Leaf litter translocation and consumption in mangrove ecosystems: the key role played by the sesarmid crab *Neosarmatium malabaricum*

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Nutrient cycling in mangrove forests is strongly linked to detrital processing of leaf litter, as compared to direct herbivorous consumption. Sesarmid crabs play a key role in detrital pathways in mangrove forests by processing a large amount of leaf litter produced in the ecosystem. We studied the rate of leaf litter translocation and consumption by a sesarmid crab, *Neosarmatium malabaricum*, through an *ex situ* experiment simulating field conditions. We supplied weighed senescent leaves of *Aegiceras corniculatum*, *Avicennia officinalis, Excoecaria agallocha* and *Rhizophora mucronata* to the crab. When provided separately, the crab translocated leaf litter of *E. agallocha* the maximum, and that of *Rhizophora mucronata* the minimum to the burrows. When litter mixed together was provided, the rate of translocation was the highest. The crabs consumed up to 80.24% of the litter that they translocated. We found this species capable of translocating 4.39 ± 1.68 g of leaf litter m^{-2} per day and that its population had the potential to translocate 1.81 times more leaf litter than the ecosystem produced, based on comparisons of translocation rate, density of *N. malabaricum* and leaf litter production in the study area. Our experiments emphasize the key role played by this crab in detrital pathways of mangrove ecosystem.

Keywords: *Aegiceras*, *Avicennia*, detrital pathways, *Excoecaria*, *ex situ* experiments, leaf litter translocation, mangroves crabs, *Neosarmatium malabaricum*, nutrient cycling, *Rhizophora.*

PRIMARY level consumption of live mangrove leaves by terrestrial herbivores is very little or practically nil in mangrove forests. This is because these leaves are not palatable as they contain large amounts of tough and comparatively indigestible cellulose, tannin, lignin and wax[1]. It is the detritus-dependent fauna present in mangrove ecosystem, that act upon considerable quantities of leaf litter generated by mangrove forests and influence the nutrient cycling at different trophic levels. Among these detritus-dependent fauna, crustaceans constitute an important group. Of these, sesarmid crabs play a major role in litter processing because their morphological, physiological and behavioural attributes are more adapted for this function[2,3]. Compared to grazing food webs in terrestrial ecosystems, detrital pathways govern the flow of energy and matter in mangrove ecosystems.

Litter processing of sesarmid crabs involves translocation of litter into their burrows, shredding and eating them, and dropping as partly digested faecal material. Crabs help conserve nutrients within the forest by translocating litter into their burrows. By shredding and eating, they increase the surface area available for bacteria and fungi to colonize the litter. This accelerates the rate of litter decomposition, facilitating cycling of nutrients within the ecosystem[2–7]. This is the most important role of the crab community in nutrient cycling in mangrove ecosystems among other services like aerating sediments, modifying topography, trapping energy, creating microhabitat for other fauna, contributing to secondary production and influencing forest structure[3,8]. However, variations in texture, size, nutritional value and chemical composition of leaf litter influence the crab's potential in litter processing[6,9].

Mangrove ecologists have published a few studies on translocation and consumption of litter by crabs in mangrove ecosystem, though literature from India is wanting. Robertson and Daniel[6] observed that crabs could translocate 33% of annually produced litter to their burrows in mangrove forests of northeastern Australia. The amount translocated was more than 57% in mangroves of Hong Kong[3], 79–85% in Peninsular Malaysia[9], and 79% in tropical Australia[2]. Crabs were found to consume leaf litter either partly or fully, after translocating it to their burrows. In Malaysian mangrove forests, crabs consumed 42–54% of annual litter produced[10]. A study by Emmerson and McGwynne[11] with *Neosarmatium meinerti* showed that crabs consumed 44% of annual litter produced by

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Avicennia species in southern Africa. By comparing leaf litter removal of the crab *Gecarcinus quadratus* with annual litter fall in coastal forests of Costa Rica, Sherman[12] demonstrated that the crab has potential to translocate more than 100% leaf litter to its burrows for consumption. Experiments with *Rhizophora* leaf litter using *Perisesarma onycophorum* and *Perisesarma eumolpe* showed that the annual litter consumption was as drastically low as 9% in Malaysia[13]. It was 28% when the crab *Perisesarma messa* was used in another experiment in tropical Australia[2]. These studies clearly indicate that the percentage of litter translocation and consumption varied with geographic localities, and crab and mangrove species. Variations in crab density, temperature of environment, forest structure[3], crab species[6], topography[9], chemical composition of litter[6,11] and seasonal variation in crab activity[12] account for such high fluctuations. However, all these studies emphasized the importance of sesarmid crabs as an important functional guild influencing litter consumption and nutrient cycling in mangrove ecosystems[14].

