Hydrobiologia (2017) 803:307–315
DOI 10.1007/s10750-017-3319-8

MANGROVES IN CHANGING ENVIRONMENTS

Chemical changes in detrital matter upon digestive processes in a sesarmid crab feeding on mangrove leaf litter

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Received: 19 November 2016 / Revised: 19 July 2017 / Accepted: 21 July 2017 / Published online: 3 August 2017

Abstract Pathways and rates of decomposition of detrital matter partly depend on its chemical composition. Digestive processes of detritivores drive changes in the chemical composition of detritus, and these changes translate into the chemical composition of the organic matter sequestered into soils and sediments. The latter, in turn, determines how stable organic matter stocks are towards further decay and release of climate-active gases thereupon. We used metabolic fingerprinting to monitor changes in the chemical composition of mangrove detritus upon digestion by a mangrove crab. According to analyses through pyrolysis-GC/MS, the decaying leaf litter of three mangrove species of the Indo-West Pacific, *Bruguiera gymnorhiza* (L.) Savigny ex Lam. and Poiret 1798, *Ceriops tagal* (Perr.) C.B. Robinson 1908, and *Rhizophora mucronata* Lam. 1804, clearly differed from each other in their chemical signature. The feces of detritivorous crabs (*Sesarma bidens* de Haan 1835) feeding on these detrital sources differed from the source litter in their chemical composition, obviously owing to digestive processes. However, the chemical signatures of feces were more similar to those of their source litter than to those of feces from different litter sources, indicating that the origin of organic matter can be tracked in fecal material. Moreover, male and female crabs appear to exhibit sex-specific digestive processes, as they produced feces that clearly differed from each other in their chemical signature. The 15 chemical compounds most relevant for distinguishing litter sources and fecal material provide first hints on which compounds discriminate the different tree species and characterize digestion by *S. bidens.* For instance, coumaran (dihydro-benzofuran), indicative of certain carbohydrates, was abundant as a pyrolysis product of the litter of *R. mucronata* and, to a much lesser degree, *C. tagal*. Hence, the carbohydrates that were pyrolysed into coumaran seem to discriminate the former two litter sources. Similarly, a pyrolysis-derivate of plant phenolics or proteins, discriminated *C. tagal* from the other litter sources. From this, we conclude that even subtle differences in litter chemistry and digestive processes of detritivores can be characterized and followed with high resolution through (py-)GC/MS. Further, we propose that the origin of

Guest editors: K. W. Krauss, I. C. Feller, D. A. Friess, R. R. Lewis III / Causes and Consequences of Mangrove Ecosystem Responses to an Ever-Changing Climate

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fecal material can be identified with the aid of this technique, and we are currently studying whether the origin of organic matter in the sediment can also be inferred from (py-)GC/MS-data.

Keywords Mangrove leaf litter · Detritivorous crabs · Digestive processes · Organic matter composition · *Bruguiera gymnorhiza* · *Ceriops tagal* · *Rhizophora mucronata* · *Sesarma bidens* · Metabolomics fingerprint · Environmental metabolomics

Introduction

Most ecosystems, both aquatic and terrestrial, are driven by the detritus food-chain and corresponding decomposition processes. More specifically, decomposition underlies element- and nutrient-cycling, and thus, supports the ecosystem's productivity. However, the mechanisms that underlie decomposition processes differ between terrestrial and aquatic systems (Treplin & Zimmer, 2012). Further, the stability of organic matter towards decay and release of climate-active gases (e.g., CO_2 and N_2O) depends not only on the environment but also on chemical composition and structure of the organic matter which, in turn, depends on its origin. Hence, being able to determine the chemical structure and origin of organic matter is pivotal to understanding organic matter dynamics and how this changes upon environmental change.

The decomposition of detritus derived from mangrove trees has become a focal point of interest upon discovering the high potential of mangroves to sequester and store carbon and nitrogen, which would otherwise be released as climate-active gases, not only in their above- and below-ground biomass but also in relatively stable organic matter in anoxic and saline sediments (Spalding et al., 2010). The storage of organic matter (often referred to as "blue carbon") in mangrove sediments (e.g., Alongi, 2012) is a direct consequence of decomposition processes. About 30–60% of the annual primary production of a mangrove forest enters the detritus pool (Ashton et al., 1999), and despite exchange with adjacent ecosystems, more than 70% of the total detrital materials of a mangrove is derived from mangrove leaves (Mfilinge & Tsuchiya, 2008).

