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Research Article

Seed dispersal of *Vitex glabrata* and *Prunus ceylanica* by Civets (Viverridae) in Pakke Tiger Reserve, north-east India: spatial patterns and post-dispersal seed fates

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ABSTRACT
Civets are considered potentially important seed dispersers in tropical forests of Asia, but relatively little is known about spatial patterns of dispersal and post-dispersal fates of civet-dispersed seeds. We explored these aspects of civet seed dispersal for two tree species *Vitex glabrata* (Lamiaceae), also known as smooth chaste tree and *Prunus ceylanica* (Rosaceae), in Pakke Tiger Reserve, a tropical forest reserve in north-east India. Pakke has five known species of viverrids: small Indian civet (*Viverricula indica*), large Indian civet (*Viverra zibetha*), common palm civet (*Paradoxurus hermaphroditus*), masked palm civet (*Paguma larvata*) and the binturong (*Arctictis binturong*). For both tree species, civets as a group dispersed seeds (100% of scats that we found) within 50 meters from fruiting trees and deposited seeds onto multiple substrates including tree branches, forest floor, and fallen logs. However, the distribution of seeds among substrates differed for the two tree species: while most seeds of *V. glabrata* (> 90%) were deposited onto canopy branches and fallen logs, the majority of *P. ceylanica* seeds (> 70%) were deposited on the forest floor. For both tree species, seeds deposited on logs experienced higher seed predation than seeds on the forest floor, especially when local seed densities (number of seeds in $1m^2$ area around the scat and in the scat) were high. Further, seed viability of *P. ceylanica* was significantly lower on logs (~35%) than on the forest floor (~65%). For both tree species, civets neither dispersed seeds far from fruiting trees nor to sites where seeds experienced either low predation or high survival, suggesting that while civets were legitimate dispersers, they were not especially effective.

KEYWORDS Civets, North-east India, *Prunus ceylanica,* seed dispersal, seed deposition substrates, seed predation, seed viability, *Vitex glabrata*.

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Introduction

In tropical forests, seeds from the vast majority of tree species are dispersed by vertebrates, primarily birds and mammals [1–3]. For these animal-dispersed plants, the biology and behaviour of their seed dispersers directly influence various aspects of seed dispersal, such as distances over which seeds are dispersed, spatial patterns of seed rain, and microhabitats where seeds are deposited. For example, many large-bodied birds and mammals that either range over large distances or retain seeds in their gut for long periods may disperse seeds over long distances (>100 m) [4–6]. Similarly, many birds and mammals deposit disproportionately large numbers of seeds at their resting sites, nesting sites or middens, leading to spatially clumped seed dispersal [7–9]. Some dispersers such as seed-caching rodents deposit seeds at distinct microhabitats such as beneath forest litter or under nurse trees [10,11]. Arboreal frugivores such as hornbills and spider monkeys that drop seeds beneath their nesting or sleeping trees may result in seeds being deposited in shaded habitats, while terrestrial frugivores such as foxes, badgers, and civets often deposit seeds in open habitats [8,12–15]. These spatial patterns of seed deposition in turn drive post-dispersal rates of seed predation and seed germination, ultimately influencing both individual plant reproductive success and whole plant community structure [16].

Amongst frugivorous mammals in tropical Asia, civets, especially palm civets, are considered potentially important seed dispersers in tropical forest tree communities [2,17]. Although they are small carnivores, many species of civets are highly frugivorous and consume a wide variety of fruits [17–19]. Some species of civets are largely arboreal and often feed on fruits directly from trees [2]. Their large gape width allows them to swallow fruits whole without damaging them, while passage through their gut leaves most seeds intact [2,15,17,20,21]. Their large home ranges (ranging from 6 - 451 ha for palm civets in Nepal, India, Borneo and China) suggest that civets have the potential to be long-distance dispersers [22–26]. Some species, such as the common palm civet and masked palm civet, are relatively abundant in fragmented and logged tropical forests without hunting pressures [2,19]. With global losses of large-bodied frugivorous birds and primates from these disturbed habitats, the potential role of civets as seed dispersers may be critical [17,19]. However, there is a dearth of quantitative information about the spatial patterns of dispersal and post-dispersal fates of civet-dispersed seeds, with the result that we still know little about how effective civets actually are as dispersers.

Past research on the natural history of civets reports that many species routinely deposit seeds in specific and conspicuous sites such as fallen logs, while a few species repeatedly defecate seeds at fixed “civeteries” [2,23]. Most studies however, did not systematically quantify all civet seed dispersal sites or track seed fates. A recent study from northern Borneo (among the few to search arboreal layers) reports that common palm civets, *Paradoxurus hermaphroditus,* non-randomly dispersed seeds of the tree *Leea aculeata* to ‘open sites’ including rainfall runoff paths, abandoned trails, stream banks and tree fall gaps [15]. They dispersed a disproportionately large number to stream banks and tree fall gaps, where seeds experienced both increased survival and germination, suggesting that seed dispersal by civets had a strong positive impact on recruitment and fitness for this tree species. In contrast, two studies on seed dispersal by the African civet (*Civettictis civetta*), which deposits seeds in large civeteries, found highly variable recruitment success for different tree species at these sites [27,28].

In our study, for two tropical forest tree species known to be dispersed by civets, *Vitex glabrata* (smooth chaste tree) and *Prunus ceylanica*, we investigated: (1) spatial patterns of seed dispersal by civets, particularly distance of seed deposition from fruiting tree, and substrates of seed deposition; (2) rates of post-dispersal seed predation and factors affecting these rates; and (3) the viability of civet-dispersed seeds and factors affecting viability. Using these data, we draw some inferences about the effectiveness of seed dispersal by civets for these tree species.

Methods

Study area and study species

This study was conducted in the Pakke Wildlife Sanctuary and Tiger Reserve (hereafter PTR) located in the East Kameng district, Arunachal Pradesh, India (26° 85' 49'' N to 27° 81' 69'' N; 92° 83' 69'' E to 93° 80' 99'' E) during the period from December 2011 to April 2012 (Fig. 1).

