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SHORT COMMUNICATION

Secondary removal of *Myristica fatua* (Myristicaceae) seeds by crabs in *Myristica* swamp forests in India

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Abstract: Little is known about the role of crabs as seed dispersers and predators. Recently, there has been interest in understanding their influence on plant recruitment in coastal forests. Secondary seed removal by crabs in a swamp-specialist tree, *Myristica fatua*, was investigated in the rare and patchy freshwater *Myristica* swamps in the Western Ghats in India. Tethered-line experiments were used to determine the role of crabs as secondary seed-removal agents in two study sites. Crabs transported a large percentage (63.3%) of seeds (n = 60) placed on the forest floor compared with rodents (25%) and other unknown agents (13.3%). Simultaneous choice experiments suggested that the nutrient-rich arils covering seeds were consumed, but there was no evidence for seed predation by crabs. A small percentage (13.3%) of monitored seeds (n = 60) germinated from within crab burrows. The spatial scale of secondary removal by crabs was restricted to < 10 m. In these fragmented swamp forests, secondary removal by crabs retains seeds largely within the swamps, where conditions for their establishment and survival are optimal. Thus, secondary seed removal by crabs could provide temporal and spatial refugia from seed predators such as rodents in *Myristica fatua*.

Key Words: freshwater crabs, nutmegs, seed dispersal, seed fate, seed predation, Western Ghats

Primary seed dispersal has long been credited with facilitating survival in plants (Howe & Smallwood 1982, Janzen 1970, Wenny & Levey 1998), thereby shaping the spatial structure of plant communities and enhancing gene flow among populations (Herrera *et al.* 1994, Nathan & Muller-Landau 2000). However, the final fate of dispersed seeds might be a template generated by primary dispersal and subsequently rearranged by secondary seed removal (Nathan & Muller-Landau 2000). Thus, understanding the consequences of secondary seed removal is crucial as it directly influences plant population dynamics (Crawley 2000), specifically in tropical tree species which overwhelmingly depend on animal-rendered services (Howe & Smallwood 1982), have specialized habitat needs and limited microsites for recruitment (Clark *et al.* 2007, Dalling *et al.* 2002).

Seeds experience contrasting fates following secondary removal. For example, seeds removed by rodents are predominantly consumed, but some seeds may escape predation via hoarding (Forget 1996, Forget *et al.* 1999). Challenges involved in tracking seeds after secondary removal hampers the exact determination of seed fates. Therefore, many studies have considered secondary removal a proxy for predation, although it can also result in dispersal and establishment (Vander Wall *et al.* 2005). In addition to rodents, secondary seed removers include diverse groups such as ants, beetles, armadillos and coatis (reviewed in Chambers & MacMahon 1994). However, the role of some agents such as crabs (Capistrán-Barradas & Moreno-Casasola 2006, Sherman 2002, Smith 1987) remains poorly understood. Some studies have elucidated the role of crabs as key players in the recruitment of plants in coastal, mangrove and island ecosystems (Lee 1985, Louda & Zedler 1985, Lindquist *et al.* 2009, O'Dowd & Lake 1991, Osborne & Smith 1990). In this study, we evaluate the importance of crabs in secondary seed removal of an endangered tree species, *Myristica fatua* var. *magnifica* (Bedd.) Sinclair (Myristicaceae) (IUCN 2000) that occurs exclusively in the *Myristica* swamp forests of the Western Ghats in India (Champion & Seth 1968). These freshwater swamps are dominated by the Myristicaceae, and exist as small fragments due to special abiotic requirements and added anthropogenic impacts

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(Chandran & Mesta 2001). In this study system, we test the hypothesis that crabs are major secondary removers of *Myristica fatua* seeds in a small fragmented and a large contiguous site.