Even though often neglected, feeding on detrital material by detritivorous animals and their digestive processes are an integral part of decomposition and organic matter-turnover, as they directly and indirectly mediate the microbial mineralization of organic matter. Among mangrove detritivores, sesarmid crabs play a significant role by burying and consuming leaf litter in their burrows, and thus, preventing them from being washed out by outgoing ebb tides (Kaiser, 2005; Alongi, 2009; Spalding et al., 2010). Upon digestion and subsequent defecation, the organic matter of mangrove origin contained in crab feces is incorporated in the anoxic and saline sediments. The fecal matter, exhibiting a greatly increased surface area and differing in chemical composition from the initial leaf litter, serves as substrate for further microbial decay, chemical transformation, and eventually mineralization. However, these processes are slowed-down and largely restricted to anaerobic microbes, due to anoxic conditions in deeper sediment layers.

Digestive processes can be studied either by quantifying the activities of different digestive enzymes (e.g., Zimmer et al., 2002, 2004; Linton et al., 2009; Hübner et al., 2015, and references therein), or by comparing the chemical composition of food sources and feces (e.g., Zimmer, 1999; Zimmer et al., 2002, 2004, 2005, and references therein). As many digestive enzymes are known to be induced by the ingested food, the relative activity of different classes of gut enzymes, such as proteases, lipases, hydrolases, and oxidases, provides information on the nature of major food sources (Hübner et al., 2015). At the same time, these specific activities allow for an assignment of consumers to different functional groups in terms of their contributions to decomposition processes, but the outcome of such measurements reflects potential digestive capabilities rather than actual digestive processes.

A more accurate picture of digestive processes can be derived from a quantitative and qualitative comparison of the chemical composition (metabolic fingerprint sensu Du & Zeisel, 2013) of consumer feces with that of the food sources they derived from (Viant & Sommer, 2013). Thus, a decrease in the content of a certain compound indicates its digestive breakdown, be it through hydrolysis or through oxidation, in particular if the simultaneous increase of the breakdown product can be detected (Zimmer et al., 2005). However, depending on the nature of the

compounds of interest, such analysis can be demanding, expensive, or time-consuming. Hence, (pyrolysis-) Gas Chromatography coupled with Mass Spectrometry [(py-)GC/MS] provides a high-throughput alternative to conventional wet-chemical methods with potentially high resolution for the characterization of the chemical signature of organic matter, be it detritus or the corresponding feces of detritivorous animals (c.f., Tolu et al., 2015).

The present study aims at showcasing chemical differences and changes in the organic matter composition of leaf litter of different mangrove species upon feeding by detritivorous crabs. More specifically, we aim at detecting and characterizing chemical compounds that can serve in distinguishing organic matter of different origins (leaf litter of different mangrove species) and recovering those compounds in the feces of detritivores (and ultimately in sediments). We hypothesize that (1) differences in the chemical composition of leaf litter of different mangrove species is reflected in their metabolic fingerprint; (2a) changes in the chemical composition of leaf litter upon digestive processes by litter-feeding crabs can be detected as changes in metabolic fingerprints of the crab feces, and (2b) male and female crabs change the chemical composition differently due to sex-specific digestive processes (c.f., Hübner et al., 2015); (3) the origin of unidentified organic matter (e.g., in feces) can be identified through its metabolic fingerprint. If (3) proves true, we will be able to monitor changes in the origin of organic matter in sediments over time (i.e., in sediment cores). Thus, focusing on (1) and (2) is a first step in this direction that, however, does not yet include microbial processing of feces and detrital matter in addition to digestive processes of detritivores. Future studies will serve as proof-of-concept for the distinction of organic matter of different origins in sediments.