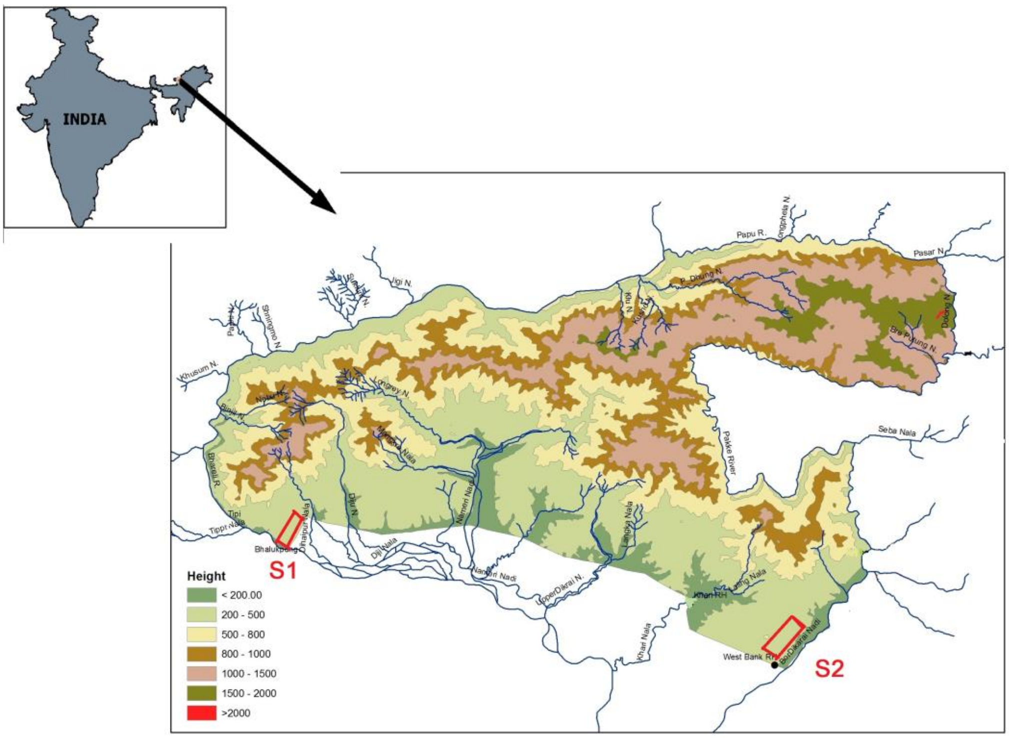


Fig. 1. Map of the Pakke Tiger Reserve, Arunachal Pradesh, in north east India where this study was conducted. The intensive study sites S1 (~8 km^2) and S2 (~10 km^2) are shown in red.

PTR has five known species of viverrids: small Indian civet (*Viverricula indica*), large Indian civet (*Viverra zibetha*), common palm civet (*Paradoxurus hermaphroditus*), Himalayan or masked palm civet (*Paguma larvata*) and the binturong (*Arctictis binturong*). Other important seed dispersers in PTR whose diet considerably overlaps with civets are mountain imperial pigeons (*Ducula badia*) and three species of hornbills: great hornbill (*Buceros bicornis*), wreathed hornbill (*Rhyticeros undulatus*) and oriental pied hornbill (*Anthracoceros albirostris*) [29].

We chose two tree species: *Vitex glabrata* (Lamiaceae; syn *Vitex pentaphylla*) and *Prunus ceylanica* (Rosaceae; formerly *Pygeum acuminatum*) as focal tree species. These tree species were chosen because a) they were fruiting during the study period, and b) they are known to be eaten by civets in large numbers. *V. glabrata* fruitjs from November through December and is a medium-height, lower-canopy tree, with a wide canopy (radius 8 – 10m) which branches low from the ground and is often associated with lianas and other climbers along its trunk and branches. The fruits are small single-seeded drupes (1 – 1.5 cm across) and form bunches at the ends of branches. They are known to be consumed by civets, bulbuls, barbets and imperial pigeons (pers.obs.). *P. ceylanica* fruits from December to February and is a tall, mid-canopy tree, with a smaller canopy (radius 3.5 – 6m) which branches high from the ground and is not usually associated with lianas or climbers. The fruits are fleshy single-seeded drupes (2.25 +- 0.15 cm across), typically eaten by hornbills, imperial pigeons, barbets and civets [12,31, pers.obs.].

Study Design

We collected data in two focal study sites S1 (~8 km^2) and S2 (~10 km^2), located about 25 km apart in a continuous stretch of lowland semi-evergreen forest in PTR (Fig.1). S1 was chosen at the start of the study period based on the presence of several fruiting trees of *V.glabrata*. When the fruiting of *V.glabrata* drew to a close and we found no new fruiting individuals, we moved east to S2 where we found several *P.ceylanica* trees that had begun fruiting. At both sites, we had access to relatively safe base camps from where we could walk to all focal fruiting trees within 2-3 hours.

To generate some direct information on the nature of the seed disperser communities for our focal tree species, we conducted ad-hoc fruiting tree watches during the day, and camera-trapped platforms containing ripe fruit during the night. Three fruiting trees of each species were watched for one hour each on 10 fruiting days. Camera-traps were placed at two fruiting trees of each species for 10-15 nights during fruiting. Fruit platforms were placed both on the trees, and at the base of the trees on the forest floor. Our sample sizes in these surveys were limited and preclude any formal analyses. We merely use this information as observational evidence for the identity of seed dispersers and predators.

Civet scats were identified based on their size (< 2.5cm diameter), and their cylindrical shape with rounded ends usually deposited in a straight manner [23]. Because our camera-traps did not capture other small carnivores and most scats exclusively contained seeds and fruit coats with little to no hair and no pungent odour, we ruled out the possibility of the scat belonging to other small carnivores. This identification was also confirmed when we found scat of a camera-trapped common palm civet at a fruiting platform.

In a pilot survey to determine a sampling methodology for finding civet scats, we conducted scat searches as follows: At site S1, we chose 12 random points that were distributed over most of the accessible areas of this site (points were on average 1km (700-1,400m apart). At each of these points, we laid 10 parallel belt transects (100m x 5m; 50 m apart) running east from the start point. Each transect was thoroughly searched for scats. As this method yielded very few scats (13 scats/120 transects), and we observed scats near fruiting trees, we then laid non-random belt transects (100m x 5m) in four cardinal directions around 12 fruiting trees. These transects yielded many more scats (35 scats/ 48 transects) and confirmed our observations that scats were clustered around fruiting trees.

