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Crab-driven processing does not explain leaf litter-deposition in mangrove crab burrows

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Abstract

Many mangrove crab species drag freshly fallen leaf litter into their burrows and store it there for some time prior to consumption. Potential explanations for this behavior include (a) avoidance of competition for a scarce resource, (b) prevention of removal of a scarce resource upon tidal outwelling, or (c) processing of an initially unpalatable food source, be it physically through leaching, through the activity of the sediment microbiota, or driven by the activity of the crab itself. To test the latter, we study the effect of burying mangrove leaf litter on two relevant physicochemical litter characteristics and on its digestibility to crabs in a laboratory experiment, using artificial substratum with low microbial activity. Freshly fallen leaves of two common mangrove species, *Bruguiera gymnorhiza* and *Ceriops tagal*, were left for two weeks either inside burrows used by *Neosamartium asiaticum* (Sesarmidae), or on top of the substratum, before they were offered to the crabs as food. Leaf toughness and total phenolic content differed significantly between mangrove species. Upon two weeks of decay, phenolic content of both leaf litter species and toughness of ***B. gymnorhiza*** changed significantly. However, neither litter characteristcs nor assimilation efficiency differed between treatments. We conclude that storing mangrove leaf litter in crab burrows in a microbe-poor environment does not affect litter digestibility. Hence, crabs themselves do not contribute to litter processing during storage inside the burrow. If it is litter processing, rather than the avoidance of competition or litter removal by tides, that renders the storage of litter inside the burrow advantageous, it will be microbial activity that drives this process. Further studies should explicitly focus on processing through the activity of the sediment microbiota.

KEYWORDS

assimilation efficiency, interference competition, litter burying, litter processing, Mangrove crab, *Neosarmatium asiaticum*, tidal outwelling

1 | INTRODUCTION

Crab communities are conspicuous components of mangrove forests worldwide. Many mangrove crabs are active burrowers. Burrowing behavior is seen in the small species of Dotilidae (Gherardi et al., 1999; Hartnoll, 1973), in the conspicuous fiddler crabs (Mokhlesi et al., 2010; Weis & Perlmutter, 1987; Wolfrath, 1993), throughout the abundant members of Sesarmidae, to the biggest Gecarcinidae (Miculka, 2009; Schlacher et al., 2016). Most of the latter species are detritivores or omnivores that feed on decaying plant material (Nordhaus et al., 2011; Thongtham et al., 2008). Their food, mangrove leaf litter, is sturdy, poor in nutrients, and hard to digest. For instance, C:N ratios of 70–90 have been reported in leaves of mangrove trees of the Rhizophoraceae, and concentrations of secondary compounds that inhibit digestion, such as phenolics (Giddins et al., 1986; Steinke et al., 1993; Zimmer, 2019), are high, especially in the Rhizophoraceae (Micheli, 1993; Quadros & Zimmer, 2017).

Besides its low quality as a food source, leaf litter is a scarce resource in the intertidal of a mangrove forest, because leaf fall is a rather rare event for tropical evergreen trees, and tidal currents wash out leaves that lie on the forest floor. Crabs may start consuming a fallen leaf where they found it, whereas others carry fragments inside their burrows prior to feeding (Masagca, 2009). In fact, mangrove leaves are often removed from the mangrove floor and dragged into the burrows by sesarmid crabs immediately after they fell to the ground (Dahdouh-Guebas et al., 1997; Giddins et al., 1986). Leaves may be stored inside burrows for 2 weeks before being consumed by the crab (Micheli, 1993). This litter-burying and -storing activity has a strong impact on sediment organic matter dynamics and element fluxes (Kristensen, 2008) and on sediment structure and chemistry (Emmerson & McGwynne, 1992).