Neosarmatium malabaricum (Henderson, 1893) inhabits India, Sri Lanka and Seychelles[15]. It is a dominant and widely distributed species in the mangroves of Peninsular India and Nicobar Islands, though the species has not been studied in mangrove ecosystems with regard to its specific role in nutrient cycling. This paper describes experiments conducted in a field laboratory set up to quantify the amount of leaf litter translocated and consumed by *N. malabaricum*, in relation to the amount of leaf litter produced in Kunhimangalam mangrove forest in Kerala, India. The estimate of litter translocation potential of crab population is a strong indication about the health of mangrove ecosystems as crabs form the most important functional link in nutrient cycling, operated through detrital pathway.

Methods

Study area

Kunhimangalam mangrove forest, located at 12°08′N lat. and 75°22′E long. in Kannur district of Kerala, India, along the Perumba-Kauvay estuary (Figure 1), covers an area of about 5 sq. km. It is the largest and least disturbed mangrove forest in Kerala (Figure 2 *h*). The state experiences tropical warm and a humid climate and pronounced monsoon (June to October), winter (November to February) and summer (March to May). *Aegiceras corniculatum* (L.) Blanco, *Avicennia officinalis* L., *Excoecaria agallocha* L. and *Rhizophora mucronata* Poir. are the dominant species among the 10 species of mangroves occurring in the forest[16]. The forest harbours 10 species of crabs with the dominance of *N. malabaricum* (Henderson, 1893) and *Parasesarma plicatum* (Latreille, 1803)[17]. *Neosarmatium malabaricum* is a blue crab (Figure 2 *a*) that inhabits elevated landward areas to avoid frequent tidal inundation and actively translocates fallen leaves into its burrows (Figure 2 *b*, *c*) and feeds on them. They have an average density of 3.85 ± 4.68 (mean ± SD) individuals m^{-2} in Kunhimangalam mangroves[17]. As *P. plicatum* prefers feeding on leaf litter directly on the forest floor rather than translocating litter to their burrows, we did not use this species in this study.

Standardization of leaf litter quantity

Surplus quantities of weighed senescent leaves of *A. corniculatum*, *A. officinalis*, *E. agallocha* (Figure 2 *d*) and *R. mucronata* (Figure 2 *e*) were separately placed in twenty tubs (five tubs for each mangrove species), each tub with 30 cm height and 50 cm diameter filled to a height of 15 cm with mud taken from the mangrove forest. We introduced 20 adult crabs into these tubs, 1 crab per tub, selected out of 75 individuals trapped at random from forest floor, after measuring the carapace width and wet weight of all of them.

We left the tubs undisturbed for crabs to build burrows (Figure 2 *g*) and translocate the desired amount of leaf litter to their burrows. After 24 h, the remaining leaf litter

Figure 1. Map of the study area showing major mangrove areas.

