Seed fates of four rainforest tree species in the fragmented forests of Anamalais in the southern Western Ghats, India

Abhishek Gopal [a,b,*], Divya Mudappa [b], TR Shankar Raman [b], Rohit Naniwadekar [b]

[a] Post-Graduate Programme in Wildlife Biology and Conservation, Wildlife Conservation Society-India, National Centre for Biological Sciences, GKVK Campus, Bangalore, 560065, Karnataka, India
[b] Nature Conservation Foundation, 1311, "Amritha", 12th Main, Vijayanagar 1st Stage, Mysore, 570017, Karnataka, India

ARTICLE INFO

ABSTRACT

Seed predation is one of the key ecosystem processes governing the plant population and community structure in forests. Forest fragmentation and habitat loss have been shown to affect seed predation, leading to altered tree recruitment. However, the effects of fragmentation and habitat loss on seed predation are highly variable and context-specific, with limited information from South Asia. For four rainforest tree species in a production landscape of tea and coffee, we examined the influence of forest type (benchmark, $N = 3$, and fragmented, $N = 5$, forests) and seed size on the proportion of seeds, 1) predated by vertebrate seed predators, 2) predated by invertebrate seed predators, and 3) removed by vertebrate seed predators. The seed fates were tracked by placing the seeds in four 1×1 m plots under the canopy of the tree ($N \geq 11$ individuals per tree species and 48 trees overall), and camera traps were placed under a subset of trees ($N = 29$, trap-nights $= 712$). Overall, we recorded nine species of seed predators, and that the seed predator species composition differed among the four tree species. However, there was no significant difference in either seed predator species composition or their visitations across the forest types. The seeds were more likely to be predated (on average 6% higher predation) by vertebrate seed predators in the fragments than in the benchmark forests. Medium-seeded species were more likely to be predated by vertebrate seed predators than large-seeded species (on average 41% higher predation). Invertebrate seed predation and seed removal by vertebrate seed predators had a weak relationship with forest type, with higher invertebrate seed predation in the fragments and higher seed removal in the benchmark forests. With altered seed dispersal patterns resulting from habitat fragmentation and habitat loss, differential seed predation can alter regeneration patterns, thereby influencing adult tree communities in fragmented forests.

1. Introduction

Habitat loss and forest fragmentation are one of the major drivers of biodiversity loss in the tropics (Haddad et al., 2015; Laurance et al., 2011). While forest fragments harbour a significant portion of biodiversity and aid in maintaining diversity at a landscape level (Anand et al., 2010; Turner and Corlett 1996), their long-term conservation value depends on the continuity of key ecological processes. With increasing anthropogenic pressures, the existing tropical forests are likely to become more fragmented and isolated (Haddad et al., 2015; Lewis et al., 2015). Therefore, it is crucial to examine the ecological processes that are likely to be affected by these changes.

Seed predation is one such process, which by reducing the number of seeds that can survive and establish, plays a crucial role in structuring plant populations and plant communities (Crawley, 2000; Germain et al., 2013; Janzen, 1971; Paine et al., 2016). This top-down control can play an essential role in maintaining tree diversity through density-dependent predation by both specialist and generalist seed predators (Comita et al., 2014; Larios et al., 2017; Paine et al., 2016; Terborgh, 2012). Plants respond to seed predation pressures through a diverse suite of physical and chemical defenses (Xiao et al., 2008; Zhang and Zhang 2008; Zhang et al., 2016). While several seed traits influence predation levels, one key trait that mammalian seed predators respond to is seed size (Lichti et al., 2017; Sidhu and Datta, 2015; Wang and Chen 2009; Wang et al., 2013). Through differential predation on large-seeded species (Chen et al., 2017; Sidhu and Datta, 2015), they can

---

reduce their fitness advantage and potentially favour the regeneration of small-seeded species.

Although forest fragmentation has been shown to affect seed predation, the magnitude and the direction of its impact on plants is highly variable and context-specific. This is evident from studies which show either higher seed predation (Aliyu et al., 2014; Donoso et al., 2004; Mendes et al., 2016) or lower seed predation (Hanson et al., 2006; Wright and Duber, 2001) or no difference in seed predation (Farwig et al., 2008; Zambrano et al., 2015) in fragmented forests. These differences are likely due to the differences in the corresponding plant-animal systems, and the fragment and matrix characteristics studied in the different sites. Additionally, one key factor driving these contrasting results is the shift in specialist and generalist seed predator communities after fragmentation (Arce-Peña et al., 2019; Mendes et al., 2016; Palmer and Catterall, 2018; Soares et al., 2015). Small mammalian seed predators have also been shown to cache seeds, leading to secondary dispersal (Jansen et al., 2012), and in some cases partially compensating for the loss of primary frugivores in defaunated forest fragments (Cao et al., 2011). The influence of fragmentation on the seed predator community and the subsequent shift in the seed predator assemblage can influence the spatial template of seeds in the forests via altered predation and displacement of seeds. In dispersal-limited fragmented forests, such altered plant-seed predator interactions along with the abiotic factors can potentially lead to an altered trajectory of regeneration.