While hypotheses for why it is advantageous for a crab to store litter inside the burrow have been proposed, they have hardly ever been rigorously tested. Depositing a leaf inside the burrow will (i) prevent it from being flushed out during the next outgoing ebb tide. At the same time, (ii) competitors are prevented from access to this valuable and limited resource. An alternative explanation of this behavior is (iii) processing of a low-quality food source during storage prior to consumption. Such litter-processing could either (iii.a) be driven by the crab itself and pure physical processes (see Gillis et al., 2019, for effects of crab burrow mimics on microbial metabolism), such as leaching, or (iii.b) by sediment microbes that colonize and start decaying the litter while being stored for several days to weeks. In fact, crabs (and other detritivores) prefer feeding on aged, decaying leaves (Nordhaus et al., 2011; Steinke et al., 1993), because soluble leaf compounds, such as phenolics, decrease rapidly over time due to a combination of leaching and microbial decay (Treplin & Zimmer, 2012; Zimmer, 2019). Thus, if storing leaf litter inside a burrow decreased leaf toughness and phenolic content, this behavior would increase the digestibility of leaf litter by the crab consumer.

Skov and Hartnoll (2002) had challenged hypothesis (iii) through field observations. They did not find any differences in the C:N ratios of senescent leaves and leaf fragments from excavated burrows of *Neosarmatium meinerti*. Hence, they rejected the hypothesis that leaf storage in crab burrows ("leaf aging") would change the litter chemistry into more favorable conditions for consumption by crabs. Later, Nordhaus and Wolff (2007) came to the same conclusion of rejecting the "leaf aging" hypothesis. However, from their field surveys, both author teams could not get any information about the "age" of the excavated leaves, that is, the time these leaves had spent in the crab burrows. Further, the only chemical parameters they measured were C and N contents (and the resulting C:N ratio). While this is often used as a first proxy for food quality, many leaf compounds, such as phenolics, can vary in their content within a given C:N ratio value. Thus, the quality of litter as substrate for decay and decomposition cannot adequately be described by only the C:N ratio (c.f., Pradisty et al., 2021), and other parameters have been used as proxies for the quality of leaf litter as food for detritivores, for example, phenolic content (Micheli, 1993; Bärlocher & Graça, 2020, and references therein; Pradisty et al., 2021) and physical toughness (Graça & Zimmer, 2020, and references therein). The ultimate test for changes in litter characteristics that affect the feeding and nutrition of consumers, however, is quantifying the actual uptake and utilization of the respective food sources (see, e.g., Nordhaus & Wolff, 2007). Hence, we test hypothesis (iii) (more explicitly iii.a) through monitoring the changes in leaf characteristics (phenolic content, physical toughness) and in leaf digestibility to crabs. Nordhaus and Wolff (2007) had rejected the "leaf aging" hypothesis partly because of the lack of differences in microbial abundance between senescent and burrowed leaves in their field study, and Lee (1997) stated that sesarmid crabs can consume large quantities of litter prior to microbial enrichment. Thus, we explicitly choose an artificial laboratory setup that minimizes the effects of sediment microbes on litter but allows for crab-driven processing (if any) of, and leaching of water-soluble compounds from, mangrove leaf litter inside crab burrows. With this approach, we aim at disentangling microbial processes (largely excluded herein) from animal-driven processes.

2 | MATERIALS AND METHODS

2.1 | Study species

To test our hypothesis, we used the sesarmid crab *Neosarmatium asiaticum*. Species of *Neosarmatium* are known to drag leaves into burrows (Dahdouh-Guebas et al., 1997; Emmerson & McGwynne, 1992; Giddins et al., 1986; Micheli, 1993). Their burrows are usually 1–2 m deep and spread over the upper intertidal up to the supratidal zone. Hence, while their complex burrows usually reach down to below the water level, the tidal regime is less extreme in their habitat than further down in the lower intertidal. *Neosarmatium asiaticum* belongs to the *N. meinerti* species complex (Ragionieri et al., 2012), inhabiting tidal mangroves and estuaries from Sri Lanka (Dahdouh-Guebas et al., 2011) through the Andamans, to Indonesia and Taiwan (Ragionieri et al., 2012).

Bruguiera and *Ceriops tagal* are common and abundant mangrove tree species in the same region of the Indo-West Pacific realm of mangrove distribution. They both belong to Rhizophoraceae and colonize the mid- to upper intertidal of estuarine and coastal areas.