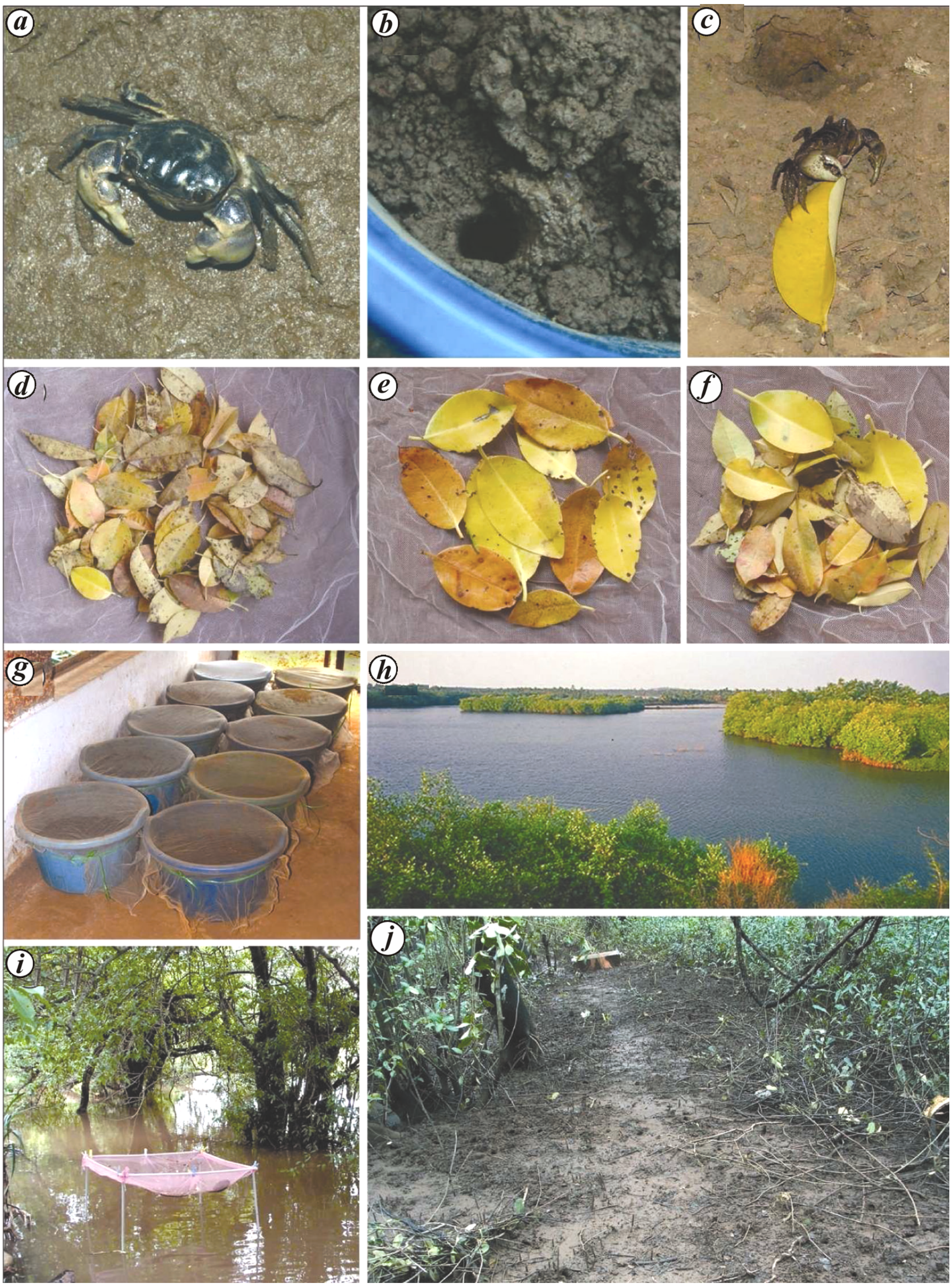

Figure 2. ***a***, Mangrove crab *Neosarmatium malabaricum*. ***b***, A burrow constructed by *Neosarmatium malabaricum* in tub. ***c***, *Neosarmatium malabaricum* translocating leaf of *Avicennia officinalis* to its burrow. Leaf litter of: ***d***, *Excoecaria agallocha*; ***e***, *Rhizophora mucronata*; ***f***, Mix of four species; ***g***, Experimental tubs with crabs; ***h***, View of Kunhimangalam mangrove forest; ***i***, Litter trap established under tree canopy; ***j***, Mangrove forest floor in Kunhimangalam dominated by *Neosarmatium malabaricum* showing the characteristic 'swept away' appearance.

in each tub was removed and weighed. From this, the amount of leaf litter translocated by a crab in a day for a single mangrove species was estimated. This procedure was repeated for five consecutive days with the twenty individuals and the maximum quantity of leaf litter translocated by any crab was estimated to be 4.4 g per day. Hence, we decided to provide 10 g of leaf litter slightly more than double the amount of leaves recorded in the standardization experiment, per crab per day.