Based on our pilot survey, we chose the following methodology to maximize the probability of finding civet scats: For each fruiting tree, we laid a 100m X 100m plot with the fruiting tree at its centre. This area was then systematically and thoroughly searched, one quadrant (50m x 50m) at a time (see Fig.2), by three persons trained in locating civet scat. Searches were intensive and included looking for scat on all substrates: trees, lianas, logs, and ground. The branches in the canopy were searched by climbing up the tall trees, as high as needed for vantage points to search the branches of shorter trees. Each quadrant was searched at least twice before the search was discontinued. In order to confirm that scats were clumped around fruiting trees, we also searched areas around non-fruiting trees using the same methodology. Non-fruiting trees were chosen *ad libitum*, on the condition that there were no fruiting trees of either study species within 50m of the non-fruiting tree. For each fruiting tree searched, a paired non-fruiting tree was searched. This process was repeated for 12 and 10 pairs (fruiting and non-fruiting) of *V.glabrata* and *P.ceylanica* trees respectively (all but one pair of *P.ceylanica* trees were more than 100m away from each other). We found only two civet scats from all plots around non-fruiting trees, confirming that scat deposition did not occur far from fruiting trees. In the rest of the study, the data we report are from the 100m X 100m plots around fruiting trees.

For each fresh civet scat pile that was located, data on GPS position, substrate of deposition (tree, liana, fallen log, or ground), and the following microhabitat characteristics were noted: neighbourhood seed density (number of seeds in 1m^2 plot centred at the scat, but not including seeds in the scat), canopy density, leaf litter depth (the average of four measures obtained by jabbing a sharp knife into the litter and counting the number of pierced leaves [31]). Searches for new scats within the plots were continued every alternate day until the tree stopped fruiting.

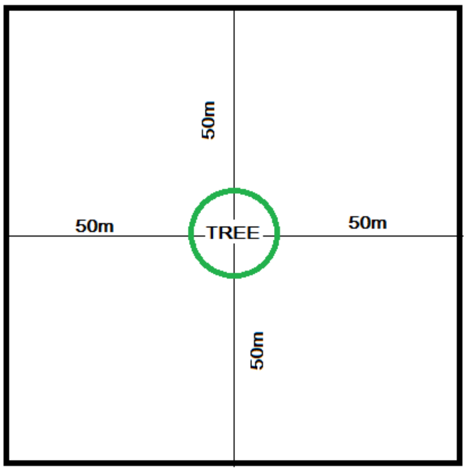


Fig. 2. A diagram showing the 100m X 100m area around focal trees that was searched for scat. The area was systematically searched, one 50m X 50m quadrant at a time.

Scat locations were marked with numbered tags, and scats were then monitored once a week until the fruiting stopped and once every 14 days thereafter. In each monitoring we noted the number of seeds remaining in the scat as well as the aforementioned microhabitat characteristics. Scats were monitored for a minimum of 14 days (when all seeds disappeared) to a maximum of 56 days (when the study ended), after which all remaining seeds were collected to test for seed viability. Seeds that disappeared from scat piles and from the substrate immediately surrounding them were assumed to have been predated. While it is also possible that these could have been cached by seed predators, an earlier study in the same site shows minimal seed recruitment for multiple tree species from the caches of rodents, which are the major seed predators in this system [32]. Therefore, for the purpose of this study, we assume that all seeds that disappeared from scats were lost to predation. We were unable to track the fate of seeds that might have dropped to the ground from scats deposited in the canopy of focal *V. glabrata* trees, as these were not distinguishable from other seeds fallen under the tree. At the end of the study period, none of the seeds that remained in the scat piles had germinated. We therefore harvested these seeds and tested all of them for seed viability in the laboratory using the tetrazolium dye test [33].

In order to check for bias in detection of scats from a particular substrate, five scats per substrate were placed in separate undisclosed locations in the 100 m x 100 m plot around a fruiting tree of each species. The scats were placed by an observer on three substrates: tree, fallen log and ground. Two other observers then intensively searched the plot for scats. The proportion of scats found in each substrate was later calculated. For *V. glabrata,* 86.6 percent scats on trees and ground and 100 percent scats on fallen logs were detected, and for *P. ceylanica*, 93.3 percent scats on trees, 86.6 percent scats on ground and 100 percent scats on fallen logs were detected. We concluded that when all areas were thoroughly searched, bias in detection for civet scats on different substrates was negligible.

Statistical Analysis

All statistical analyses were carried out using the statistical software R [34]. We used bootstrapping techniques to test for differences between the mean distances (from fruiting trees) at which scats on different substrates were deposited. We generated a distribution of the mean by re-sampling the mean 1,000 times with replacement, and plotting 95% of the distribution of means as confidence intervals. Non-overlapping confidence intervals were interpreted as significant differences between the compared means. Since confidence intervals generated in this manner include the entire 95th percentile range of values, these tests result in a conservative interpretation of the differences between means. Using the bootstrapping techniques outlined above, we tested for the effect of substrate of scat deposition on two measures of post-dispersal seed fate: rates of seed predation from scats and the viability of seeds that remained in scats at the end of the study period.

We also conducted a more detailed survival analysis, specifically Cox proportional hazards model with mixed effects modified for time dependent variables, to analyse which factors significantly influenced seed predation from scats. The factors included in the analysis were: substrate of seed deposition, distance from fruiting trees, local seed density (the sum of neighbourhood seed density and the number of seeds in the scat), leaf litter and canopy density. As predictor variables that varied with time violated the proportional hazards assumption, variables were stratified into multiple shorter time intervals during which they are assumed to remain constant, a modification that accounts for model assumptions [*sensu* 27]. As seed predation rates are likely to be dependent on the fruit crop of a tree, as well as the scat characteristics such as the number of seeds in the scat, tree identity was included as a random effect. Finally, scat identity was included as an additional random effect nested within tree identity. Our analysis included all ecologically meaningful interactions, and significant predictors were chosen using a stepwise backward elimination of predictors with the highest p value.