This study was conducted from June to October 2013 within the Kulathupuzha reserve forest (8°51′N, 77°5′E), southern Western Ghats of India. A small, fragmented swamp (Marappalam; hereafter fragMP; area 1.5 ha) and a large contiguous swamp (Munnamchal; hereafter contMC; area > 20 ha) were chosen as study sites. *Myristica fatua* trees are dioecious and fruit from May to October (unpubl. data). Capsules enclose a single large seed, which is covered by a bright yellowish-orange lacy aril. Freshly collected arillate seeds weigh 24.8 ± 2.98 g (n = 10, Mean ± SD), while seeds alone weigh 20.9 ± 2.93 g (n = 10). Primary frugivores include *Ocyceros griseus* Latham (Malabar grey hornbill), *Buceros bicornis* Linnaeus (great hornbill), *Macaca radiata* Geoffroy (bonnet macaque), *Ratufa indica* Erxleben (Malabar giant squirrel), *Macaca silenus* Linnaeus (lion-tailed macaque) and *Presbytis johnii* Fischer (Nilgiri langur). Entire dehisced capsules can also passively drop from trees. Two common freshwater crab species (burrow densities in fragMP = 0.27 m^{-2} and contMC = 0.12 m^{-2}), *Barytelphusa guerini* (H. Milne-Edwards) and *Travancoriana schirnerae* Bott, secondarily remove seeds in the *Myristica* swamp forests.

To determine the identity of secondary removers, aril-intact (passively dropped) and aril-removed seeds (dropped by frugivores) were tethered to 2-m long fishing lines (Experiment A). Three aril-intact and three aril-removed seeds were placed under each of 10 trees in both sites. The fate of these seeds was monitored on days 1–5, 7, 9, 14 and weekly thereafter until week 14. The displacement distance was measured for recovered seeds from the location of placement to the seed-end of the tether. Depending on location of recovery, seeds were categorized as (1) crab-removed (line recovered from crab burrow), (2) rodent-removed (line recovered 2–10 m above ground), (3) unknown (line detached and seed removed), (4) infected or (5) not removed. Ten of these crab burrows with recovered fishing lines were excavated to check the fate of seeds.

To check whether crabs were seed predators or dispersers, simultaneous choice experiments were performed using tethered and waterproof-paint-marked seeds and arils (Experiment B). In both cases, an aril-intact seed, an aril-removed seed and an aril alone were placed at a distance of 0.5 m from the entrance of burrows (n = 15 burrows in each case). Experiment B was monitored using infrared surveillance cameras and direct observations (18h00–23h00) until complete removal. Tethered seeds (15 aril-intact + 15 aril-removed) and marked seeds (15 aril-intact + 15 aril-removed) that were carried by crabs into burrows were monitored weekly for signs of predation or germination. All statistical analyses were performed using R software (version 3.0.2) and the SURVIVAL package was used for analysing seed removal rates (R Foundation for Statistical Computing, Vienna, Austria).

In Experiment A, there was no difference between sites in the removal of tethered aril-intact ($\chi^2 = 0.63$, df = 1, P = 0.429) and aril-removed seeds ($\chi^2 = 0.60$, df = 1, P = 0.437), so the data were pooled for further analysis. Compared with rodents, crabs removed significantly higher proportions of aril-intact ($\chi^2 = 7.84$, df = 1, P < 0.05) as well as aril-removed seeds ($\chi^2 = 6.56$, df = 1, P < 0.05) (Figure 1). The distance of seed removal varied significantly between crabs and rodents (Wilcoxon rank sum test, W = 40, P < 0.0001; Crabs = 1.48 ± 1.74 m, n = 23, maximum = 8 m; Rodents = 3.56 ± 4.06 m, n = 23, maximum = 20 m).

Simultaneous choice experiments (Experiment B) indicated that removal rates of arils were higher than aril-intact and aril-removed seeds (Kruskal–Wallis test, tethered seed, $\chi^2 = 39.5$, df = 2, P < 0.0001; marked-seed, $\chi^2 = 40.7$, df = 2, P < 0.0001). Direct observations showed that arils covering seeds were partially eaten at the placement location and the rest was carried into burrows (Supplementary material). Excavations of burrows revealed no signs of seed predation (fragments of seeds) or intact seeds. However, 13.3% of the 60 seeds monitored at crab burrows germinated successfully at a depth of approximately 15 cm within burrows. The mean height of seedlings, which emerged from burrows, was 35.3 ± 12.1 cm (n = 8).