Materials and methods

Detritivorous crabs, *Sesarma bidens*, originating from the Indo-West Pacific, were obtained from Interaquaristik (https://www.interaquaristik.de) in spring 2016. A total of 13 female and 14 male crabs were used for feeding experiments on leaf litter of *Rhizophora mucronata* Lam.1804, *Bruguiera gymnorhiza* (L.) Savigny ex Lam. & Poiret 1798, and *Ceriops tagal* (Perr.) C.B. Robinson 1908. This leaf litter was obtained from young saplings of the three species that had been raised in the greenhouse of the Leibniz Centre for Marine Tropical Research (ZMT GmbH), Bremen (Germany), from seedlings collected in Zanzibar in summer 2014. There is essentially only anecdotal information on feeding preferences of *S. bidens* available (but see Islam & Uehara, 2008; Mchenga & Tsuchiya, 2010), but the high abundance of both the detritivorous crab and these tree species in the same areas suggests a close trophic relationship that we assume for this study.

Nine leaves of each species were hand-picked from individual saplings and maintained in brackish water (18 psu) for 45 days to initiate decay until leaves appeared brown, known to be preferred by *S. bidens* (Islam & Uehara, 2008), and decaying upon visual inspection. After this pre-conditioning of the leaves, each leaf was cut in two halves, of which one was used as food for an individual crab, whereas the other one remained in the brackish water until the end of the experiment.

For feeding with the different litter sources, crabs were maintained in translucent plastic boxes (15 cm × 8 cm × 10 cm) that contained a slope of wet sand (playground sand, BWL, 04509 Löbnitz, Germany) and brackish water (18 psu) that left half of the sand slope immersed. Twice per week, the brackish water was renewed, and the sand was washed with tap water. Individual crabs were randomly assigned to one of the different litter sources. Hence, male and female crabs were not equally distributed to the different litter sources (for sample sizes, refer to Fig. 1).

Individual crabs were kept under the above conditions, while feeding on their experimental food for at least three days to make sure that their digestive tract was filled with, and they had time to acclimate to, the experimental food source. Then, they were transferred into another plastic box of the same size that contained the brackish water in a smaller plastic box (7.5 cm × 7.5 cm × 4 cm) with a metal mesh to ease the crabs getting out of the water onto the sand. In this box, they were offered their assigned litter source, and fecal pellets were collected from the water box or the sand surface. Fecal pellets and remnants of each litter source were stored frozen (−20°C) until freeze-drying and homogenization to a grain size of <200 µm. 50–100 µg of these samples were used for pyrolysis-GC/MS-analysis.

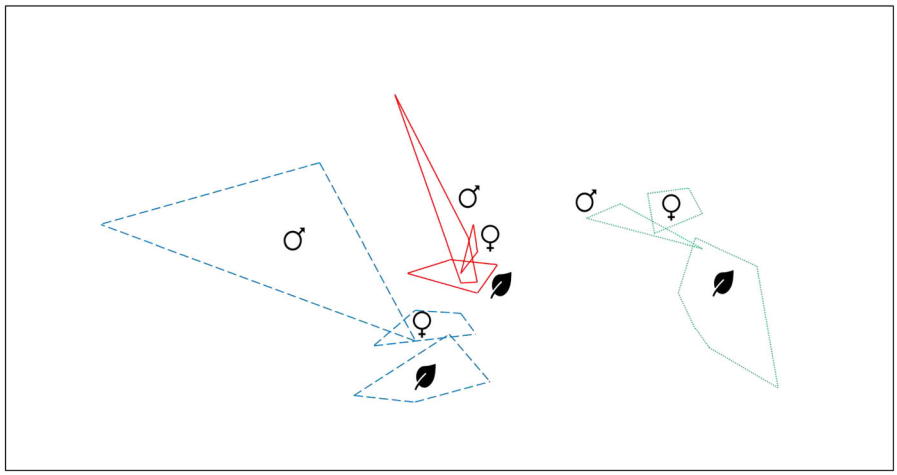

Fig. 1 nMDS plot of Bray–Curtis similarity indices among different mangrove litter sources and the corresponding feces of male and female *Sesarma bidens*. *Blue broken* lines: *Ceriops tagal*; *Red solid* lines: *Bruguiera gymnorhiza*; *Green dotted* lines: *Rhizophora mucronata*; leaf litter; ♀ feces of female crabs; ♂ feces of male crabs. *Polygons* encompass all samples of the respective group ($N = 9$ for each litter source; $N = 5$ for male, $N = 4$ for female crabs on *C. tagal*; $N = 6$ for male, $N = 3$ for female crabs on *B. gymnorhiza*; $N = 3$ for male, $N = 6$ for female crabs on *R. mucronata*)