The Western Ghats mountain chain in India is a global biodiversity hotspot having a high level of richness and endemism of various taxa (Myers et al., 2000; Kumar et al., 2004). Despite being a vital eco-region, it faces severe anthropogenic pressures, resulting in a loss of forest cover and an increase in fragmentation of forested habitats (Jha et al., 2000; Krishnadas et al., 2018; Nayak et al., 2020). Currently, the majority of the forests in the Western Ghats exist as fragments interspersed in human-modified landscapes. There are very few studies from South Asia and from this region examining seed predation in the context of fragmentation. In a production landscape of tea and coffee plantations, interspersed with rainforest fragments, we compared the seed fates of four rainforest bird-dispersed tree species (two large-seeded species and two medium-seeded species) between the benchmark forests ($N = 3$) and the fragmented forests ($N = 5$) under the canopy of the tree. The specific aims of the study were, 1) to document the seed predator assemblage for the four tree species and across the forest types, 2) to examine if there is any difference in the visitation rates of seed predators across forest types, and 3) to examine the influence of forest type and seed size on seed predation by vertebrate and invertebrate seed predators, and on seed removal by vertebrate seed predators. A study by Osuri et al. (2017) in this landscape, shows that these fragments are dispersal limited, especially for bird-dispersed old-growth tree species, primarily due to the lower densities of large-bodied avian frugivores in the fragments (Raman, 2006). A recent study has also demonstrated lower visitation rates of frugivores for certain tree species (Gopal et al., 2020a). Additionally, Kumar et al. (2002) report higher richness and abundance of rodents in the fragments due to invasion of commensal species from the surrounding matrix. Sridhar et al. (2008) also reports higher mean densities of some large-bodied seed predators in the fragments. As such, we expected more generalist seed predators and higher visitations of seed predators in the fragments. Given the reduced seed dispersal and a shift in the seed predator composition, we examined if trees in the fragments were more likely to face higher seed predation, and if seed predation was influenced by seed size.

2. Methods

2.1. Study area

The study was conducted on the Valparai Plateau (220 km², 10°15′–10°22′N, 76°52′–76°59′E) and in the Anamalai Tiger Reserve (958 km², 10°12′–10°35′N, 76°49′–77°24′E) in the southern Western Ghats, India (Supplementary Fig. 1). The study area has an undulating terrain ranging from 600 to 1400 m above mean sea level. It receives an average of 2500 mm of rainfall annually, and the majority of it falls during the south-west monsoon from June to September (Rathod and Aruchamy, 2010). The natural vegetation is classified as mid-elevation tropical wet evergreen forests of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type (Pascal et al., 2004). The plateau is mainly a production landscape of tea and shade coffee interspersed with rainforest fragments of varying sizes (1–300 ha) on privately-owned land and is surrounded by relatively undisturbed forests within Protected Areas (Supplementary Fig. 1). The forests in this landscape have a long history of extraction and disturbance (since the late 1800s) in terms of logging for timber, and clearing and conversion of forested lands for plantations (Mudappa and Raman, 2007). For further information about the study site and detailed history of the landscape, refer to Mudappa and Raman (2007). Here, in three benchmark forest sites (Iyerpadi-Akkamalai, Manamboli, Panathiar) and five forest fragments (Andiparai, Iyerpadi-Akkamalai, Old Valparai, Candura, Varuttuparai), we examined the seed fate of four rainforest bird-dispersed tree species (Supplementary Fig. 1; Supplementary Table 1). We classified five trees that were in benchmark forests (Andiparai and Iyerpadi-Akkamalai) as being in forest fragments as they were close to the road and a tribal settlement (10 − 30 m; HETR09, CAST01, CAST08, PEMA04, and PEMA05; Supplementary Table 1).