The proportions of aril-intact and aril-removed seeds removed by crabs did not differ significantly in fragMP ($\chi^2 = 0$, df = 1, P = 1) and contMC ($\chi^2 = 3.28$, df = 1, P = 0.070) (Figure 1; 32 seeds each were removed by crabs in fragMP and contMC). However, aril-intact seeds were removed at much faster rates (< 3 d, mean = 1.89 ± 0.94 d) than aril-removed seeds (up to 98th day, mean = 32.6 ± 27.0 d) in both sites (Gehan-Wilcoxon test, fragMP $\chi^2 = 23.5$, df = 1, P < 0.001; contMC $\chi^2 = 11.9$, df = 1, P < 0.001).

Crabs removed a greater proportion of *M. fatua* seeds compared with rodents and unknown agents, which could include *Sus scrofa* Linnaeus (wild boar), *Viverricula indica* Geoffroy Saint-Hilaire (small Indian civet), *Moschiola indica* Gray (mouse deer) and *Muntiacus muntjak* Zimmerman (barking deer). Rodents were the major seed predators of *Myristica hypargyraea* in lowland rain forests of Tonga, Western Polynesia (Meehan *et al.* 2005). Similarly, rodents such as *Platacanthomys lasiurus* (Malabar spiny dormouse), *Rattus rattus wroughtoni* (white-bellied wood rat) and *Funambulus sublineatus* (dusky striped squirrel) are major predators of *Myristica beddomei* seeds in the Western Ghats, India (Chetana & Ganesh 2013). In addition to these species, rodent species