2.2 | Acclimatization of crabs

Individuals of *N. asiaticum*, originating from Indonesia, were obtained from a commercial trade shop (www.interaquaristik.de) in Germany. All crabs used in the experiment were of similar size (~38 mm carapace width), and there were no ovigerous females (Figure 1). Upon arrival in the laboratory, the crabs were placed individually in containers of 10 × 15 × 8 cm (height × length × depth) and fed ad libitum with a mixture of decaying mangrove leaves collected a few weeks before the experiments (see below). The containers were kept at 25°C and contained a ca 2-cm thick layer of fine sand as artificial substratum of low microbial activity. Water supply consisted of a central plastic pool with brackish water (15 psu) that was replaced every day. Before the beginning of experiments, the crabs were fed with white cabbage leaves in order to empty their digestive tract from any other food source and to flush out natural microbial gut communities as much as possible.

2.3 | Burrow formation and maintenance by crabs

We used transparent cylinders of acrylic glass (50 cm height; 11.5 cm diameter: 5,191 cm^3) to encourage burying behavior of mangrove crabs in the laboratory (Figure 1). The cylinders were filled with homogenized fine sand (see above) and flooded with brackish water (15 psu) before introducing one crab into each cylinder. A valve at the bottom allowed for controlling the water level in each cylinder by draining or replenishing the water. Three days after setting up the cylinders, the crabs were transferred to their experimental artificial substratum and kept at 25°C. The water level was kept about 10 cm below the sand surface to stimulate the burrowing by the crabs. Burrow formation lasted 14 days, while crabs were fed with cabbage leaves every other day, to allow crab acclimation and for maturation of the burrow through crab activity in a microbe-poor environment. Brackish water was drained and replaced every 3 days. To keep the burrows from collapsing, the water was added slowly to the cylinders through the valve at the bottom of the cylinder (Figure 1).

2.4 | Mangrove leaves and experimental setup

We obtained yellow leaves from mangrove treelings from Zanzibar (Tanzania) growing in the greenhouse of the Leibniz Centre for Tropical Marine Research (Bremen, Germany). Prior to the experiment, freshly fallen leaves were collected daily and kept at 4°C to slow down decay. To keep the within-species physicochemical variation among leaves as low as possible, we selected only yellowish leaves of similar size that had been shed without human intervention, resulting in a total of 12 leaves from *B. gymnorhiza* and 18 leaves from *C. tagal*.

Each leaf was divided into two halves, and each half was placed inside a mesh bag of 25 cm^2 (5 × 5 mm mesh) (Figure 1). Each bag was attached to a nylon thread to allow for its recovery from the cylinders after the experiment. The mesh bags prevented the crabs from consuming the leaves while allowing for physical contact. Both halves of the same leaf were added to one cylinder: One half was placed inside the burrow and the other was placed on the surface of the artificial substratum. The crabs were present in the cylinders but fed with cabbage leaves. After 14 days (natural duration of litter storage, according to Micheli, 1993), the bags were recovered, and leaves were gently washed with tap water to remove sand from their surface. Each half was then divided into two halves again (Figure 1): One quarter of the leaf was freeze-dried to obtain the fresh weight:dry weight ratio and