2.2. Study species

The tree species were classified as medium-seeded (seed width ≤ 1.5 cm and seed length ≤ 3 cm) or large-seeded (seed width > 1.5 cm and seed length > 3 cm) following Naniwadekar et al. (2019). Two large-seeded tree species, *Canarium strictum* and *Myristica dactyloides* (Burseraceae, mean $\pm$ SE seed width $= 1.82 \pm 0.02$ cm, mean $\pm$ SE seed length $= 4.02 \pm 0.04$ cm, $N = 110$ and Myristicaceae, mean $\pm$ SE seed width $= 2.38 \pm 0.01$ cm, mean $\pm$ SE seed length $= 3.69 \pm 0.04$ cm, $N = 109$, respectively), and two medium-seeded tree species, *Heynea trijuga* and *Persea macrantha* (Meliaceae, mean $\pm$ SE seed width $= 1.30 \pm 0.01$ cm, mean seed length $= 1.19 \pm 0.01$ cm, $N = 113$ and Lauraceae, mean seed width $\pm$ SE $= 1.25 \pm 0.01$ cm, mean seed length $\pm$ SE $= 0.93 \pm 0.01$ cm, $N = 139$, respectively), hereafter referred by their respective genera, were selected for the study. These tree species were selected based on their relative abundance, fruiting period and seed sizes (Muthuramkumar et al., 2006; NCF − ARP unpubl. data; Osuri et al., 2017). For furtherdetails about the selected tree species, please see Gopal et al. (2020a).

2.3. Field methods

This study was conducted between November 2017 and May 2018. We selected at least 11 individual trees per species that were spread across the benchmark and forest fragments (Table 1; Supplementary Fig. 1; Supplementary Table 1). The benchmark forests are relatively contiguous and are protected whereas the forest fragments are primarily on private lands owned by plantation companies (Supplementary Fig. 1). While both forest types face disturbance in terms of firewood collection, non-timber forest produce collection, and pole cutting, the fragments are relatively more disturbed as compared to the benchmark forests (Muthuramkumar et al., 2006). We identified the trees through field surveys and prior knowledge of existing trees in the landscape. The trees chosen were not randomly located but were selected based on their distribution with respect to forest type and ease of access for monitoring.

Ripe fruits were selected from under the fruiting tree during the peak fruiting season of each tree species, and the pulp or aril was cleaned with a clean, dry cloth and air-dried to obtain seeds. As we were often unable to find enough fruits under the fruiting trees, we collected seeds from under different trees from which a randomly picked set of seeds were

Table 1

The details of the sampling effort and the number of days seeds were monitored for the four tree species.

Tree species	Number of trees		Number of plots	Number of seeds	Days monitored	
	Benchmark	Fragments			Min	Max
Canarium strictum	4	7	44	440	67	162
Myristica dactyloides	6	7	52	520	9	40
Heynea trijuga	5	6	44	440	14	138
Persea macrantha	8	5	52	520	24	44
Total	**23**	**25**	**192**	**1920**	—	—

placed under the focal trees. To assess the viability of seeds, they were visually examined for signs of predation and subjected to a water flotation test.

Under the canopy of the fruiting tree (~1–2 m from the base of the trunk), in four cardinal directions, four 1 × 1 m plots were cleared of leaf litter, and 10 seeds marked with a non-toxic marker were tagged and placed in each plot to monitor the seed fate (minimum distance between the plots was 2 m). All the seed plots were laid within the fruiting period of the respective tree species. Seeds were tagged using a 50 cm long Dacron fishing line attached to the seed surface with a non-toxic super glue (Loctite® Super Glue Ultra Gel™) to track cached seeds by seed predators following methods outlined in Sidhu and Datta (2015).

Camera traps were placed under a subset of trees (N = 29 trees) in the benchmark and fragmented forests to determine the seed predator assemblage and the visitation rates (Table 2; Supplementary Table 1). We had a limited number of camera traps, six Reconyx HC500 and four Moultrie M-990i, and these were placed randomly in one of the four plots per tree under the canopy. The camera traps were placed until all the seeds were removed from the plot or for a minimum of three weeks (Table 2). The uneven sampling is primarily due to the malfunctioning of some of the camera traps and camera displacements by large mammals.

The plots were monitored every 7–10 days except in the case of three trees of *Myristica* (MYDA11, MYDA12, and MYDA13) and *Persea* (PEMA11, PEMA12, and PEMA13), which were monitored only at the start and at the end of the study as they were in a remote area and weekly monitoring was not possible (Supplementary Table 1). Additionally, for *Canarium*, three trees (CAST09, CAST10, and CAST11) were monitored weekly for the first two months from the start of the study in November and less frequently (at least twice a month) after that until the end of the study period in May because of logistical constraints (Supplementary Table 1). During each visit, we recorded the following seed fates, 1) intact – when seeds showed no signs of predation (vertebrate or invertebrate predation); 2) vertebrate predation – when seeds had visible bite marks, or when there were remains of the eaten seeds; 3) invertebrate predation – when seeds had a hole in them, typically caused by weevils and beetle borers; 4) removed – seeds missing from the plots were classified as removed; 5) dead – when the seeds were spoilt or were shrivelled up due to desiccation; and 6) germinated – when there was

radicle emergence. Whenever seeds were missing from the plot, two observers searched for the seeds in a radius of 10 m around the plot following the method of Sidhu and Datta (2015). Away from the plot, we found tags with no evidence of seed predation. These could be mostly due to seed predators removing the tags and either caching the seeds or eating the seeds at safe sites at distances greater than 10 m.