Leaf translocation and consumption experiments

The set up for these experiments was the same as that used for the standardization procedure, except for the fact that an additional set of five tubs was prepared with 40 g of freshly fallen senescent leaves, 10 g from each of the four species (Figure 2*f*). We preferred to use 40 g leaf litter for the mixed category because, if a mixture of 10 g was used and if the crab preferred only one species, it could amount to only 2.5 g, much less than 4.4 g, the estimated optimum amount of consumption. Another set of five tubs, four with 10 g litter of four species and one with 40 g mixed leaves, but without crabs, were kept as controls. So, altogether we maintained 30 tubs. After 24 h, the remaining leaves in the tubs were collected, cleaned and weighed. Translocation rate was calculated as weight removed per day. Weight reduction from the control treatments (natural weight reduction in leaf litter in 24-hour duration) was subtracted from values obtained from experimental treatments to get net translocation rate. Dry weight, corresponding to fresh weight of translocated leaves of each species, was estimated through a predetermined fresh-dry weight ratio following Ashton *et al.*[18]. This experiment was continued for 10 days. The quantity of leaves translocated by 25 crabs in 25 tubs was estimated and the average and Standard Error (SE) of the quantities were calculated.

Burrows in each tub were excavated on the eleventh day. Unconsumed leaf litter from the burrows was retrieved, washed, dried and weighed. This quantity was deducted from the quantity of leaf litter translocated to get the amount of leaf litter consumed by the crab. All the crabs were released into mangrove habitat after our experiments.

Quantification of leaf litter production

We established 20 litter traps made of nylon net (mesh size 2 mm^2) spread over 1 sq. m PVC frames randomly in the mangrove forest, one meter above the high tide mark to quantify leaf litter production (Figure 2 *i*). Litter was collected weekly for two years from August 2008 to July 2010 and species-wise segregated and weighed by its dry weight. This provided total leaf litter production per day per m^2 in dry weight.

Data analysis

We extrapolated the rate of leaf litter translocation calculated from *ex situ* experiments to the field density of the crab and compared it with the rate of leaf litter production in Kunhimangalam mangrove forest. Ratio of these two variables gave the translocation potential of *N. malabaricum*. One way ANOVA followed by Tukey's HSD post-hoc analysis was performed to find out (i) the difference among translocation rates of leaf litter used for five categories and (ii) the difference in rates of leaf litter production in different seasons. We carried out student's *t*-test to assess the significance of difference in translocation rates of male and female crabs. Feeding preference of *N. malabaricum* to leaf litter from different mangrove species was determined using Ivlev's electivity index[19]. All values are expressed as average ± SE unless otherwise specified.

Results

An adult *N. malabaricum* has an average carapace width of 25.5 ± 2.54 mm and an average wet weight of 12.3 ± 3.75 g. The average leaf litter translocation rate per day, based on the 10 day observation period, varied significantly ($F = 4.6$, $P < 0.001$) among the 5 treatments (Table 1). It was 0.39 ± 0.12 g in dry weight for *Aegiceras corniculatum*, 0.51 ± 0.16 g for *A. officinalis*, 0.64 ± 0.20 g for *E. agallocha* and 0.37 ± 0.12 g for *R. mucronata*. Interestingly, 1.14 ± 0.36 g leaves were translocated daily from tubs provided with mixed leaves from all four species (Figure 3). Tukey's HSD test showed a significantly higher rate of translocation for the mixed category than that for *A. corniculatum* ($Q = 5.08$, $P < 0.01$), *A. officinalis* ($Q = 4.29$, $P < 0.05$) and *R. mucronata* ($Q = 5.26$, $P < 0.01$). An analysis of translocation rates (Figure 4), when a mixture of leaf litter from four

Table 1. Results of one-way ANOVA performed to analyse the difference in translocation rates of the five categories of leaf litter used for the *ex situ* experiment

	SS	d*f*	MS	F	P
Between groups	4.00	4	1.00	4.60	0.003
Within groups	9.79	45	0.22		
Total	13.80	49			

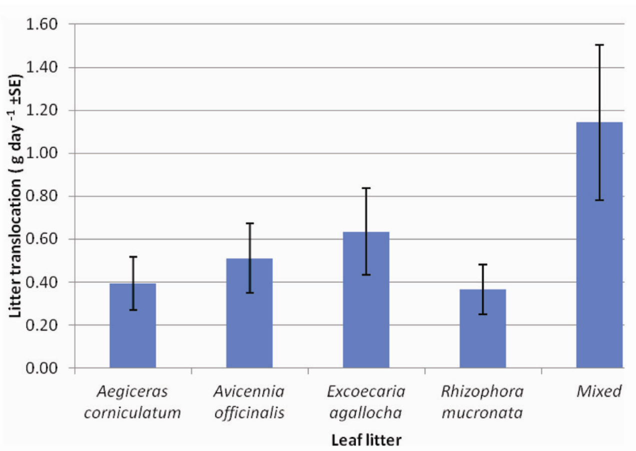

Figure 3. Rate of leaf litter translocation by *Neosarmatium malabaricum* in the *ex situ* experiment.