The pyrolysis unit (Thermal Desorption Unit, Gerstel, Deutschland), was set to an initial temperature of 40°C, a transfer temperature of 320°C, and a pyrolysis temperature of 600°C. The settings of the GC-unit (7890B GC-System, Agilent Technologies, USA) with a 30 m column of 250 µm inner diameter and a 0.25 µm silarylene-coating (Optima 17MS, Macherey–Nagel, Germany) and helium as carrier were: 2 min initial oven temperature of 40°C; increment of 4°C min^{-1} to 100°C, an increment of 4°C min^{-1} to 200°C, an increment of 8°C min^{-1} to 300°C for 15 min., and a final increment of 10°C min^{-1} to 320°C for 5 min. The MS-unit was set to a detection range of *m*/*z* 45–600, and data were collected with Gerstel Maestro 5.04.

Peaks were separated from each other and characterized based on the basal mass of the underlying compounds and their retention time (Agilent MassHunter B.07.00). Relative peak area was calculated as percent of the total peak area of each individual sample, after having limited the detection to the 100 largest peaks of each sample. Alignment of peaks was automated with a routine (developed by T.B.) within MS-Excel.

Peak identity and the corresponding relative peak area for each sample were treated like species and their relative abundances in faunistic analyses. Using PAST 3.14, we estimated Bray–Curtis similarities among samples and performed Analyses of Similarity (ANOSIM) to detect significant differences among samples in their chemical composition. A subsequent SIMPER analysis allowed for determining which peaks best explained differences among samples.

Comparing different litter sources provided information on differences in chemical composition among the "litter" of the studied tree species, whereas comparing litter and feces yielded insight into digestive processes by male and female crabs. We will refer to the latter as "decomposition stage" hereafter.

Results

We detected a total 216 compounds (peaks) of which several differed remarkably among litter source, between litter and feces, and between feces of male and female crabs. These peaks do not necessarily represent litter compounds but rather their pyrolysis products. For the sake of ease of reading, however, we will hereafter refer to them as being compounds detected in our samples.

Based on the relative area of each peak, ANOSIM detected highly significant differences in the chemical composition of the leaf litter of the three mangrove species, *B. gymnorhiza*, *C. tagal*, and *R. mucronata* ($P = 0.0001$; Fig. 1). The chemical composition of feces differed significantly from that of their corresponding litter source, but feces were more similar to

their litter source than to feces from different litter sources (Fig. 1; two-way ANOSIM: $P = 0.0001$ for both litter source and decomposition stage). Polygons that comprise all samples of the same treatment were visually distinguishable (Fig. 1) and represent clusters that are statistically distinct between male and female crabs (two-way ANOSIM: $P = 0.0001$ for litter source, $P = 0.02$ for sex). However, this sex-effect was significant only for *C. tagal* (one-way ANOSIM: $P = 0.03$) but not for *B. gymnorhiza* ($P = 0.22$) or *R. mucronata* ($P = 0.16$), possibly due to too small sample size (see Fig. 1).

According to statistical comparison through SIMPER analyses, the relative peak area of 15 compounds explained about 30% of the differences among all samples in the chemical composition of their pyrolysates (Table 1). We were able to identify with >85% probability eight out of these 15 compounds. A not further identified phenolic compound and another unidentified compound were characteristic for *C. tagal* litter, both being efficiently digested by female crabs (i.e., it had a significantly reduce relative peak area in female feces) but much less so by male crabs (increased or unchanged relative peak area in male feces). Characteristic of litter of *R. mucronata* were catechol, squalene, a not further identified terpenoid, and another unidentified compound. Catechol and the terpenoid were mostly digested by males, squalene by both sexes equally, but heptacosanone (in *R. mucronata* litter) seemed undigested by female crabs and enriched in male feces. Two unidentified compounds, present in all tree species, were not or only weakly digested. Hydroxy-cyclopentenone was also present in all litter types (but relatively more abundant in *R. mucronata*), but interestingly this compound seemed to be digested only when present in small quantities (i.e., in *B. gymnorhiza* and *C. tagal*) but not at higher content (as in *R. mucronata*), and only by females. Present mainly in *B. gymnorhiza* and, to a lesser extent, in *C. tagal*, pristene was digested by males but not by females. Coumaran (dihydro-benzofuran) and falcarinol, present mainly in *R. mucronata* and *C. tagal* versus *B. gymnorhiza* and *C. tagal*, respectively, seemed equally efficiently digested by both sexes. Finally, two compounds found in low content in the litter, were enriched in female feces (thus supposedly highly indigestible for them): nonacosaene and an unidentified compound. The significant sex-effect on the digestion of compounds in *C. tagal* litter seem to be mostly driven by hydroxy-cyclopentenone, an unknown phenolic compound and two unidentified compounds.