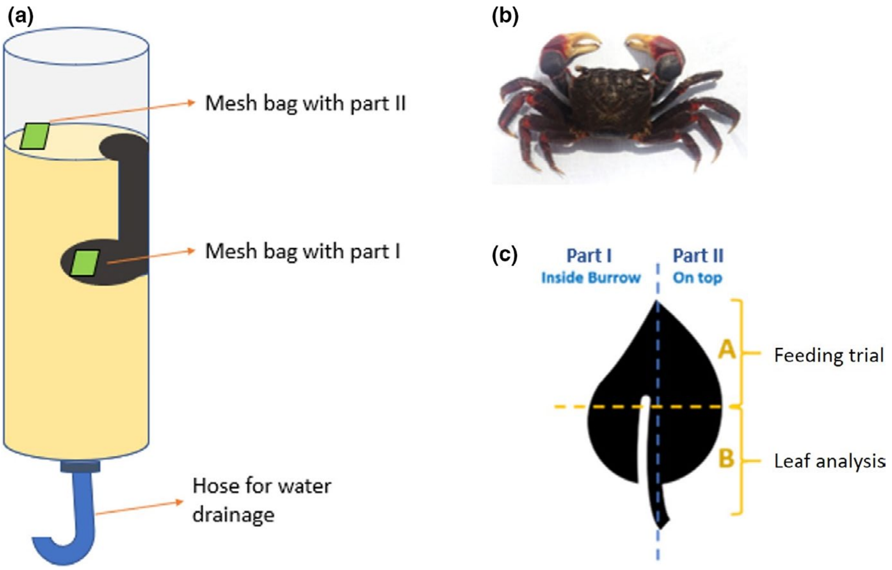

FIGURE 1 Experimental setup. (a) Cylinders filled with sand and water where crabs built their burrows. (b) *Neosarmatium asiaticum*, used as model species, in dorsal view (carapace width = 35 mm). (c) Schematic view of the procedures applied to the mangrove leaves. First, each leaf was divided into two halves (blue line). After decay for 14 days, leaves were recovered and further divided into two halves (yellow line; portions A and B), which were used in feeding trials and for physicochemical analysis

the phenolic content, and the other quarter was weighed, used to measure leaf toughness (following the procedure described by Graça & Zimmer, 2020), and offered to crabs in the feeding experiments (see below). Total phenolic contents were measured upon extraction in 50% methanol, following a modified Folin–Ciocalteu assay (Zimmer et al., 2014), with tannic acid as standard. Thus, results are presented as mean ± standard deviation tannic acid equivalents (TAE, mg/g dry weight).

2.5 | Feeding experiment

We used 26 crabs in the feeding experiments: 16 (eight females and eight males) received *C. tagal* leaves and 10 (five females and five males) received *B. gymnorrhiza* leaves. The crabs were rinsed with water and fed with a randomly assigned quarter (either from the surface or from inside the burrow) in a fresh container for 24 hr, after which fecal pellets were collected, and the crabs were fed again with cabbage. No mangrove leaf remnants were found in the containers after feeding for 24 hr. Dark fecal pellets, that is, pellets from mangrove leaves, were collected until whitish pellets, that is, derived from cabbage, occurred. After 1–4 days, when the crab guts were completely empty from mangrove leaves, the complementary part (stored on the surface vs. stored inside a burrow) of the same experimental leaf was fed to the same crab, and feces were collected as above. Feces were freeze-dried and weighed.

We compared leaf toughness and phenolic contents between treatments (i.e., burrow vs. surface) through paired *t* tests. Assimilation efficiency (AE %), on a dry weight basis, was calculated as follows: AE = (amount ingested − feces)/amount ingested × 100. Results are presented as mean ± standard deviation.

3 | RESULTS AND DISCUSSION

The two mangrove species studied here differed in toughness ($p = .0249$) and phenolic content ($p < .0001$) (Table 1). Before the experiment, the leaves of *B. gymnorhiza* were ~30% tougher than those of *C. tagal*. A similar difference between *Bruguiera* spp. and *C. tagal* was recorded by Choong et al. (1992). In the comparative study of Micheli (1993), by contrast, leaves from *C. tagal* were more sturdy than those of *Bruguiera exaristata*. Overall, and as expected, toughness (Table 1A) decreased over the two weeks of experimental treatment for *B. gymnorhiza* [by 62% inside burrows ($p < .0001$) vs. 28% on the surface ($p = .001$)] but not for *C. tagal* (by 20% inside burrows ($p = .097$) vs. 11% on the surface ($p = .223$). We did not detect any significant difference between treatments (*B. gymnorhiza*: $p = .267$; *C. tagal*: $p = .245$). Hence, while decaying the litter for two weeks slightly decreased litter toughness, this change over time was not affected by the storage conditions (surface vs. burrow).