Table 2. Leaf litter translocation and consumption rates of *Neosarmatium malabaricum* obtained from *ex situ* experiment and the percentage of leaf litter consumption by the crab out of translocated leaf litter (values: average ± SE)

Species	Translocated g/10 days	Retrieved g/10 days	Consumed g/10 days	Consumed g/day	Consumed (%)
Aegiceras corniculatum	3.93 ± 0.51	0.86 ± 0.39	3.07 ± 0.35	0.31 ± 0.03	78.12
Avicennia officinalis	5.11 ± 1.46	1.62 ± 0.74	3.49 ± 0.81	0.35 ± 0.08	68.30
Excoecaria agallocha	6.34 ± 0.67	1.46 ± 0.44	4.88 ± 0.71	0.49 ± 0.07	76.97
Rhizophora mucronata	3.67 ± 1.76	1.80 ± 0.86	1.90 ± 1.05	0.19 ± 0.11	51.77
Mixed category	11.44 ± 0.64	2.26 ± 0.35	9.18 ± 0.55	0.92 ± 0.05	80.24

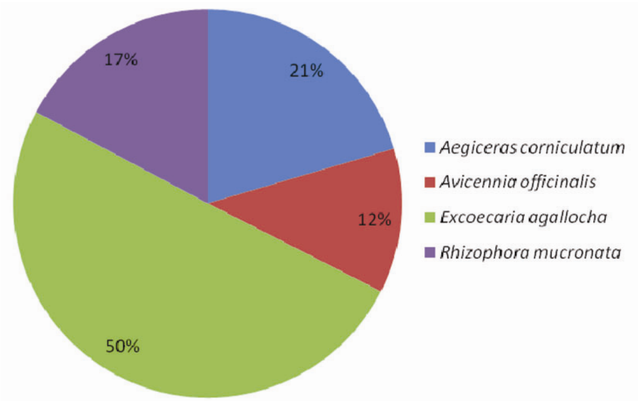

Figure 4. Preference shown by *Neosarmatium malabaricum* to leaf litter of different mangrove species when they were given mixed together in the *ex situ* experiment.

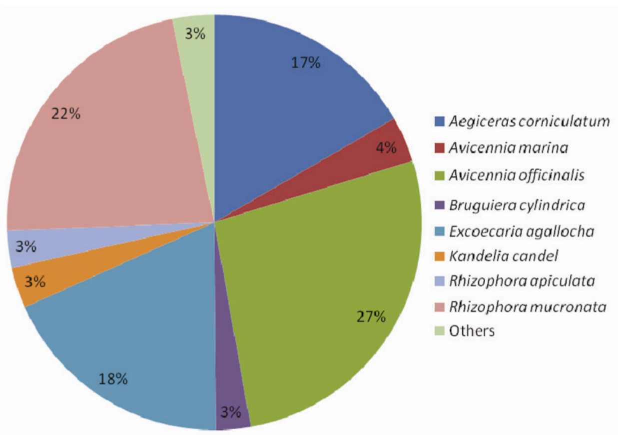

Figure 5. Percentage composition of different mangrove species towards total leaf litter production in Kunhimangalam mangroves.

species was supplied, showed that crabs preferred *E. agallocha* by 50%, *A. corniculatum* by 21%, *R. mucronata* by 17% and *A. officinalis* by 12%. Evlev's Electivity Index also supported this pattern of preference where *E. agallocha* scored the highest index ($E = 0.52$) followed by *A. corniculatum* ($E = 0.09$), *R. mucronata* ($E = -0.26$) and *A. officinalis* ($E = -0.48$). Paired two tailed *t*-test gave no significant difference between translocation rates of male and female crabs ($t = 0.38$, $P > 0.05$).