Discussion

The present findings clearly demonstrate significant differences in the chemical composition of decaying leaves of *B. gymnorhiza*, *C. tagal*, and *R. mucronata*. Such differences in litter chemistry not only affect palatability to, and preference by, detritivores (Ashwini & Sridhar, 2005; Nordhaus & Wolff, 2007; Catalán et al., 2008; Nordhaus et al., 2011; Quadros et al., 2015) but also drive digestibility, and thus, decomposition rates of detrital matter (Zimmer et al., 2004, 2005). Digestive processes by *S. bidens* clearly changed the chemical composition of fecal matter relative to the original leaf litter, but differences among litter sources remained, and some compounds that appeared characteristic for different litter sources were still detectable in crab feces. This observation opens the opportunity to detect and identify particular plant sources of organic matter in (mangrove) sediments (c.f. Vancampenhout et al., 2009; Schellekens et al., 2011), and, if different pathways of decay or decomposition result in different classes of organic compounds in the sediment (c.f. Buurman et al., 2009a, b; Vancampenhout et al., 2009; Schellekens & Buurman, 2011), to even hindcast which organisms were present and active drivers of decomposition processes in past (mangrove) communities. The ability of this technique to detect even sex-specific (thus intra-specific) differences in digestive processes demonstrated in this study provides strong support for the potential of unraveling different decomposition pathways among detritivore species.

Indeed, not only did mangrove crabs, through digestion, change the chemical composition of the organic matter of mangrove origin, but females and males did so sex-specifically. Sex-specific feeding (behavior) and digestion has rarely been studied in invertebrates (but see Weissburg, 1993; Hübner et al., 2015) but has been explained in birds (e.g., Markman et al., 2006) and fish (e.g., Thongprajukaew & Kovitvadhi, 2013) with respect to differences in body size and growth rates. Mitten crabs (*Eriocheir sinensis*) show sex-biased gene expression patterns (Liu et al., 2015). Saltmarsh crabs (*Neohelice granulate*

Table 1 The 15 compounds that most strongly contribute to the distinction of litter sources and the corresponding crab feces

			Relative contribution (%) to[b]								
			Bruguiera gymnorhiza			*Ceriops tagal*			*Rhizophora mucronata*		
Compound	common synonym	Contribution (%) to overall dissimilarity[a]	Litter	female Feces	male Feces	Litter	female Feces	male Feces	Litter	female Feces	male Feces
unidentified compound[c]		3.1	0.1	0.1	0.1	6.4	2.9	5.8	<0.1	<0.1	0.1
2-hydroxy-2-cyclopenten-1-one[d]		2.8	2.0	1.6	1.0	2.1	0.3	2.1	5.4	7.0	5.1
unknown phenolic compound[e]		2.6	0.1	0.4	0.3	4.4	2.1	5.8	0.6	<0.1	<0.1
1,2-dihydroxybenzol[f]	catechol	2.6	0.3	0.9	0.4	0.1	0.3	0.9	4.8	4.5	2.3
2,3-dihydro-benzofuran	coumaran	2.4	0.2	0.3	<0.1	2.2	<0.1	0.3	6.1	0.4	0.7
unidentified compound[g]		2.3	6.5	7.6	5.9	2.8	2.7	3.3	3.3	4.5	4.8
prist-1-ene[h]		2.3	3.1	7.6	0.4	1.6	1.5	0.9	0.8	0.4	1.3
unidentified compound[i]		1.9	3.1	3.2	3.9	2.4	4.6	3.4	2.2	5.4	4.5
(3,9)-Heptadeca-1,9-dien-4,6-diin-3-ol[j]	falcarinol, panaxynol	1.7	2.7	1.0	1.6	2.5	1.6	1.0	0.6	0.5	0.4
nonacosa-1-ene[k]		1.6	0.4	0.4	1.1	0.9	1.3	0.5	0.7	4.2	1.8
2,6,10,15,19,23-hexamethyltetracosa-2,6,10,14,18,22-hexaene	squalene	1.6	0.5	0.7	0.6	0.6	<0.1	<0.1	4.3	0.2	0.3
unidentified compound[l]		1.6	0.1	0.1	0.2	<0.1	0.1	0.2	3.0	2.7	2.2
2-hepatcosanone[m]		1.4	0.9	0.9	0.8	0.3	0.4	0.4	1.5	1.2	4.5
unknown terpenoid[n]		1.3	<0.1	0.3	<0.1	<0.1	<0.1	<0.1	2.2	2.7	1.3
unidentfied compound[o]		1.0	1.2	3.4	0.6	0.1	0.6	0.1	0.8	0.4	0.5