The maximum number of days the plots were monitored for *Canarium*, *Myristica*, *Heynea*, and *Persea* were 162, 40, 138, and 44, respectively (Table 1). For *Persea* and *Myristica,* as the peak fruiting period was only in April, the plots could not be monitored for a longer duration, and the seeds were removed at the end of the study period in May after 40–44 days (Table 1). However, at the end of the monitoring period, only a small proportion of seeds (0.07, N = 520 seeds, for *Persea;* 0.05, N = 520 seeds, for *Myristica*; Table 3) were intact. This is unlikely to change the overall results of the study.

Away from the plot, we mostly found instances of just tags being present and the seeds missing with very few visible signs of predation. It is likely that the rodents would have removed the tags before transporting the seeds, for either caching or for eating at the feeding sites, as has been reported by Sidhu and Datta (2015). Hence, we considered this as the primary displacement of the seeds with the fates of the seeds being unknown; following Vander Wall (2010), we do not infer seed predation. We examined if there was any difference in the displacement distance of the seeds across forest types for each tree species.

Table 3

Proportion of seeds that were intact, predated and removed for the four tree species.

Tree species	Intact	Predated		Removed
		Vertebrate	Invertebrate	
Canarium strictum (N = 440)	0.89	0.06	0.01	0.04
Myristica dactyloides (N = 520)	0.05	0.14	0.31	0.49
Heynea trijuga (N = 440)	0.00	0.45	0.00	0.55
Persea macrantha (N = 520)	0.07	0.56	0.30	0.06
Overall (N = 1920)	**0.24**	**0.31**	**0.17**	**0.28**

Table 2

Summary of the camera trap sampling effort and the number of visits by large-bodied (>1 kg) and small-bodied (≤1 kg) seed predators for each of the four tree species is shown.

Tree species	Number of trees		Trap-nights			Visitor species type	Total visits	Mean ± SD visits trap-night^{-1}
	Benchmark	Fragments	Total	Min	Max			
Canarium strictum	2[a]	4	267	28	65	Large-bodied	64	0.24 ± 0.30
						Small-bodied	122	0.51 ± 0.53
Heynea trijuga	4	5	173	4	54	Large-bodied	66	0.45 ± 0.48
						Small-bodied	320	4.00 ± 4.21
Myristica dactyloides	4	4	124	5	27	Large-bodied	38	0.29 ± 0.37
						Small-bodied	187	1.88 ± 1.50
Persea macrantha	5	1[a]	148	4	42	Large-bodied	25	0.23 ± 0.16
						Small-bodied	87	0.45 ± 0.74
Total	**15**	**14**	**712**	—	—	—	**909**	—

[a] Equal number of camera traps were placed in the benchmark and fragmented forests. However, camera trap malfunctioning and displacement by wild animals resulted in an unbalanced effort.

2.4. Analysis

To examine if the visitations of seed predators differed between forest types, we used a generalized linear mixed model (GLMM) framework with a Poisson error structure and tree species as random intercept. We used the offset function, which is the log-transformed observation effort, to account for variable trap-nights.

To examine the differences in species composition of the seed predators visiting the focal trees across the forest type, we used non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity metric from the "vegan" package in R 3.5.2 (Oksanen et al., 2019; R Core Team, 2018). The visits per focal tree were standardized by the total visits to the respective tree species to account for variable trap effort among the four tree species (Table 2). The difference in community composition was tested with a permutation test (999 permutations, using the function 'Adonis' in R package "vegan"; R Core Team, 2018; Oksanen et al., 2019).

To examine the influence of forest type and seed size on the proportion of seeds 1) predated by vertebrate seed predators, 2) predated by invertebrate seed predators, and 3) removed by vertebrate seed predators, we used GLMM with a binomial error structure and tree species as random intercept. As the primary focus of the study was on comparing the seed fate between the forest types, the seed fate information was pooled from the four plots laid out under the tree (controlling for the potential correlations between the plots), and the data were analysed at the level of the individual tree with tree species as a random intercept. In the case of overdispersion, observation-level random effect was included in the model. The goodness of fit of the GLMM to the data was evaluated by calculating marginal R^2 and conditional R^2 (Nakagawa and Schielzeth, 2013). Additionally, we examined the primary displacement of the seeds from the plots and whether it varied with respect to forest type for each tree species using a linear model. All the analysis was done in R (R Core Team, 2018) using the following packages, "tidyverse" (Wickham, 2017), "MuMIn" (Barton, 2019), and "lme4" (Bates et al., 2015).