Senescent leaves of *B. gymnorhiza* had higher phenolic content than those of *C. tagal* (Table 1B; $p < .0001$). Senescent leaves of *B. gymnorhiza* are known to contain a high phenolic content in general (Camilleri, 1989). This difference persisted over the experiment, irrespective of whether they had been buried or kept on the surface, although contents decreased over the course of the experiment (by 96% for *B. gymnorhiza* ($p < .0001$); by 94% inside burrows vs. 96% on the surface for *C. tagal* [$p < .0001$]). Such a drastic reduction in the phenolic content of mangrove litter over the first weeks of decay has recently been described by Pradisty et al. (2021). Like for toughness, there were no significant differences between treatments (*B. gymnorhiza*: $p = .445$; *C. tagal*: $p = .142$). Hence, while litter decay over two weeks drastically reduced the phenolic content of the litter, this change over time was not affected by the storage conditions (surface vs. burrow).

Given that the leaf litter did not differ regarding phenolic content and toughness when it decayed on the surface vs. inside a burrow, it is not surprising that assimilation efficiencies did not differ between treatments either (Table 1C; *B. gymnorhiza*: $p = .708$; *C. tagal*: $p = .249$). The digestibilities of different food sources observed herein are remarkably lower than previously recorded values of 82% for *N. meinerti* (= *N. africanum*, see Ragionieri et al., 2012) feeding on 6-week-old *Avicennia marina* leaves (Emmerson & McGwynne, 1992), possibly because of the supposedly very low microbial activity in our experimental setup (but see Lee, 1997, stressing that sesarmid crabs consume fresh senescent leaves already prior to microbial enrichment).

Mangrove crabs prefer senescent and decayed leaves when given a choice (Christofoletti et al., 2013; Dahdouh-Guebas et al., 1997; Kristensen et al., 2010; Nordhaus et al., 2011). Such feeding preferences of detritivores are likely due to changes in the content of water-soluble secondary compounds, such as phenolics, and toughness during early decay (Zimmer, 2019). For instance, tannin contents of leaf litter decreased by 68% over 8 weeks through leaching in *B. gymnorhiza* (Steinke et al., 1993), and even more in *B. parviflora* (Pradisty et al., 2021). Accordingly, *N. smithi* assimilated little of 2-week-old litter, but assimilation efficiencies increased to 30%–60% when fed with 4- to 8-week-old litter (Giddins et al., 1986).

Considering that sesarmid crab burrows usually reach the water table and, thus, contain water at the bottom (Andreetta et al., 2014; Pülmanns, 2014), leaching would be more intense inside the burrow than on the sediment surface, and phenolic contents and toughness would be lower in leaves stored inside the burrow. Our results, however, indicate that burying of leaf litter did not change its toughness or phenolic content over two weeks, as compared to leaves decaying on the surface, when feeding by crabs and/or microbial sediment processes were essentially excluded. Thus, the physical conditions inside the burrow per se, or the presence of the crab itself, do not foster leaf processing or decay ("leaf aging hypothesis": see above) beyond what would happen if the leaf remained on the sediment surface (hypothesis iii.a). If litter-processing was promoted by litter-storing inside the burrow, this would be driven by sediment microbes (which we largely excluded in our experimental design). This hypothesis (iii.b) needs to be tested in future studies (but see Skov & Hartnoll, 2002 and Nordhaus & Wolff, 2007, suggesting a negligible role of microbes).

TABLE 1 Toughness (A) and total phenolic content (B) of leaves prior to decay ("initial") and after two weeks on the sediment "surface" or inside the "burrow," and the assimilation efficiency (C) of *Neosarmatium asiaticum* crabs feeding on these leaves

(A) Toughness (g/mm^2)			
	Initial	**Surface**	**Burrow**
Bruguiera gymnorhiza	399 ± 62 (5)^a	286 ± 112 (9)^b	150 ± 21 (9)^b
Ceriops tagal	307 ± 42 (5)^a	269 ± 15 (17)^a	240 ± 20 (17)^a
(B) Phenolic content (mg/g)			
	Initial	**Surface**	**Burrow**
Bruguiera gymnorhiza	30 ± 1 (5)^a	1.2 ± 0.8 (9)^b	1.2 ± 0.7 (9)^b
Ceriops tagal	11 ± 3 (5)^a	0.5 ± 0.3 (19)^b	0.7 ± 0.4 (19)^b
(C) Assimilation (%)			
		Surface	**Burrow**
Bruguiera gymnorhiza		60 ± 16 (9)^a	57 ± 15 (9)^a
Ceriops tagal		52 ± 21 (17)^a	45 ± 17 (17)^a

Note: Values are mean ± *SD*; sample size is given in parentheses; and different superscript letters indicate statistically significant differences between values within the same mangrove species.