Results

We found 69 scats with *V. glabrata* seeds around 10 (of 12) fruiting trees. The number of seeds in each scat varied from 11 to 350, with a modal class of 45-55 seeds. We found 101 scats with *P. ceylanica* seeds around seven (of 10) fruiting trees. The numbers of seeds in each scat varied from one to 51 seeds per scat with a modal class of 10-15 seeds. Most scats (>95%) contained seeds of only one species. Based on fruit tree watches and camera-traps of fruit displays, *V.glabrata* fruits were eaten by common palm civet *(Paradoxurus hermaphroditus),* lineated barbet (*Megalaima lineata*), blue throated barbet (*Megalaima asiatica*), black crested bulbul (*Pycnonotus melanicterus*), pin tailed green pigeon (*Treron apicauda*), wedge tailed green pigeon (*Treron sphenurus*), and predated by hoary bellied squirrel (*Callosciurus pygerythrus*) and rodents *(Rattus sp.). P. ceylanica* fruits were eaten by common palm civet, large Indian civet (*Viverra zibetha*), Malay tree shrew (*Tupaia glis*), lineated barbet and wreathed hornbill (*Rhyticeros undulatus*), and predated by hoary bellied squirrel (*Callosciurus pygerythrus*), Malayan giant squirrel (*Ratufa bicolour)* and rodents (*Rattus* sp.) The data from the camera-traps of fruit displays show that *V. glabrata* fruits were eaten from the tree while most *P. ceylanica* fruits were eaten from the ground (see Fig. 3). They also indicated that the bulk of seed dispersal by civets for both species could be attributed to the common palm civet, which was camera-trapped on 25 of the 35 trap nights, and accounted for 23/26 civet captures on *P.ceylanica* and 6/6 civet captures for *V.glabrata*.

Spatial Patterns of Seed Dispersal by Civets

For both our focal tree species, scats were clustered near the fruiting tree and decreased with increasing distance (Fig. 4). The farthest scats we detected were ~ 40m from the fruiting tree. However, within this general pattern, there were distinct variations in the substrates of seed deposition for each tree species: In *V. glabrata*, 58 percent of scats were deposited on the fruiting tree and on neighbouring trees and lianas, off the ground and in the lower reaches of the forest canopy around the focal tree. Another 38 percent were deposited on logs on the forest floor, and only four percent of the scats were deposited directly on the ground. In contrast, 73.2 percent of *P. ceylanica* scats were deposited directly on the ground under the fruiting tree, while 25.7 percent of scats occurred on logs on the forest floor (Appendix 1). Further, for both species, there appeared to be an interaction between distance from the fruiting tree and the substrate of scat deposition. Specifically, most scat deposition away from fruiting trees was found to be on logs, while scats found on the ground tended to occur close to fruiting trees (Fig. 5).

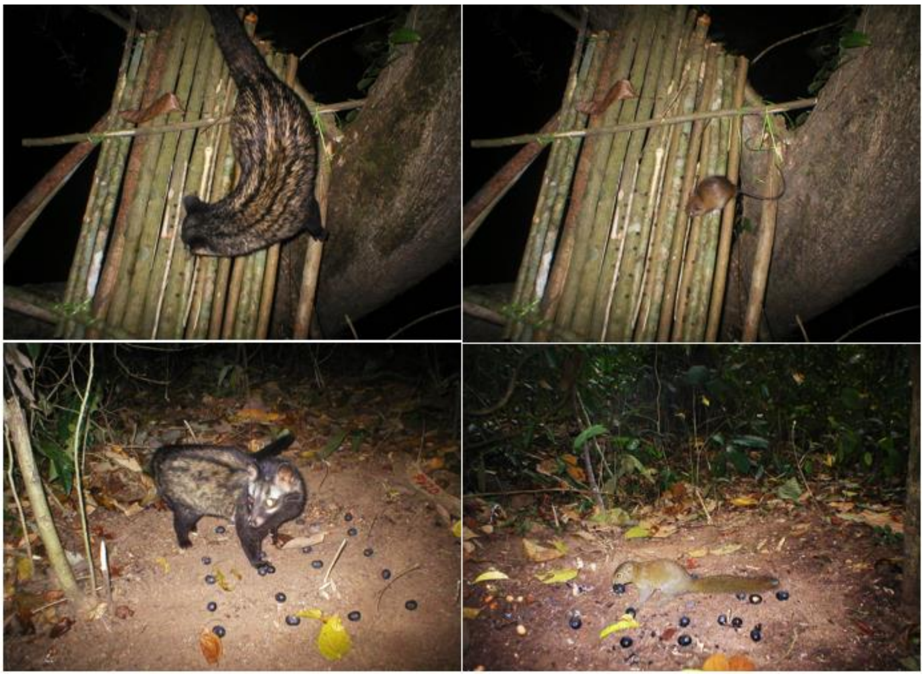
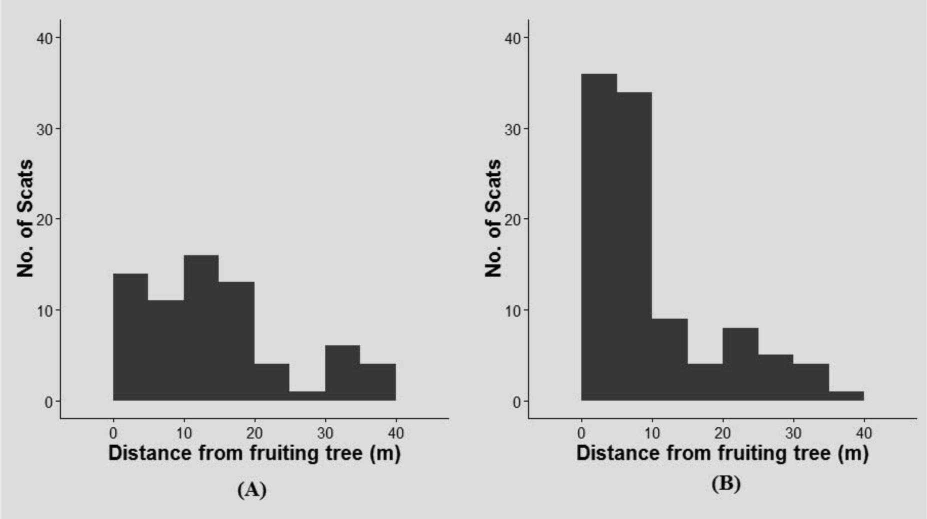


Fig.3. Camera-trapped images of seed dispersers and seed predators frequently captured at fruit platforms: Common palm civet (*Paradoxurus hermaphroditus)* and *Rattus sp* with *V.glabrata* fruits (top row); Common palm civet and hoary bellied squirrel (*Callosciurus pygerythrus*) with *P.ceylanica* fruits (bottom row). Photo credits: Dayani Chakravarthy.