3. Results

3.1. Seed predator composition and visitations across the forest type

Overall, we recorded 909 visits by nine species of seed predators in 712 camera trap-nights placed under 29 trees (Table 2, Supplementary Table 2). Among the small-bodied seed predators (body mass ≤ 1 kg), Jungle-striped squirrel (*Funambulus tristriatus*), Murid sp1, Murid sp2, Malabar spiny dormouse (*Platacanthomys lasiurus*), and Sahyadris forest rat (*Rattus satarae*), the most frequent visits were by the Sahyadris forest rat (48% of the total 909 visits) followed by the Jungle-striped squirrel (21% of the total 909 visits). These seed predators were the most frequent visitors both in the benchmark and in the fragmented forests. Among the large-bodied seed predators (body mass > 1 kg), Indian porcupine (*Hystrix indica*), Indian spotted chevrotain or Mouse deer (*Moschiola indica*), Indian muntjac or Barking deer (*Muntiacus muntjak*), and Wild pig (*Sus scrofa*), the most frequent visitors were the Indian spotted chevrotain (11% of the total 909 visits) in the benchmark forests and the Barking deer (9% of the total 909 visits) in the forest fragments. For the large-seeded *Canarium* and *Myristica,* the most frequent visitations were by the Jungle-striped squirrel (43% of total 186 visits and 44% of total 225 visits, respectively; Supplementary Table 2). For the medium-seeded *Heynea* and *Persea,* the most frequent visits were by the Sahyadris forest rat (79% of total 386 visits and 67% of total 112 visits, respectively; Supplementary Table 2). However, there was no statistical difference in overall visitations of seed predators between the two forest types (Supplementary Table 3).

The results of the 'Adonis' analysis showed that there was a significant difference in the seed predator composition for the four tree species, $R^2 = 0.34$, $p = 0.001$, and stress $= 0.18$, with *Myristica* and *Heynea,* having the most distinct communities, and *Canarium* and *Persea* having

an overlapping seed predator community and being "in-between" the former two species (Fig. 1). However, there was no significant difference in the seed predator community composition between the benchmark and fragmented forests ($R^2 = 0.02$, $p = 0.7$).

3.2. Seed fates

The seed fates of 1920 seeds of four rainforest tree species across 48 trees were tracked. Overall, around 48% of the seeds were predated (31% by vertebrate and 17% by invertebrate seed predators; Table 3). Among the four tree species, the large-seeded *Canarium* had the least predation, with almost 90% of the seeds remaining intact. In contrast, the medium-seeded *Persea* had the highest predation with 86% of the seeds being predated both by vertebrate and invertebrate seed predators. The large-seeded *Myristica* had the highest predation by invertebrate seed predators, whereas the medium-seeded *Heynea* had no predation by invertebrates (Table 3). Almost 50% of the seeds of *Heynea* and *Myristica* were removed (Table 3). Only 0.01% (5 seeds) seeds of *Persea* were dead, and seed germination of 0.01% (overall) was recorded onsite over the study period (2 seeds of *Canarium*, and 5 seeds each of *Myristica* and *Persea* had germinated).

The results of the GLMM for the proportion of seeds predated by vertebrates showed that seeds were more likely to be predated in the fragmented forests, on average 6% higher predation than in benchmark forests. Medium-seeded species were more likely to be predated, on average 41% higher predation than the large-seeded species (Fig. 2A; Table 4). The marginal and conditional R^2 were 0.31 and 0.34, respectively (Table 4), indicating a moderate fit and inter-species variation in the proportion of seeds predated (Supplementary Fig. 2A).

Although the difference in invertebrate predation was significant across forest type, the low marginal R^2 indicates that the variation in invertebrate predation explained by forest type was limited (Fig. 2B; Table 4; Supplementary Fig. 2B).