Alternatively, removing leaves from the forest floor into burrows right after they fell might avoid a scarce food source from being washed out by tidal currents (hypothesis ii). The benefits of dragging freshly fallen leaf litter into a burrow might also be related to avoiding competition for a scarce resource between detritivorous mangrove crabs (hypothesis i). In fact, Steinke et al. (1993) observed that, if two crabs grab the same leaf when it falls, a fight will usually ensue with the stronger individual eventually pulling the leaf out of the other's grasp and retreating to its burrow. More recently, Cannicci et al. (2018) proposed that interference competition for food may be a major force shaping the spatial distribution of sesarmids in the mangroves of Sri Lanka. Thus far, however, rigorous testing of hypothesis (i) or (ii) has not been undertaken. Admittedly, either of them is difficult, if not impossible, to test, as we can assume that crabs would show this behavior even if no other crabs were around or tidal inundation was prevented experimentally. Rather, the leaf-burying behavior seems to be genetically fixed in these crab species and to occur irrespective of the biotic or abiotic environmental conditions. If, however, neither the presence of a crab or leaching (iii.a; this study) nor the activity of sediment microbes (iii.b; to be tested) increases the digestibility of leaf litter to the crab, it becomes more likely that one of the above explanations (i. or ii.) applies to leaf-burying behavior in mangrove crabs. As a two-week phase of litter decay prior to consumption by crabs, however, slightly decreased leaf toughness and drastically reduced phenolic contents (even under conditions of presumably low microbial activity), both being relevant predictors of food quality, food storage might prove advantageous for the consumer in terms of digestibility under natural conditions with high microbial activity (iii.b)—this hypothesis remains to be tested. Because, in turn, storage of litter in a mangrove forest is not feasible on the sediment surface because of the risk of tidal removal (i) or competition for food with other crabs (ii), litter processing ("leaf aging"; iii) will require storage inside a burrow. Hence, the explanation for this conspicuous behavior might be a combination of all three hypotheses discussed herein.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

Sophie J. Forgeron: Formal analysis (equal); Investigation (lead); Writing-original draft (equal). **Aline Ferreira de Quadros:** Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing-original draft (equal). **Martin Zimmer:** Conceptualization (equal); Formal analysis (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing-review & editing (lead).

DATA ACCESSIBILITY STATEMENT

The data have been deposited with PANGAEA: https://doi.org/10.1594/PANGAEA.931484.

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REFERENCES

Andreetta, A., Fusi, M., Cameldi, I., Cimò, F., Carnicelli, S., & Cannicci, S. (2014). Mangrove carbon sink. Do burrowing crabs contribute to sediment carbon storage? Evidence from a Kenyan mangrove system. *Journal of Sea Research*, *85*, 524–533. https://doi.org/10.1016/j.seares.2013.08.010

Bärlocher, F., & Graça, M. A. S. (2020). Total phenolics. In F. Bärlocher, M. O. Gessner, & M. A. S. Graça (Eds.), *Methods to study litter decomposition – A practical guide* (2nd ed., pp. 157–161). Springer.

Camilleri, J. (1989). Leaf choice by crustaceans in a mangrove forest in Queensland. *Marine Biology*, *102*, 453–459. https://doi.org/10.1007/BF00438346

Cannicci, S., Fusi, M., Cimó, F., Dahdouh-Guebas, F., & Fratini, S. (2018). Interference competition as a key determinant for spatial distribution of mangrove crabs. *BMC Ecology*, *18*. https://doi.org/10.1186/s12898-018-0164-1

Choong, M. F., Lucas, P. W., Ong, J. S. Y., Pereira, B., Tan, H. T. W., & Turner, I. M. (1992). Leaf fracture toughness and sclerophylly: Their correlations and ecological implications. *New Phytologist*, *121*, 597–610. https://doi.org/10.1111/j.1469-8137.1992.tb01131.x