(A) (B)

Fig. 4. Pooled frequency distributions of the number of civet scats found at different distance classes from focal fruiting trees of A) *Vitex glabrata (N=10)* and B) *Prunus ceylanica (N=12)*

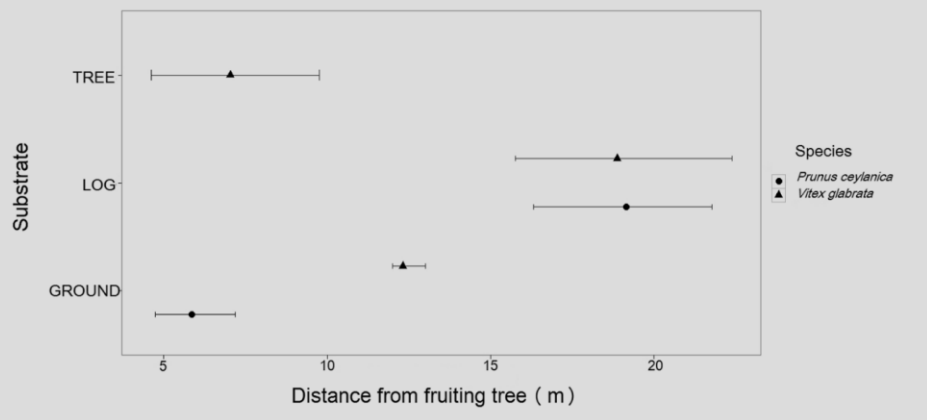


Fig. 5. Mean distances from focal fruiting trees of scats on different substrates for *Vitex glabrata* and *Prunus ceylanica.* The bars represent the 95th percentiles of 1000 bootstrapped means.

Post-dispersal seed fates

Seed predation rates over 56 days in monitored natural scat piles varied from 2 percent to 100 percent in *V. glabrata* and 0 percent to 100 percent in *P. ceylanica*. Overall, mean seed predation was higher in *P. ceylanica* (57.25%) than in *V. glabrata* (30.42%). For both species, scats on logs had significantly higher rates of seed predation than those on the ground (Fig. 6 [A]). At the end of the study, we harvested the seeds that were remaining in the monitored scats. Since these could potentially have been taken by predators, these estimates of predation rates probably underestimate actual predation.

Our analyses of seed removal rates from monitored scats indicated strong effects of substrate and local seed densities on post-dispersal seed predation for both tree species. We found that for *V. glabrata,* local seed density (the sum of neighbourhood seed density and the number of seeds in the scat) interacted with substrate (Log: z = - 5.27, *P* < 0.0001, Tree: z = - 4.92, p < 0.0001), distance from fruiting tree (z = - 4.38, *P* < 0.0001) and leaf litter depth (z = - 4.11, *P* < 0.001) to negatively influence seed survival. For *P. ceylanica,* local seed density interacted with substrate log (z = - 2.99, *P* = 0.0028) and distance from the fruiting tree (z = - 2.17, *P* = 0.03) to decrease seed survival, and leaf litter depth was also found to negatively influence seed survival (z = - 3.45, *P* < 0.001). Thus, for both tree species, seeds on logs experienced high levels of seed predation, especially when local seed densities were high. In contrast, such effects of local seed density on predation were not evident for seeds on the ground (Fig.7).

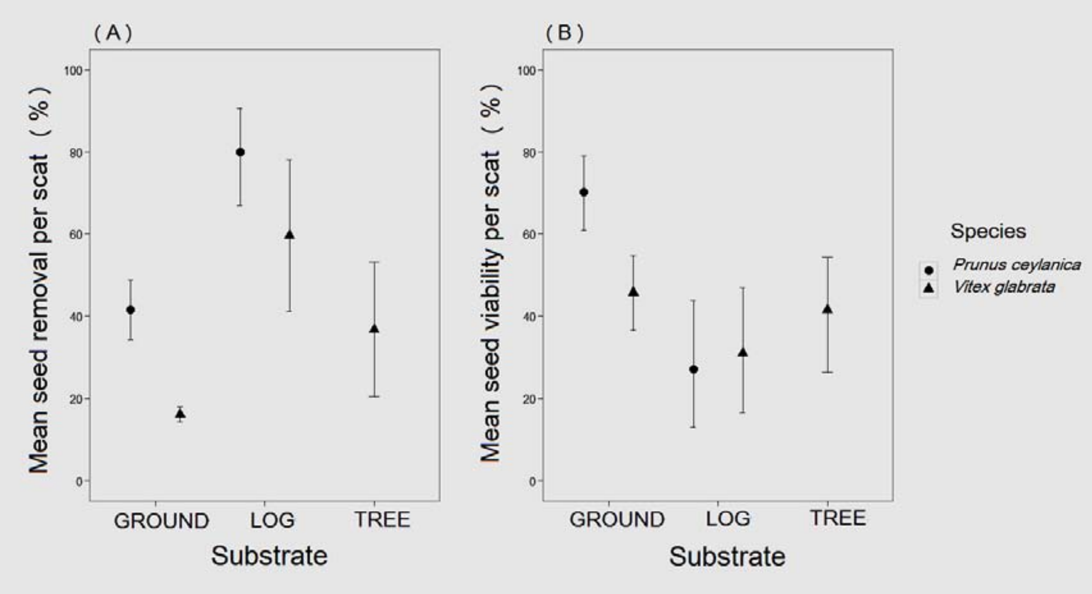


Fig. 6. Seed predation (A) and seed viability (B) on different substrates for *Vitex glabrata* and *Prunus ceylanica*. The points represent the means (% per scat) and the bars represent the 95th percentiles of 1000 bootstrapped means

At the end of the study, all remaining seeds in scats were collected and tested for seed viability. Seed viability varied from 0 percent to 100 percent in both *V. glabrata* and *P. ceylanica*. Overall, mean seed viability was higher in *P. ceylanica* (57.25%) than *V. glabrata* (27.21%). For *V. glabrata*, seed viability did not appear to be affected by substrate, whereas seed viability varied significantly with substrate for *P. ceylanica*, with seeds deposited on logs found to be significantly less viable than those deposited on the ground (Fig. 6 [B]).