Similarly, in the case of seed removal, while the seeds were more likely to be removed in the benchmark forests (Fig. 2C; Table 4), the low marginal and moderate conditional R^2 indicated a limited influence of
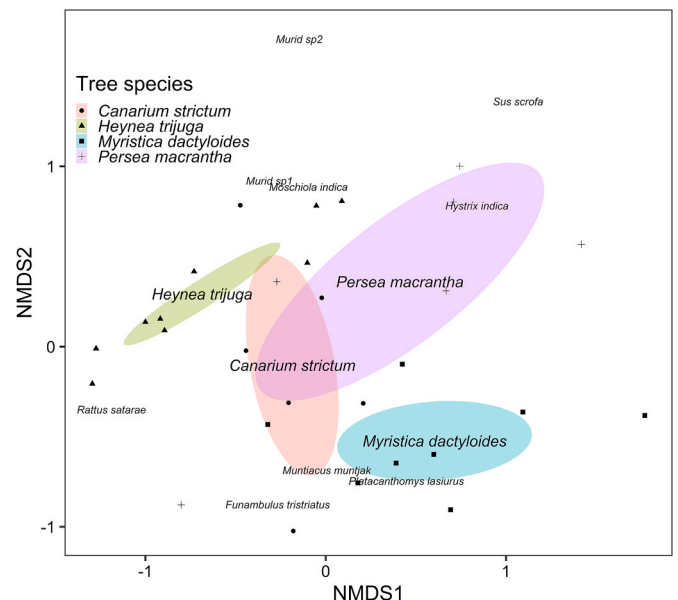

Fig. 1. Species composition of the seed predators that visited the four tree species. *Heynea* and *Myristica* have the most distinct communities, and there is an overlap in seed predator communities between *Canarium* and *Persea*. Each point represents the focal trees where the camera traps were placed and the ellipses correspond to the 95% confidence interval based on the standard error. *Canarium* and *Myristica* are large-seeded, and *Heynea* and *Persea* are medium-seeded tree species.
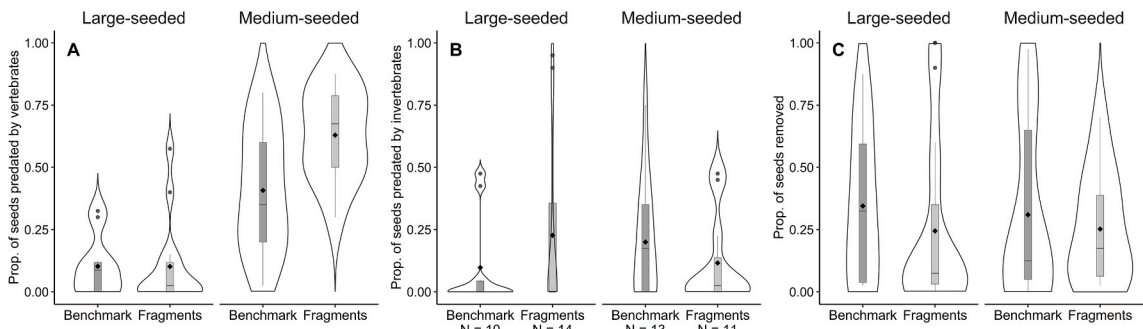
Fig. 2. Violin plots showing the seed fates with respect to seed size and forest type. (A) Proportion of seeds predated by vertebrate seed predators, (B) proportion of seeds predated by invertebrate seed predators, and (C) proportion of seeds removed by vertebrate seed predators. *Canarium* and *Myristica* are large-seeded, and *Heynea* and *Persea* are medium-seeded tree species. The shape of the violin plots are determined by kernel density estimation with wider areas corresponding to higher proportion of the data. Embedded within the violin plots are boxplots indicating the medians and the quartiles, the whiskers indicate 1.5 times the inter-quartile range and the diamonds represent the mean value. The *N* in the figure corresponds to the number of trees in each forest type (Benchmark, *N* = 3 sites, and Fragments, *N* = 5 sites).

Table 4
Results of the generalized linear mixed model with binomial error structure examining the influence of forest type and seed size (large- and medium-seeded) on the seed fates with tree species as random intercept. Also shown are the coefficients with 95% lower and upper confidence limits (LCL & UCL) and the conditional and marginal R^2 of the models. Parameter coefficients whose 95% confidence limits do not overlap zero have been highlighted in bold.

Model	Intercept: Benchmark and Large-seeded	Forest type: Fragment	Seed size: Medium	Marginal R^2	Conditional R^2
(a) Proportion of seeds predated by vertebrate seed predators					
Forest type + Seed size + (1|Tree species)	−2.79 (−3.60 − −2.04)	**0.77 (0.54 − 1.00)**	**2.45 (1.40 − 3.55)**	0.31	0.34
(b) Proportion of seeds predated by invertebrate seed predators					
Forest type + Seed size + (1|Tree species)	−3.08 (−7.49 − 1.26)	**0.52 (0.25 − 0.79)**	−0.62 (−6.98 − 5.47)	0.02	0.63
(c) Proportion of seeds removed by vertebrate seed predators					
Forest type + Seed size + (1|Tree species)	−1.23 (−4.03 − 1.55)	**−0.65 (−0.89 − −0.41)**	0.24 (−3.70 − 4.19)	0.02	0.43

forest type on seed removal and high variation among tree species (Table 4; Supplementary Fig. 2C).

