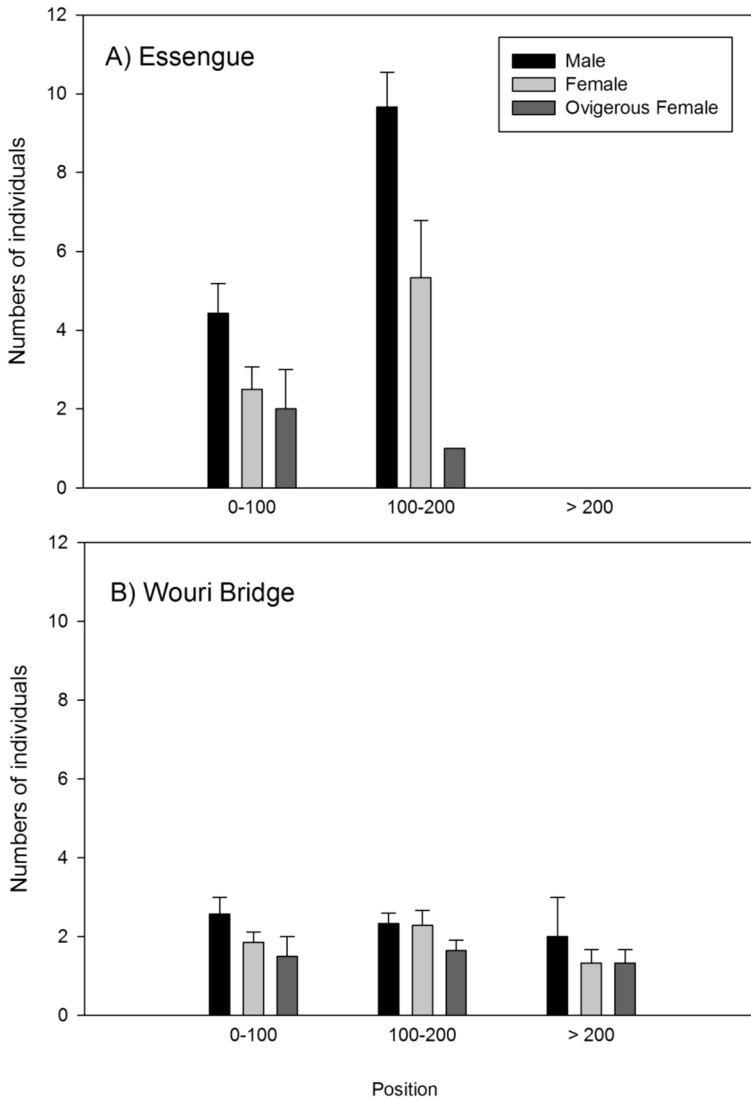


Fig. 3. Average number of *Platychirarma buettikoferi* (De Man, 1883) specimens found in *Pandanus candelabrum* P. Beauv. leaf clusters at three different heights from the ground, in: A, Essengue Forest ($N = 10$); and B, Wouri bridge Forest ($N = 37$). Data are expressed as mean \pm standard error.

other mangrove litter (Sousa & Dangremond, 2011). Additionally, we consistently found males, females and ovigerous females in every cluster analysed. Faecal pellets were found in almost all of the axils analysed, which suggests a high fidelity to the leaf. The leaf clusters could also provide refuge from the high predation pressure exerted by the mudskipper *Periophthalmus papilio* (Bloch & Schneider,

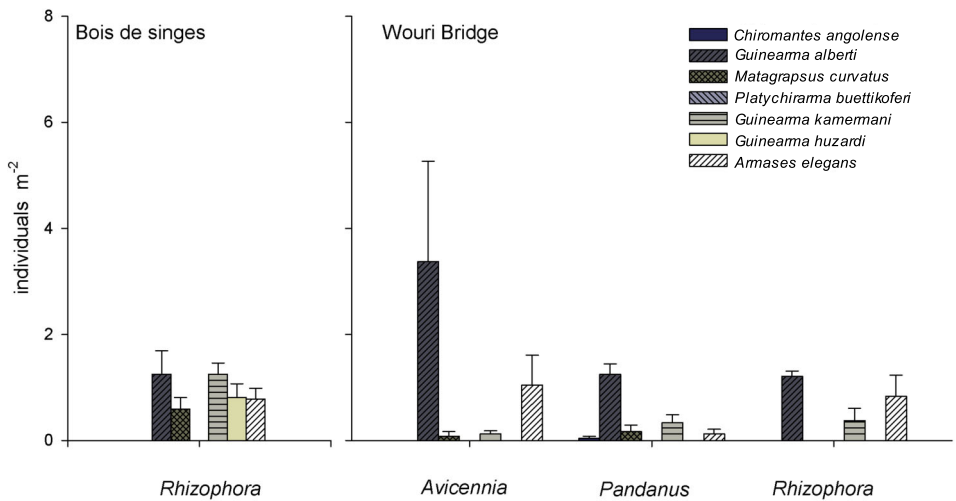


Fig. 4. Mangrove macrobenthos density in the study sites expressed as mean \pm standard error; ($N = 6$ for each site). Data not available for Essengue forest (see Material and Methods section).

1801), found in very high densities in WB on the forest floor (Etim et al., 1996), and other predators (Cannicci et al., 1998).