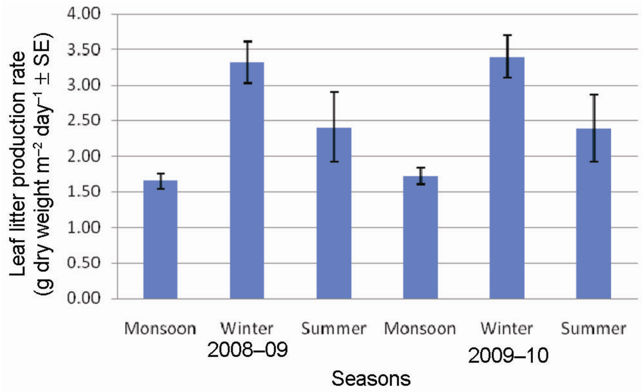

Figure 6. Seasonal variation in the leaf litter production rates in Kunhimangalam mangroves during the study period from 2008–2010.

Excavation of crab burrows yielded 0.86 g of *A. corniculatum,* 1.62 g of *A. officinalis*, 1.46 g of *E. agallocha*, 1.8 g of *R. mucronata* and 2.26 g of mixed leaves. This indicated that 3.07 g (78.12%) of *A. corniculatum*, 3.49 g (68.30%) of *A. officinalis*, 4.88 g (76.97%) of *E. agallocha*, 1.9 g (51.77%) of *R. mucronata* and 9.18 g (80.24%) of mixed leaves were consumed by one crab, during the ten-day experiment (Table 2).

We estimated average leaf litter production in the mangrove forest at 2.42 ± 0.26 g m^{-2} per day. *A. corniculatum* (17%), *A. officinalis* (27%), *E. agallocha* (18%) and *R. mucronata* (22%) were the major litter producing species (Figure 5). Rates of litter production varied significantly ($F = 24.25$, $P < 0.001$) across the three seasons studied. Highest leaf litter production occurred in winter (3.36 ± 0.20 g m^{-2} per day), followed by summer (2.40 ± 0.30 g m^{-2} per day) and monsoon (1.68 ± 0.08 g m^{-2} per day). We observed this pattern in both the years of our study (Figure 6).

The experiments showed that an adult *N. malabaricum* is capable of translocating 1.14 ± 0.36 g dry weight of senescent leaves per day to its burrow. As average density of *N. malabaricum* was 3.85 ± 4.68 crabs m^{-2}, this species alone is capable of translocating 4.39 ± 1.68 g of leaf litter m^{-2} per day. As the highest density of this crab estimated at Kunhimangalam mangroves was 10.56 ± 0.38 individuals m^{-2}, the translocated amount would be 12.04 ± 0.13 g dry weight of leaf litter m^{-2} per day.

Discussion

A comparison of rate of leaf litter translocation by *N. malabaricum* with rate of leaf litter production in Kunhimangalam mangrove forest indicates that the crab population has the potential to translocate 1.81 times more leaf litter than what is produced in the ecosystem. When we compared seasonality of leaf litter production with translocation potential of *N. malabaricum*, we found that the crab population could translocate 2.61, 1.31 and 1.83 times more leaf litter than what was produced during monsoon, winter and summer respectively. In coastal forests of Costa Rica, Sherman[12] made similar observations and found that *Gecarcinus quadratus* could translocate 2.5 times more litter to burrows than that gathered in leaf fall traps. In this context, the observations made by Nordhaus *et al.*[20], while discussing litter consumption experiments using *Ucides cordatus*, in intertidal forests of northern Brazil, are important: 'consumption rates determined in field experiments probably overestimated the average consumption rate since crabs were provided with a surplus of leaves during the experiments. A single crab consumed 6.5 g dry weight per day, whereas daily litter fall was only 4.5 g dry weight m^{-2} at *Rhizophora* forest. Such results therefore show potential rather than actual ingestion rates'. *Neosarmatium malabaricum* could potentially translocate all leaf litter from the forest floor below the canopy of mangrove trees. This provides the mangrove forest floor a 'swept away' appearance (Figure 2*j*). Ashton[9] and Emmerson and McGwynnne[11] have made similar observations with reference to Merbok mangrove forests in Malaysia and Mngazana mangrove forests in South Africa respectively.