Compounds with marked difference in their relative contents ("relative peak area") among samples are highlighted by grey background

[a] SIMPER-output on how strongly the corresponding compound contributes to the dissimilarity of all samples

[b] Average area of the respective peak relative to the total area of all peaks in the corresponding chromatograms

[c] 3.5% contribution to sex-effect on *Ceriops feces*

[d] 3.3% contribution to sex-effect on *Rhizophora feces*; 2.1% contribution to sex-effect on *Ceriops feces*

[e] 4.4% contribution to sex-effect on *Ceriops feces*

[f] 5.8% contribution to sex-effect on *Rhizophora feces*

[g] 2.9% contribution to sex-effect on *Bruguiera feces*; 2.4% contribution to sex-effect on *Rhizophora feces*

[h] 10.6% contribution to sex-effect on *Bruguiera feces*

[i] 3.4% contribution to sex-effect on *Ceriops feces*; 2.3% contribution to sex-effect on *Rhizophora feces*

[j] 2.3% contribution to sex-effect on *Bruguiera feces*

[k] 5.2% contribution to sex-effect on *Rhizophora feces*

[l] 2.9% contribution to sex-effect on *Rhizophora feces*

[m] 6.3% contribution to sex-effect on *Rhizophora feces*

[n] 3.3% contribution to sex-effect on *Rhizophora feces*

[o] 4.2% contribution to sex-effect on *Bruguiera feces*

and *Armases cinereum*, respectively) exhibit sex-specific enzyme activities and microbial gut communities (Lancia et al., 2012; Hübner et al., 2015), possibly due to slightly different habitats and, thus, food sources under natural conditions. The present results, and documented sex-specific feeding preferences (Mchenga & Tsuchiya, 2010), suggest a similar mechanism in *S. bidens*, but the current early stage of implementing the method used in this study does not yet allow for unambiguous conclusions. Nonetheless, we hold that any bias in the sex ratio of a given crab population (e.g., da Silva et al., 2007; Chatterjee & Chakraborty, 2015; Hübner et al., 2015), be it through sex-specific behavior and habitat choice or through human activities, might have implications on organic matter-turnover and stability.

In fact, the observed changes in the chemical composition upon digestion of all litter sources followed the same consistent pattern, being a shift "upwards" in the nMDS plot (Fig. 1) from litter to feces, suggesting that similar digestive processes are involved for all three litter sources. Further, feces of females always clustered more on the "right side" of the plot than those of male, suggesting sex-specific digestive processes that are relatively independent of the litter source. Along this line, notwithstanding the partly small sample size, the feces of female crabs derived from the same litter source were always more similar to each other than feces of male crabs were, possibly suggesting a greater variability in male than in female digestive processes. All this together corroborates the above conclusion about the potential use of the approach we used for distinguishing sources of organic matter and pathways of decomposition. However, future detailed studies on which compounds and digestive processes cause these shifts will be needed before we can interpret these consistent patterns adequately.