Christofoletti, R. A., Hattori, G. Y., & Pinheiro, M. A. A. (2013). Food selection by a mangrove crab: Temporal changes in fasted animals. *Hydrobiologia*, *702*, 63–72. https://doi.org/10.1007/s10750-012-1307-6

Dahdouh-Guebas, F., Koedam, N., Satyanarayana, B., & Cannicci, S. (2011). Human hydrographical changes interact with propagule predation behaviour in Sri Lankan mangrove forests. *Journal of Experimental Marine Biology and Ecology*, *399*(2), 188–200. https://doi.org/10.1016/j.jembe.2010.11.012

Dahdouh-Guebas, F., Verneirt, M., Tack, J. F., & Koedam, N. (1997). Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. *Hydrobiologia*, *347*, 83–89.

Emmerson, W. D., & McGwynne, L. E. (1992). Feeding and assimilation of mangrove leaves by the crab Sesarma meinerti de Man in relation to leaf-litter production in Mgazana, a warm-temperate southern African mangrove swamp. *Journal of Experimental Marine Biology and Ecology*, *157*, 41–53. https://doi.org/10.1016/0022-0981(92)90073-J

Gherardi, F., Russo, S., & Anyona, D. (1999). Burrow-orientated activity in the ocypodid crab, *Dotilla fenestrata*, living in a mangrove swamp. *Journal of the Marine Biological Association of the UK*, *79*, 281–293.

Giddins, R. L., Lucas, J. S., Neilson, M. J., & Richards, G. N. (1986). Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae). *Marine Ecology Progress Series*, *33*, 147–155. https://doi.org/10.3354/meps033147

Gillis, L. G., Snavely, E., Lovelock, C., & Zimmer, M. (2019). Effects of crab burrows on sediment characteristics in a *Ceriops australis*-dominated mangrove forest. *Estuarine Coastal & Shelf Science*, *218*, 334–339. https://doi.org/10.1016/j.ecss.2019.01.008

Graça, M. A. S., & Zimmer, M. (2020). Physical litter properties: Leaf toughness and tensile strength. In F. Bärlocher, M. O. Gessner, & M. A. S. Graça (Eds.), *Methods to study litter decomposition – A practical guide* (2nd ed., pp. 187–193). Springer.

Hartnoll, R. G. (1973). Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. *Estuarine and Coastal Marine Science*, *1*, 137–152. https://doi.org/10.1016/0302-3524(73)90066-2

Kristensen, D. K., Kristensen, E., & Mangion, P. (2010). Food partitioning of leaf-eating mangrove crabs (Sesarminae): Experimental and stable isotope (13C and 15N) evidence. *Estuarine Coastal and Shelf Science*, *87*, 583–590. https://doi.org/10.1016/j.ecss.2010.02.016

Kristensen, E. (2008). Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, 30–43. https://doi.org/10.1016/j.seares.2007.05.004

Lee, S. Y. (1997). Potential trophic importance of the faecal material of the mangrove sesarmine crab *Sesarma messa*. *Marine Ecology Progress Series*, *159*, 275–284. https://doi.org/10.3354/meps159275

Masagca, J. T. (2009). Feeding ecology of tree-climbing mangrove sesarmid crabs from Luzon, Philippines. *Biotropia - Southeast Asian Journal of Tropical Biology*, *16*, 1–10.

Micheli, F. (1993). Feeding ecology of mangrove crabs in North Eastern Australia: Mangrove litter consumption by *Sesarma messa* and *Sesarma smithii*. *Journal of Experimental Marine Biology and Ecology*, 165–186. https://doi.org/10.1016/0022-0981(93)90002-6

Miculka, B. (2009). *Burrowing habits, habitat selections, and behaviors of four common Dominican land crabs;* Guinotia dentata, Gecarcinus lateralis, Gecarcinus ruricola, *and* Cardisoma guanhumi. Texas A&M University.

Mokhlesi, A., Kamrani, E., Backwell, P., & Sajjadi, M. (2010). Study on the behaviour of two fiddler crabs, *Uca sindensis* and *Uca annulipes* (Decapoda: Ocypodidae), in Bandar Abbas, Iran. *Journal of the Marine Biological Association of the UK*, *91*, 245–249.