Mangroves export a substantial amount of organic material to the coastal ocean through tidal currents and this amount increases during spring tides[21]. By translocating all leaf litter produced in Kunhimangalam mangroves, *N. malabaricum* prevents export of leaf litter through tidal flushing and thus effectively helps in trapping nutrients within the ecosystem. In Kunhimangalam mangrove forest, litter from lower intertidal zones is washed off daily through tidal currents but that in upper intertidal zones is accumulated on the forest floor as daily tides do not normally reach these zones. *N. malabaricum* being a crab which inhabits in upper intertidal zones has access to the leaf litter produced in this zone for translocation except for 5–8 days in a month during spring tides. Leaf litter translocation in high intertidal forests is more crucial when compared to low intertidal forests because nutrient import from regular tidal cycles via sedimentation is negligible in upper intertidal areas[7].

The percentage of litter translocation and consumption varies depending on crab species and forest composition. Robertson[2] showed that crabs translocated up to one-third of the annual litter fall and consumed 80% or more of this within six hours in Indo-Pacific mangrove forests. Other studies have also shown similar results, though percentage of translocation and consumption varied with respect to crab and mangrove species in a given habitat. In Hong Kong, Lee[3] found that crabs were capable of removing more than 57% of the daily litter production. Ashton[9] reported that 79–85% of the leaves were taken to burrows from *Bruguiera* dominated areas, in Sungai Paris and Lower Merbok locations in Peninsular Malaysia and 82–89% of them were processed, though they could process only 66% of leaf litter from *Rhizophora* dominated locations. Ong *et al.*[10] concluded that 42–54% of the leaf litter was consumed by crabs in Sungai Merbok mangrove ecosystem. Emmerson and McGwynne[11], showed that crabs consumed 44% of the leaf fall in southern African mangrove swamp. In tropical Australia, 79% of the total leaf litter from the floor of *Avicennia* forests was removed by sesarmid crabs[2,6]. It is reported that the New World mangrove crab *Ucides occidentalis* could remove daily production of leaf material within one hour in Ecuador[22]. Supporting this observation, Schories *et al.*[7] showed that *Ucides cordatus* could remove up to 67% of leaf litter produced in a *Rhizophora* and *Avicennia* dominated forest within one day in North Brazil. Robertson and Daniel[6] estimated that mangrove crabs could recycle more than 90% of leaf litter in high intertidal forests. Level of litter consumption by crabs is also an indicator of degradation rate and nutrient cycling within the ecosystem[9].

N. malabaricum plays a significant role in the energy pathway and carbon flow within the forest by translocating all leaf litter produced in Kunhimangalam mangrove forest. This process also supports primary production of the forest ecosystem[23,24]. Middleton and McKee[25] found that activity of sesarmid crabs could increase the rate of litter decomposition up to three times and contributed considerably to overall productivity of the ecosystem. Studies by Malley[26] on mangroves of Malaysia and those of Robertson[2] in northern Australia proved that leaf burying crabs were a major link in detrital pathways connecting primary and secondary productions within mangrove forests. Interaction of sesarmid crabs with mangrove litter helps to generate particulate organic matter, upon which depends an array of other detritivorous fauna. For example, crabs in Myora Springs on Stradbroke Island in Australia provide particulate organic matter for at least 38 species of detritivores which form the primary link in the marine food web[27]. Sesarmid crabs help the transfer of detritus to predator food chains by assimilating litter to their biomass[26–28].

In our experiments, crabs evidently preferred leaves of *E. agallocha* to those of *A. corniculatum*, *A. officinalis* and *R. mucronata* (Figure 4). *Avicennia officinalis* was the least preferred species among the four. An interesting point is that the crab translocated more leaves when offered mixed litter from the four species (Figure 3). This indicates their preference for more species diverse habitats. Moreover, there is little evidence to show that the