The compounds detected and identified through GC/MS do not directly reflect the chemical composition of the samples studied but are partly pyrolysis products of the original compounds in leaves and feces. Nonetheless, these pyrolysis products can be interpreted in terms of their chemical origin. From this, information on the composition and origin of the organic matter in soils has been inferred. Thus, furans (e.g., coumaran abundant in *R. mucronata* and, to a lesser degree, in *C. tagal*) are indicators of polysaccharides (Vancampenhout et al., 2010), especially in tropical broadleaved forests (Vancampenhout et al., 2009). The same applies to cyclopentenone (Nguyen et al., 2003) that was common in all litter types but most abundant in *R. mucronata* litter from which it was digested only weakly. Nitrogenous compounds are often pyrolysis products of amino acids, amino sugars, or pyrroles (Buurman et al., 2007), but we did not detect any to be significant for distinguishing litter sources of crab feces.

Aromatic compounds (e.g., coumaran and catechol from *R. mucronata* litter, and the unknown phenol from *C. tagal* litter) are indicative of phenolic plant compounds (lignins or polyphenols), carbohydrates (see above), or proteins (Nguyen et al., 2003; Buurman et al., 2009a, b; Vancampenhout et al., 2010): female crabs digested the precursors of coumaran and the unknown phenol, whereas male crabs digested the former and the catechol-precursor in *R. mucronata* litter. Pristene, potentially a derivate of chlorophyll (Nguyen et al., 2003), distinguished *B. gymnorhiza* litter from the others and was digested by male but not female crabs. It remains an open question why litter types would differ in the content of such a common compound as a chlorophyll-derivate. Lignins are represented by guaiacol and its derivates (Buurman & Roscoe 2011), derived from coniferyl alcohol of conifers, and by syringol, derived from sinapyl alcohol of angiosperms (Vancampenhout et al., 2009). However, none of these compounds contributed significantly to distinguishing the litter sources tested herein.

Long-chain fatty acids are common indicators of plant cutin and cutan (Tegelaar et al., 1989). Methylketones are pyrolysis products of lipids (Buurman et al., 2007); different chain-length distributions in chromatograms may indicate different plant sources (2009a, b), but we did not identify any compound from this group to be of relevance for litter distinction. The long-chain unsaturated alcohol falcarinol (mostly found in *C. tagal*) and the (long-chain unsaturated) triterpene squalene distinguished *R. mucronata* litter (rich in the latter, poor in the former) from the other two litter types. Squalene, a common component of lipids in many organisms, was highly digestible to both sexes, whereas falcarinol was digested only weakly. Falcarinol is known to exert antimicrobial effects (Li et al., 2016). How this might relate to microbial decay or digestive breakdown of the respective litter sources remains to be clarified.

Based on the above, the present results from the analysis of a simple decomposition study through

chromatography-based mass spectrometry have the potential to yield detailed insights into the basis that underlies our understanding of organic matter dynamics in mangrove sediments. Not only can we distinguish different origins of organic matter (Koch et al., 2003, 2005, 2011; Stewart, 2011; Stewart et al., 2011), but we can also depict subtle differences in digestive (and probably other) processes related to the decomposition of organic matter. The organic matter in mangrove sediments is considered stable over long time spans, owing to anoxic and saline conditions that hamper microbial decay and mineralization of organic matter and its respiratory turnover into CO_2 or N_2O. Irrespective of the stabilizing conditions found in deeper layers of terrestrial soils, however, the stability of organic matter over time strongly depends on both the physical heterogeneity of the micro-environment and the chemical structure and composition of the organic matter (Schmidt et al., 2011). Thus, both the origin of the organic matter stored in mangrove sediments and the identity of its detritivorous and microbial consumers will determine its stability and fate. As this relationship might prove relevant for understanding carbon-sequestration and -storage in mangroves and other coastal marine ecosystems ("blue carbon"), studies aiming at identifying the origin of sediment organic matter are ongoing in our laboratory.

Acknowledgements We are grateful to Lucy Gillis (ZMT) for having brought mangrove seedlings from Zanzibar in 2014, and to Matthias Birkicht (ZMT), Hans-Konrad Nettmann (University Bremen), and the entire Mangrove Ecology Group of ZMT for valuable discussions.

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