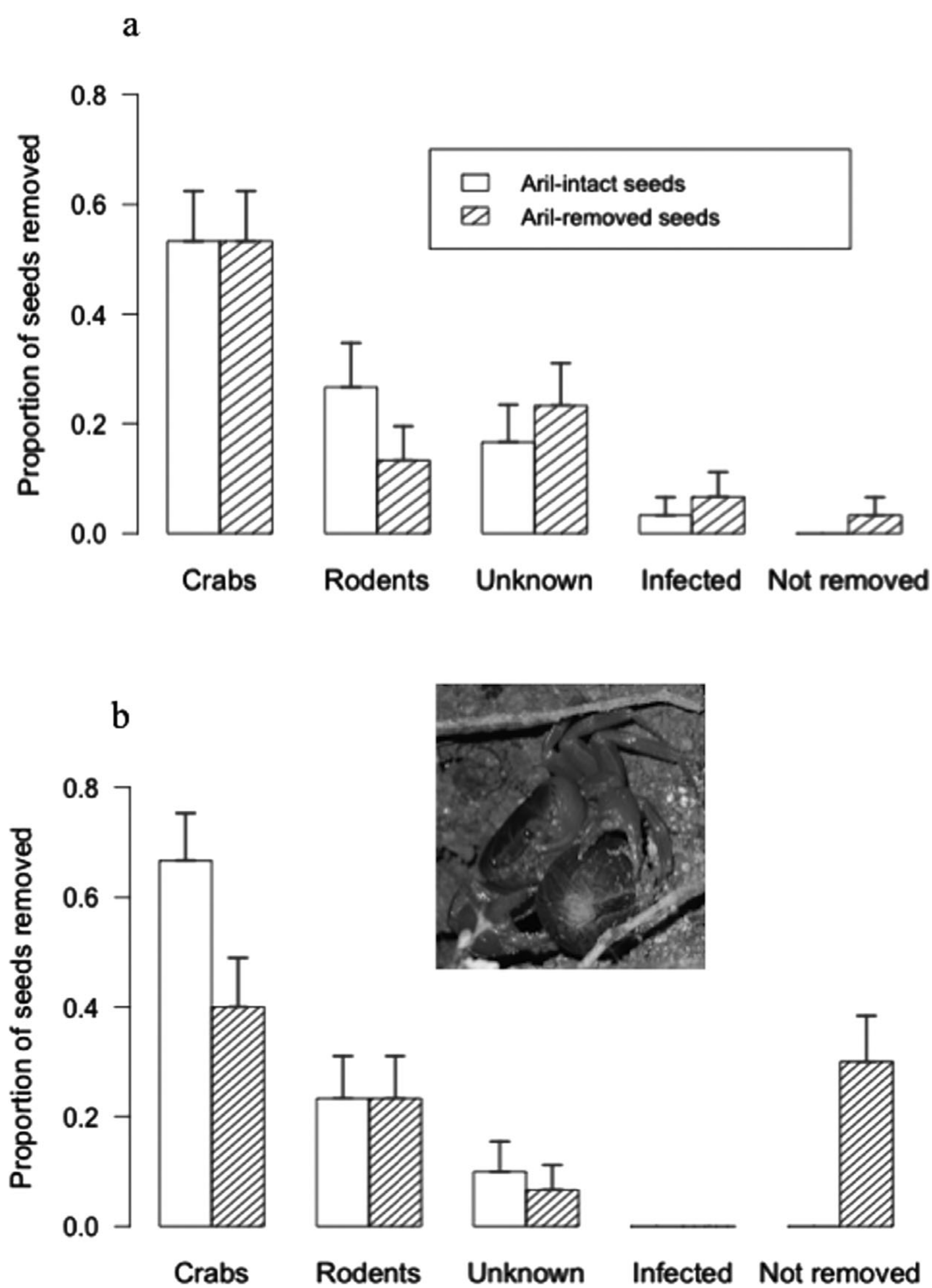

Figure 1. Secondary seed removal of *Myristica fatua* in *Myristica* swamp forests in the southern Western Ghats in India. Mean (+ SE) proportions of seeds removed in a fragmented swamp, fragMP (a) and a contiguous swamp, contMC (b) following differential seed fate i.e. crab-removed, rodent-removed, infected seeds, unknown (specific group of removers could not be identified) and seeds not removed by the 98th day are shown. Thirty tethered aril-intact and aril-removed seeds were placed in each study site (Experiment A). Inset shows the freshwater crab, *Barytelphusa guerini* holding a seed of *Myristica fatua.*

in our study area include *Bandicota indica* Bechstein (greater bandicoot rat) and *Rattus rattus* Linnaeus (black rat) (Nair *et al.* unpubl. data, pers. obs.). We did not find any signs of hoarding by rodents in the swamps. Remains of 20 seeds (fragMP + contMC) were found close to cut tethered lines that ended up on trees, suggesting predation by rodents. Crabs have been shown to cause high levels of seed predation in mangrove species such as *Avicennia marina* and *Bruguiera exaristata* (Smith 1987) and sea grasses such as *Zostera marina* and *Phyllospadix torreyi* (Fishman & Orth 1996, Holbrook *et al.* 2000). We found no direct or indirect evidence for seed predation

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by crabs, though arils were highly preferred, possibly for their high nutritive value. Arils of Myristicaceae are lipid-rich compared with many other fruits (Howe & Vande Kerckhove 1981). A few crabs were seen to push out intact seeds from within their burrows, suggesting that they consume arils but not seeds of *M. fatua*. The removal patterns in fragmented swamp and large contiguous swamp were similar; suggesting that removal of *M. fatua* seeds by crabs was not a site-specific phenomenon.

Secondary removal by crabs and rodents was highly localized within swamps. Tethering indicated that crabs carry seeds over short distances from under tree crowns to burrows (Experiment A). Fruit removal over short distances was previously reported in *Pandanus tectorius* by the crab *Cardisoma carnifex* in a Central Pacific island (Lee 1985). Territoriality and risk-averse behaviour in crabs (Dunham & Gilchrist 1988) could result in localized seed transport, thereby retaining seeds within swamps. Female *M. fatua* trees produce large-seeded fruits in small numbers (range = 50–300, unpubl. data), so even a small proportion of these seeds that escape predation from rodents and pathogens could have substantial impacts on recruitment.

Regeneration microsites for *M. fatua* are contained within the swamps exclusively (Chandran *et al.* 1999, Ramesh *et al.* 1997). Primary dispersers such as hornbills often drop seeds within the swamp forests or in the surrounding matrix. Seeds dropped within the swamp forests may either undergo predation or germinate, while those dropped outside the swamps do not survive, given the unsuitable abiotic conditions. On the other hand, secondary seed transport by crabs is confined to the swamps where conditions for survival are suitable. Additionally, crab burrows can function as refugia for seeds by facilitating spatial and temporal escape from predation in this highly endangered tree species.

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SUPPLEMENTARY MATERIAL

For supplementary material for this article, please visit http://dx.doi.org/10.1017/S0266467414000091
Video showing a freshwater crab feeding on the aril of *Myristica fatua* seed and carrying the seed into the burrow. Shivani&Somanathan_supplementaryvideo.mp4

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