The coincident distribution of *P. buettikoferi* and *P. candelabrum* in the Wouri estuary mangroves suggests that this is a tight association. We found no specimens of *P. buettikoferi* in the mature forests dominated by *Rhizophora* spp. in the same area, such as Bois de Singes (fig. 4). This association is corroborated by a previous study that placed *P. buettikoferi* at the landward side of mangrove forests and did not describe the species as a true mangrove crab (Rathbun, 1921). Furthermore, we found no specimens of *P. buettikoferi* throughout one month of observation, while other sesarmids were abundant such as *Chiromantes angolense* (de Brito Capello, 1864), *Guinearma alberti* (Rathbun, 1921), *Metagrapsus curvatus* (H. Milne Edwards, 1837), *Guinearma kamermanni* (De Man, 1883), *Guinearma huzardi* (Desmarest, 1825) and *Amases elegans* (Herklots, 1851) (fig. 4).

The adaptation to live in a pioneering plant such as *P. candelabrum* seems to be convergent among different crab species, as documented for *Metapaulias depressus* in Jamaica (Schubart, 2007), *Malagasya goodmani* (Cumberlidge, Boyko & Harvey, 2002) and the sesarmid *Labuanium gracilipes* (H. Milne Edwards, 1854) in Madagascar (Cumberlidge et al., 2005), *Geosesarma foxi* (Kemp, 1918) and *Geosesarma serenei* (Ng, 1986) in Penang, Peninsular Malaysia (Ng, 2017), and *Geosesarma batak* (Manuel-Santos, Ng & Freitag, 2016), in central-southern Palawan Island and *Geosesarma tagbanua* (Manuel-Santos, Ng & Freitag, 2016), in central-northern Palawan Island, in the Philippines (Manuel-Santos et al., 2016). In the present study, we could not prove that *P. buettikoferi* is a strictly phytotelmic

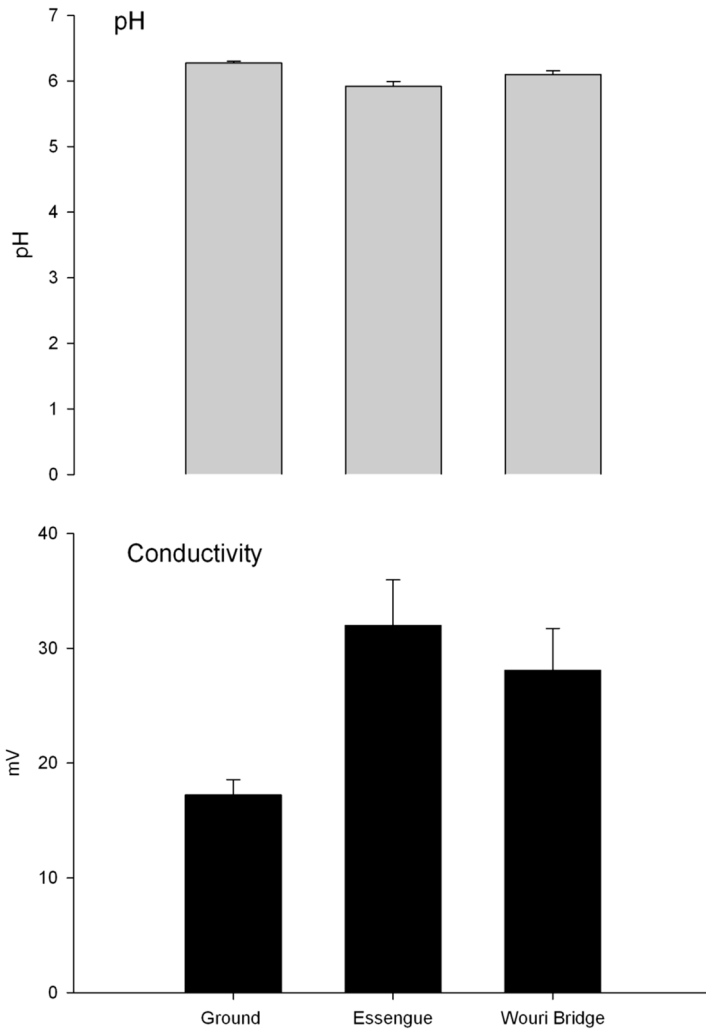


Fig. 5. The pH and conductivity of ground water (taken at ground level) and phytotelma *Pandanus candelabrum* P. Beauv. water at the two study sites. Data are expressed as mean \pm standard error. $N = 14$ for Wouri Bridge and $N = 10$ for Essengue for pH; and $N = 12$ for Wouri Bridge and $N = 10$ for Essengue, for Conductivity.

species, but our findings suggest that the vegetation shift induced by human disturbance can at least offer a phytotelmic habitat to this crab species. In fact, the colonization of phytotelmata could also be the proximate factor behind the evolution of its flat chelipeds, unique to *P. buettikoferi* and very rare in the Sesarmidae (fig. 2). Indeed, a flat cheliped can help this crab hide within the leaf axils of *P. candelabrum* and, more generally, better exploit the shelter that this vegetation provides (fig. 2A). A similar characteristic has been observed in the crab *S. lin-*

tou living in *Pandanus odoratissimus*, that exhibits conspicuously flattened fingers (Schubart et al., 2003). The permanent presence of water in these microhabitats could represent a physiological advantage for *P. buettikoferi*, providing a safe habitat in which to excrete catabolites while avoiding desiccation (Anger, 1995) and representing a water source to brood embryos (Cannicci et al., 2011; Vogt, 2013). To confirm the phytothelmic behaviour, the occurrence of ovigerous females is another proof that corroborates our result, although further investigations of egg sizes and the larval development are needed (Anger, 1995; Diesel, 1997).

In conclusion, we reveal a previously undescribed, possibly facultative, phytothelmic habit of *P. buettikoferi*, which may enable this species to colonize mangrove areas occupied by *P. candelabrum*.

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