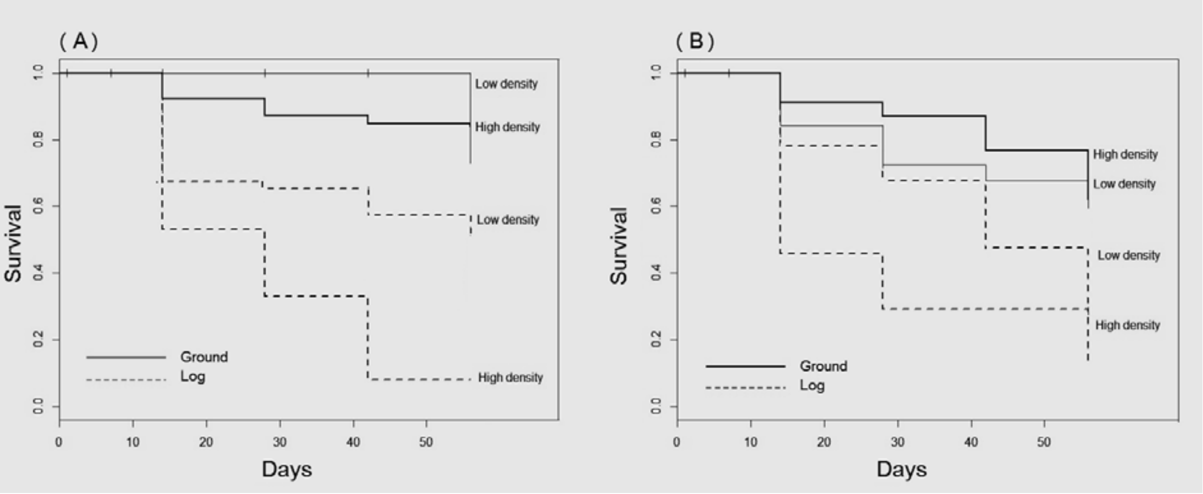


Fig.7. Kaplan–Meier seed survivorship curves (where survival is the probability that a seed escapes predation) for (A) *Vitex glabrata* at low (<50 seeds m^{-2}) and high (> 50 seeds m^{-2}) seed densities and (B) *Prunus ceylanica* at low (<15 seeds m^{-2}) and high (<15 seeds m^{-2}) seed densities. The frequency distributions of observed local seed densities were used to broadly classify low and high seed density categories for the two tree species. Dashed lines represent seeds on log substrates, while unbroken lines represent seeds on the ground. Seed fates for all scats were tracked till the 56th day from the start of monitoring.

Discussion

We found contrasting spatial patterns of civet seed dispersal for two tropical trees within the same tropical forest community. Seeds of *V. glabrata* were dispersed in a relatively large radius around fruiting trees (Fig. 4), with seeds dispersed in the canopy branches of the fruiting tree as well as on the branches of neighbouring trees and lianas. In contrast, seeds of *P. ceylanica* were concentrated into a relatively smaller radius around fruiting trees, with most seeds deposited on the ground below the fruiting tree. We suspect that this variation in dispersal is driven by differences in the way civets access fruits from the two tree species. *V. glabrata* trees branch close to the ground and have an extensive network of canopy branches, often interconnected with neighbouring trees, while *P. ceylanica* typically has a tall smooth trunk, branches far from the ground, and often has a stand-alone canopy that is not connected to neighbouring trees. A simple and intuitive explanation for the variation in feeding behaviour (and as seen from our preliminary observations from camera-trapping) is that differences in the branching architectures of the two tree species caused civets to access fruits from these trees in very different ways. While fruits of *V.glabrata* were eaten on the branches of the tree, seeds of *P.ceylanica* were generally eaten when they had fallen on the ground, as reflected in the different deposition patterns of scats. An alternate possibility could be that civets were responding to some aspect of fruit chemistry. Attached fruits at various stages of ripening differ from fallen fruits in their fruit chemistry, and many animals show preferences for fruits at a specific ripening stage [36,37]. Thus it is possible that *P. ceylanica* fruits that had fallen to the ground were nutritionally preferred to those still attached on the tree. Regardless of the causes, it is likely that this variation in civet foraging behaviour might have caused differences in the seed shadows generated by civets for *V. glabrata* and *P. ceylanica.*

Our methodology for finding civet scats, which included careful searching of both the forest floor and the canopy branches, revealed that seed deposition by civets within the canopy and on the forest floor may often be as significant as deposition on conspicuous logs or 'open' sites. These results contradict the common perception in the literature that civets predominantly defecate seeds in 'conspicuous' or 'open' sites [2,15,23]. As most studies did not specifically search canopies for civet scats, we suspect that this perception is due to higher detection of scats on conspicuous sites like fallen logs. It is also possible that some civets, being highly arboreal, recognise fruiting tree branches as conspicuous sites for scent marking, an artefact of the territorial behaviour exhibited by civets and other frugivorous carnivores [38,39]. The same might apply to scats on fallen logs or culverts.

In our study, seed predation rates were highly influenced by substrate of scat deposition, with seeds on logs experiencing higher rates of predation for both tree species. Increased seed predation on logs may have resulted from greater detection of scats on logs (through either visual or olfactory cues) than of those in the under-storey. A similar pattern of high predation from elevated substrates has been reported in a study of seed fate of a swamp tree *Nyssa aquatica* [40]. In our study site, rodents that use olfactory cues to locate prey [10] are amongst the major seed predators [32]. Olfactory cues from seed piles on logs may have been particularly strong in our study because scat piles on logs typically occurred far from fruiting trees in areas of low seed densities.