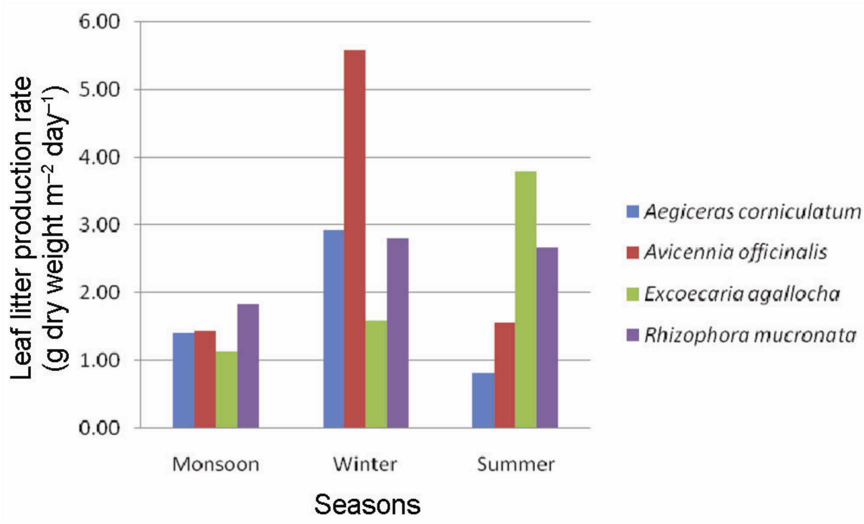

Figure 7. Differential contribution of the four dominant litter producing mangrove species in the three seasons studied.

diet of a crab species consisted of only one mangrove species, though it is possible that crab may restrict its feeding area to a forest dominated by a single species[29]. As for consumption rate, our experiments showed that *N. malabaricum*, as in translocation, preferred mixed leaf litter to that of individual species (Table 2). The thinner lamina of *E. agallocha* leaves has more flexibility, and this might have helped the crabs pull down more leaves to their burrows. Also, thicker lamina and bigger size could reduce the capacity of crabs to pull down *R. mucronata* leaves. These characters, however, do not appear to be critical in determining the rate of litter consumption. Reluctance to consume more leaves of *Rhizophora*, if there were choices for other species, has been reported with respect to Malaysian sesarmid crabs[9]. These aspects demand more attention and detailed study.

Seasonal changes influence not only quantity of litter production but also its species composition in Kunhimangalam mangrove forest (Figure 7). This is also related to quantity of leaf litter processed by *N. malabaricum*. Production of leaf litter was highest in winter and the litter constituted all four species, *A. corniculatum*, *A. officinalis*, *E. agallocha* and *R. mucronata.* Highest rate of litter translocation was recorded when we provided mixed litter to *N. malabaricum*. Similarly, preference shown by *N. malabaricum* to *E. agallocha* over other three mangrove species, helped to increase translocation potential of the crabs during summer. The highest contribution to leaf litter came from *E. agallocha* in Kunhimangalam mangrove forest in summer. Monsoon, the lean season as regards to litter production, witnessed *N. malabaricum* mainly translocating and feeding on saplings of *A. officinalis* and *E. agallocha*[17]. So, seasonal changes do influence species' preference of *N. malabaricum* in Kunhimangalam mangrove forest but hardly do both of them seriously affect annual total quantity of litter processed by the crabs.

Mutualistic interaction, as we discussed, between crab and mangrove communities, which involves multiple species and varied preferences, has conservation implications. Degradation or loss of mangroves substantially reduces availability of leaf litter to the crab community. Nicholson[30], observed that crabs could consume only 95% less litter in degraded mangroves in Zanzibar in East Africa. Such conditions may prompt the crab community to leave the area and migrate to better forested areas. They may also leave mangrove forests because of physical, chemical and biological changes in the gaps in forest floor formed due to felling of mangrove trees. Bisang reportedly observed that density of sesarmid crabs was much lower in degraded mangrove forests in Zanzibar[30]. Such situations reduce quantity of litter processing and consequently, nutrient cycling and eventually, health of the mangrove ecosystem. This imparts the lesson that mangrove restoration programmes should not only employ multiple species, but should also be coupled with reintroduction of disrupted crab species to establish the lost interactions.

Our study emphasizes the key role played by the sesarmid crab *N. malabaricum* in litter translocation and consumption in the mangrove ecosystem in Kunhimangalam, Kerala. It supports the results of allied works conducted in different parts of Asia, Africa and Australia (several works cited in the text). All these studies[2,9,12,22,25] converge to some common conclusions: (i) sesarmid crabs have a highly significant effect on weight loss of mangrove leaves (leaf degradation) by burying and consuming them, (ii) sesarmid crabs retain nutrients within forests (according to Smith *et al.*[31], the amount of leaf material exported from mangrove forests was reduced by 30%), and play a key role in carbon and nutrient cycling and (iii) by being involved in such vital functions, it is possible that sesarmid crabs function as ecosystem modifiers in mangrove ecosystems of the Old World tropics.

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