Nordhaus, I., Salewski, T., & Jennerjahn, T. C. (2011). Food preferences of mangrove crabs related to leaf nitrogen compounds in the Segara Anakan Lagoon, Java, Indonesia. *Journal of Sea Research*, *65*, 414–426. https://doi.org/10.1016/j.seares.2011.03.006

Nordhaus, I., & Wolff, M. (2007). Feeding ecology of the mangrove crab *Ucides cordatus* (Ocypodidae): Food choice, food quality and assimilation efficiency. *Marine Biology*, *151*, 1665–1681.

Pradisty, N. A., Amir, A. A., & Zimmer, M. (2021). Plant species- and stage-specific differences in microbial decay of mangrove leaf litter: The older the better? *Oecologia*, *195*(4), 843–858. https://doi.org/10.1007/s00442-021-04865-3

Pülmanns, N. (2014). The importance of burrowing and leaf litter feeding crabs for the ecosystem functioning of mangrove forests.

Quadros, A. F., & Zimmer, M. (2017). Dataset of "true mangroves" plant species traits. *Biodiversity Data Journal*, *5*, e22089. https://doi.org/10.3897/BDJ.5.e22089

Ragionieri, L., Fratini, S., & Schubart, C. D. (2012). Revision of the *Neosarmatium meinerti* species complex (Decapoda: Brachyura: Sesarmidae), with descriptions of three pseudocryptic Indo-West Pacific species. *Raffles Bulletin of Zoology*, 71–87.

Schlacher, T. A., Lucrezi, S., Peterson, C. H., Connolly, R. M., Olds, A. D., Althaus, F., Hyndes, G. A., Maslo, B., Gilby, B. L., Leon, J. X., Weston, M. A., Lastra, M., Williams, A., & Schoeman, D. S. (2016). Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research*, *112*, 55–64. https://doi.org/10.1016/j.seares.2016.04.001

Skov, M. W., & Hartnoll, R. G. (2002). Paradoxical selective feeding on a low-nutrient diet: Why do mangrove crabs eat leaves? *Oecologia*, *131*, 1–7. https://doi.org/10.1007/s00442-001-0847-7

Steinke, T. D., Rajh, A., & Holland, A. J. (1993). The feeding behaviour of the red mangrove crab *Sesarma meinerti* De Man, 1887 (Crustacea: Decapoda: Grapsidae) and its effect on the degradation of mangrove leaf litter. *South African Journal of Marine Science*, *13*, 151–160.

Thongtham, N., Kristensen, E., & Puangprasan, S. Y. (2008). Leaf removal by sesarmid crabs in Bangrong mangrove forest, Phuket, Thailand; with emphasis on the feeding ecology of *Neoepisesarma versicolor*. *Estuarine Coastal and Shelf Science*, 583–590. https://doi.org/10.1016/j.ecss.2008.09.017

Treplin, M., & Zimmer, M. (2012). Drowned or dry: A cross-habitat comparison of detrital breakdown processes. *Ecosystems*, *15*, 477–491. https://doi.org/10.1007/s10021-012-9523-5

Weis, J., & Perlmutter, J. (1987). Burrowing behavior by the fiddler crab *Uca pugilator*: Inhibition by the insecticide diflubenzuron. *Marine Ecology Progress Series*, *38*, 109–113. https://doi.org/10.3354/meps038109

Wolfrath, B. (1993). Observations on the behaviour of the European fiddler crab *Uca tangeri*. *Marine Ecology Progress Series*, *100*, 111–118. https://doi.org/10.3354/meps100111

Zimmer, M. (2019). Detritus. In: S. E. Jorgensen, & B. D. Fath (Eds.). *Encyclopedia of ecology* (2nd ed., Vol. 3, pp. 292–301). Elsevier.

Zimmer, M., Auge, H., von Wühlisch, G., Schueler, S., & Haase, J. (2014). Environment rather than genetic background explains intraspecific variation in the protein-precipitating capacity of phenolic compounds in beech litter. *Plant Ecology & Diversity*, *7*, https://doi.org/10.1080/17550874.2013.871655

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