In a recent study of seed dispersal by civets on *Leea aculeata* seeds in a Malaysian tropical forest, Nakashima et al. [15] set out seeds experimentally at random locations on the forest floor and in characteristic open sites where civets frequently deposited scat. They found higher seed recruitment at these civet dispersed sites than at random sites, suggesting that civets may sometimes act as agents of directed dispersal and enhance dispersal success [15]. Likewise, Abiyu et al. report a potentially synergistic interaction between the African civet (*Civettictis civetta*) and an Afromontane forest tree, *Mimusops kummel*, where seeds of this species that were deposited in civeteries along open forest edges experienced high germination success [28]. Our study on civet dispersal of *V. glabrata* and *P. ceylanica* seeds showed very different patterns. First, civets deposited scats on a range of substrates, in both closed and open canopy sites, such that we did not find ‘typical’ civet dispersed sites for these tree species. Further, none of these seed deposition sites were associated with enhanced recruitment. On the contrary, both *V. glabrata* and *P. ceylanica* seeds dispersed onto logs, the conspicuous and “open” deposition sites in this study, suffered higher seed predation, and the larger seeds of *P. ceylanica* suffered higher seed mortality on logs and at open sites.

We explored the spatial patterns and post-dispersal seed fates of civet-dispersed seeds of two tropical tree species, but we note that our study was short-term and occurred during a period of low fruit abundance for civets, when *V.glabrata* and *P.ceylanica*, which were not very abundant in the area (< 2.5 trees/ha) [29], were the only civet-dispersed trees fruiting at the time (pers. obs.). We expect that longer term studies in periods when fruit is highly abundant may show different patterns. Further, we did not explore the mechanisms underlying the observed patterns. Future studies that explicitly incorporate the roles of tree architecture and forager behaviour on the dispersal patterns of arboreal non-volant foragers may lead to interesting new insights on the spatial patterns of seed dispersal. We also suggest that detailed studies of how seed traits interact with conditions at deposition sites to influence post-dispersal seed fates are needed to complete our understanding of the trajectory from seed dispersal to successful seed germination. In our study, we treated all civets as a group and thus were unable to differentiate between dispersal services provided by the five species present in this area. Although this approach is valid from the plant-driven perspective of assessing dispersal services provided by this group, it may hide interesting nuances if different civet species differ in where and how far they deposit seeds, and prefer different fruit species.

We show that in this tropical forest, civet-dispersed seeds of *V. glabrata* and *P. ceylanica* differed in their spatial dispersion and in the types of substrates on which they were deposited, most likely a result of different feeding behaviours of civets on these tree species. Our results highlight the large impacts of seed deposition substrate on seed predation and seed viability, together the “*largest demographic filter in the seed to seedling transition*” [41]. As most dispersal away from fruiting trees in our study was onto logs, where seed predation was high and seed viability low for at least one species, civet seed dispersal away from fruiting trees appears to have had low success. Further, none of the civet dispersal sites in this study were associated with either reduced predation or enhanced survival of seeds. These results contrast with those from Nakashima et al. [15] who found enhanced germination success for civet-dispersed seeds for one tropical tree species. Two studies on the African civet (*Civettictis civetta*) report large variation in dispersal services provide by this species, with low germination of dispersed seeds for most tree species, but enhanced germination for one species [27,28]. Together, these studies highlight the large differences in seed dispersal services provided by the same disperser group for different tree species. They suggest that the ability of civets to provide compensatory dispersal services in disturbed forests will differ for different tree species and may often be limited. More generally, such variation cautions against drawing broad generalizations about the dispersal services provided by any disperser group.

Implications for conservation

Our results, in conjunction with other studies, suggest that the effectiveness of civets as seed dispersers is highly variable among species and ecosystems [15,27,28]. In our study, civets were not especially effective seed dispersers for *Vitex glabrata* and *Prunus ceylanica*, indicating that these species of trees must depend on other taxa (such as frugivorous birds) for dispersal services. For endangered trees like *Prunus ceylanica* [42], this can have grave implications for regeneration when other large frugivores have been extirpated.

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References

[1] Howe, H.F., Smallwood, J. Ecology of seed dispersal. *Annual Review of Ecology and Systematics.* 1982;13(1):201–28.

[2] Corlett, R.T. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological reviews of the Cambridge Philosophical Society.* 1998;73(4):413–48.

[3] McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., et al. Seed dispersal in changing landscapes. *Biological Conservation.* 2012;146(1):1–13.

[4] Fragoso, J.M. V. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology.* 1997;85(4):519–29.

[5] Shilton, L.A., Altringham, J.D., Compton, S.G., Whittaker, R.J. Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society B: Biological Sciences.* 1999;266(1416):219.

[6] Jordano, P., García, C., Godoy, J. a, García-Castaño, J.L. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences of the United States of America.* 2007;104(9):3278–82.

[7] Jordano, P., Schupp, E.W. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs.* 2000;70(4):591–615.

[8] Russo, S.E., Augspurger, C.K. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters.* 2004;7(11):1058–67.

[9] McConkey, K.R. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in Central Borneo. *Journal of Tropical Ecology.* 2005;21(3):255–62.

[10] Vander Wall, S.B. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology.* 1998;79(1):233–41.

[11] Gómez, J.M., Puerta-Piñero, C., Schupp, E.W. Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia.* 2008;155(3):529–37.

[12] Datta, A., Rawat, G.S. Foraging Patterns of Sympatric Hornbills during the Nonbreeding Season in Arunachal Pradesh, Northeast India. *Biotropica.* 2003;35(2):208–18.

[13] Martínez, I., García, D., Obeso, J.R. Differential seed dispersal patterns generated by a common assemblage of vertebrate frugivores in three fleshy-fruited trees. *Ecoscience.* 2008;15(2):189–99.

[14] Zhou, Y.-B., Zhang, L., Kaneko, Y., Newman, C., Wang, X.-M. Frugivory and seed dispersal by a small carnivore, the Chinese ferret-badger, *Melogale moschata*, in a fragmented subtropical forest of central China. *Forest Ecology and Management.* 2008;255(5-6):1595–603.