We did not find evidence of caching for the focal tree species. However, we found anecdotal evidence of *Canarium* and *Myristica* seeds cached near the respective tree species' buttresses. Furthermore, we documented one case of the seeds of *Heynea* being cached in a tree hollow of a non-native tree, *Grevillea robusta,* commonly used as a shade tree in tea plantations in this landscape.
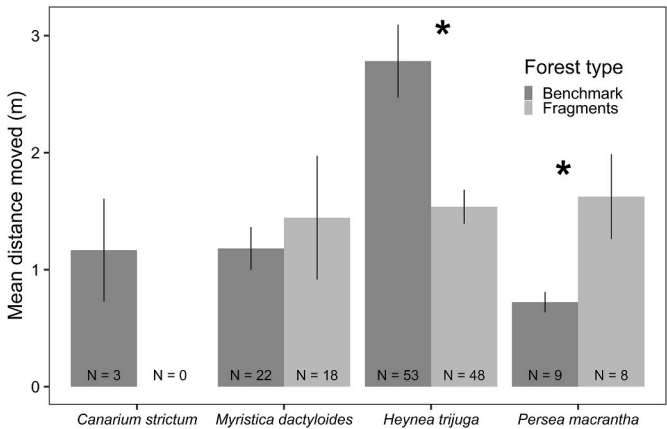
We found 161 instances of primary displacement of the seeds from the plot (Fig. 3). However, for all the tree species, the primary

Fig. 3. Displacements (mean ± SE) of the seeds from the plot. Median (range) displacement in the benchmark sites was 1 m (0.5–10 m), and in the fragments was 1 m (0.3–10 m). There was no displacement of seeds of *Canarium strictum* in the forest fragments. * indicates a statistically significant difference between forest types (*P* < 0.05). The *N* in the figure corresponds to the number of instances of the displacement of the seeds from the plot.

displacement of the seeds was less than 2 m (except in the case of *Heynea* in the benchmark forests), suggesting a limited role of dispersal by rodents for these tree species in the study site (Fig. 3; Supplementary Table 4).

4. Discussion

We found evidence for higher predation by vertebrate seed predators and weak evidence for higher seed predation by invertebrate seed predators in the forest fragments compared to the benchmark forests. Furthermore, the medium-seeded species were more likely to be predated by vertebrate seed predators than the large-seeded species. Although more seeds were removed in the benchmark forests, the relationship of seed removal with forest type was weak. The seed predator species composition differed among the four tree species, but there were was no influence of forest type on species composition and visitations.

The results of seed predation studies in fragmented forests are highly variable, with studies showing an increase (Aliyu et al., 2014; Donoso et al., 2004; Mendes et al., 2016), decrease (Hanson et al., 2006; Wright and Duber, 2001), or no change in predation level (Farwig et al., 2008; Zambrano et al., 2015). One key reason for this contrasting response is the differential response of specialist and generalist seed predators to fragmentation (Arce-Peña et al., 2020; Mendes et al., 2016). A previous study in this landscape has documented an increase in overall abundance and species richness of rodents due to the invasion of commensal species such as *Mus* spp. and *Golunda ellitoti* due to fragmentation (Kumar et al., 2002). The invasion was facilitated by the proximity to human settlements and the influence of the adjoining matrix (coffee, tea, cardamom plantation, etc.) and habitat disturbance (logging and lopping). Sridhar et al. (2008) also report a higher mean density of Indian spotted chevrotain and Indian muntjac in these fragments. Due to limited camera trapping effort, we probably did not detect the difference

in species composition between the forest types. In addition, we documented that rodents are the primary agents of seed mortality for these tree species in this study site except for *Myristica*, which had higher seed predation by invertebrates.

Interestingly, Malabar spiny dormouse, a rare rodent species, endemic to the Western Ghats (Kumar et al., 2002; Mudappa et al., 2001), was the fourth most frequent visitor to the seed plot in both the forest types. The species is sensitive to habitat alteration (Jayson, 2006; Mudappa et al., 2001), but also occurs in coffee agroforests (Sinu, 2012). Although it fed exclusively on *Myristica* during our study period, it has also been reported to feed on *Persea* in a different study site (Jayson, 2006) in the southern Western Ghats. It is an arboreal species and was frequently recorded on camera traps carrying *Myristica* seeds up tree trunks. Camera trap videos also documented predation events by Indian muntjac, which are reported as seed dispersers elsewhere (Prasad et al., 2004). Malabar giant squirrel (*Ratufa indica*) and Nilgiri langur (*Semnopithecus johnii*) are the known arboreal pre-dispersal seed predators, which we did not consider in our study as we were interested in examining seed fates on the forest floor.