[15] Nakashima, Y., Inoue, E., Inoue-Murayama, M., Abd Sukor, J.R., Sukor, J.R.A. Functional uniqueness of a small carnivore as seed dispersal agents: a case study of the common palm civets in the Tabin wildlife reserve, Sabah, Malaysia. *Oecologia.* 2010;164(3):721–30.

[16] Wang, B.C., Smith, T.B. Closing the seed dispersal loop. *Trends in Ecology & Evolution.* 2002;17(8):379–86.

[17] Mudappa, D., Kumar, A., Chellam, R. Diet and fruit choice of the brown palm civet *Paradoxurus jerdoni* , a viverrid endemic to the Western Ghats rainforest , India. *Tropical Conservation Science.* 2010;3(3):282–300.

[18] Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., et al. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia.* 2002;133(4):559–72.

[19] Zhou, Y., Zhang, J., Slade, E., Zhang, L., Palomares, F., Chen, J., et al. Dietary shifts in relation to fruit availability among masked palm civets (*Paguma larvata*) in central China. *Journal of Mammalogy.* 2008;89(2):435–47.

[20] Ho, W.P. The role of masked palm civet (Paguma larvata) and small indian civet (Viverricula indica) in seed dispersal in hong Kong, China. University of Hong Kong; 2009.

[21] Nakashima, Y., Inoue, E., Inoue-Murayama, M., Sukor, J.A. High Potential of a Disturbance-Tolerant Frugivore, the Common Palm Civet *Paradoxurus hermaphroditus* (Viverridae), as a Seed Disperser for Large-Seeded Plants. *Mammal Study.* 2010;35(3):209–15.

[22] Joshi, A.R., Smith, J.L.D., Cuthbert, F.J. Influence of food distribution and predation pressure on spacing behavior in palm civets. *Journal of Mammalogy.* Allen Press; 1995;76(4):1205–12.

[23] Mudappa, D. Ecology of the Brown Palm Civet *Paradoxurus jerdoni* in the tropical rainforests of the Western Ghats, India. Ph.D Thesis. Bharathiar University; 2001.

[24] Nakashima, Y., Nakabayashi, M., Sukor, J.A. Space use, habitat selection, and day-beds of the common palm civet (Paradoxurus hermaphroditus) in human-modified habitats in Sabah, Borneo. *Journal of Mammalogy.* 2013;94(5):1169–78.

[25] Zhou, Y., Newman, C., Palomares, F., Zhang, S., Xie, Z., Macdonald, D.W. Spatial organization and activity patterns of the masked palm civet *(Paguma larvata)* in central-south China. *Journal of Mammalogy.* 2014;95(3):534–42.

[26] Nakashima, Y., Sukor, J.A. Importance of common palm civets *(Paradoxurus hermaphroditus)* as a long-distance disperser for large-seeded plants in degraded forests. *Tropics.* 2010;18(4):221–9.

[27] Pendje, G. Frugivory of *Civettictis civetta* and its role in seed dispersal at Mayombe. *Revue d'Ecologie la Terre et la Vie.* 1994;49(2):107–16.

[28] Abiyu, A., Teketay, D., Glatzel, G., Gratzer, G. Tree seed dispersal by African civets in the Afromontane Highlands: too long a latrine to be effective for tree population dynamics. *African Journal of Ecology.* 2015;

[29] Datta, A., Rawat, G.S. Dispersal modes and spatial patterns of tree species in a tropical forest in Arunachal Pradesh , northeast India. *Tropical Conservation Science.* 2008;1(3):163–85.

[30] Viswanathan, A., Naniwadekar, R., Datta, A. Seed dispersal by avian frugivores : non-random heterogeneity at fine scales. *Biotropica.* 2015;47(1):77–84.

[31] Wenny, D.G. Seed Dispersal , Seed Predation , and Seedling Recruitment of a Neotropical Montane Tree. *Ecological Monographs.* 2000;70(2):331–51.

[32] Velho, N., Datta, A., Isvaran, K. Effect of rodents on seed fate of five hornbill-dispersed tree species in a tropical forest in north-east India. *Journal of Tropical Ecology.* 2009;25(05):507.

[33] Malone, C.R. A rapid method for enumeration of viable seeds in soil. *Weeds.* 1967;15(4):381–2.

[34] R Development Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria; 2013. Available from: http://www.r-project.org/

[35] Therneau, T., Crowson, C.. Using time dependent covariates and time dependent Coefficients in the cox model. http://cran.r-project.org/web/packages/survival/vignettes/timedep.pdf.; 2013.

[36] Dudley, R. Ethanol, fruit ripening, and the historical origins of human alcoholism in primate frugivory. *Integrative and comparative biology.* 2004;44(4):315–23.

[37] Somanathan, H., Mali, S., Borges, R.M. Arboreal larder-hoarding in the tropical Indian giant squirrel *Ratufa indica*. *Ecoscience.* 2007;14(2):165–9.

[38] Kays, R.W., Gittleman, J.L. The social organization of the kinkajou *Palos flavus* (Procyonidae). *Journal of zoology.* 2001;253:491–504.

[39] Rozhnov, V. V., Rozhnov, Y. V. Roles of Different Types of Excretions in Mediated Communication by Scent Marks of the Common Palm Civet, *Paradoxurus hermaphroditus* Pallas, 1777 (Mammalia, Carnivora). *Biology Bulletin.* 2003;30(6):584–90.

[40] Huenneke, L.F., Sharitz, R.R. Substrate heterogeneity and regeneration of a swamp tree, *Nyssa aquatica*. *American Journal of Botany.* 1990;77(3):413.

[41] Russo, S.E. Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla seeds* in Peru. *Journal of Tropical Ecology.* 2005;21(3):243–53.

[42] World Conservation Monitoring Centre 1998. *Prunus Ceylanica*. *The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>.*

Appendix 1. The percentage of civet scats recorded with seeds of *Vitex glabrata* and *Prunus ceylanica* at each substrate.

Species	Ground (%)	Log (%)	Tree (%)	Liana (%)	Fruiting Tree (%)
Vitex glabrata (N = 69)	4.41	38.23	22.05	16.17	19.11
Prunus ceylanica (N = 101)	73.26	25.74	0	0.9	0