Caching and secondary dispersal have been reported in other sites in the tropics (Cao et al., 2011; Chen et al., 2017; Sidhu and Datta 2015), but we did not find any evidence of caching and found only tags away from the plot. The mean distance of the primary displacement of seeds in the benchmark and the fragmented forest was primarily less than 2 m. Consequently, rodents may disperse the seeds under the canopy of the parent tree itself and only a small proportion of seeds are likely to be taken beyond the canopy of the tree. However, as 28% (of the total 1920) of seeds were removed, it is also possible that some of the seeds were cached at distances greater than 10 m. It needs to be further examined how prevalent dispersal by rodents is in this landscape, and if rodents can complement and partially compensate for the loss in dispersal services by primary dispersers in the fragmented forests (Gopal et al., 2020a; Osuri et al., 2017).

One key trait that influences predation by small mammals, especially rodents, is seed size, as larger seeds are likely to have higher nutritional content (Lichti et al., 2017; Wang and Chen 2009; Wang et al., 2013). In this study, we found an opposite trend, with medium-seeded species more likely to be predated than the large-seeded species. This is in line with a recent review by Dylewski et al. (2020), which shows that small-seeded species are more likely to be predated by small mammalian seed predators in the tropics. However, as the results are for only four tree species, and except for *Canarium* all the other species have softer seed coats, it needs to be examined further if these trends hold at the larger community level. Additionally, other studies have also reported lower predation for *Canarium* and have attributed it to its hard seed coat (Ganesh and Davidar, 2005; Sidhu and Datta 2015, in the case of *Canarium resiniferum*).

This study complements a previous study in the same landscape that showed that while the dispersal services were less likely to be affected for the large-seeded *Myristica*, they were more likely to be affected for the medium-seeded *Persea* on trees with low surrounding forest cover (Gopal et al., 2020a). With compromised seed dispersal and higher seed predation in fragments, altered recruitment patterns in fragments can be expected. Forest fragments are also likely to have altered microhabitat conditions (Haddad et al., 2015; Laurance et al., 2011). Thus, alteration in dispersal and post-dispersal processes will likely affect recruitment patterns of trees in the long-term. Due to logistical constraints, very few studies have examined the role of mammalian predation at the community level (but see Blate et al., 1998; Paine et al., 2016), even fewer so in the context of fragmentation. This study too focuses on four bird-dispersed tree species during a single fruiting season. A community-wide study over an extended period and covering additional sites would help substantiate the results found in this study. Furthermore, while not a trivial task, linking the various initial stages of the seed dispersal cycle (Wang and Smith, 2002) to plant establishment, especially in forest fragments, can give us key insights into the trajectory of regeneration in fragmented forests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2020.103698.

References

Aliyu, B., Adamu, H., Moltchanova, E., Forget, P.M., Chapman, H., 2014. The interplay of habitat and seed type on scatter hoarding behavior in a fragmented Afromontane forest landscape. Biotropica 46 (3), 264–267.

Anand, M.O., Krishnaswamy, J., Kumar, A., Bali, A., 2010. Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: remnant forests matter. Biol. Conserv. 143 (10), 2363–2374.

Arce-Peña, N.P., Arroyo-Rodríguez, V., San-José, M., Jiménez-González, D., Franch-Pardo, I., Andresen, E., Ávila-Cabadilla, L.D., 2019. Landscape predictors of rodent dynamics in fragmented rainforests. Biodivers. Conserv. 28 (3), 655–669.

Barton, K., 2019. MuMIn: Multi-Model Inference. R Package version 1.43.6. https://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1), 1–48.

Blate, G.M., Peart, D.R., Leighton, M., 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. Oikos 82, 522–538.

Cao, L., Xiao, Z., Guo, C., Chen, J., 2011. Scatter-hoarding rodents as secondary seed dispersers of a frugivore-dispersed tree *Scleropyrum wallichianum* in a defaunated Xishuangbanna tropical forest, China. Integr. Zool. 6 (3), 227–234.

Chen, Q., Tomlinson, K.W., Cao, L., Wang, B., 2017. Effects of fragmentation on the seed predation and dispersal by rodents differ among species with different seed size. Integr. Zool. 12 (6), 468–476.

Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M., Beckman, N., Zhu, Y., 2014. Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. J. Ecol. 102, 845–856.

Crawley, M.J., 2000. Seed Predators and Plant Population Dynamics. In: second ed. Fenner, M. (Ed.), Seeds: the Ecology of Regeneration in Plant Communities. CAB International, Oxon, pp. 167–182.

Donoso, D.S., Grez, A.A., Simonetti, J.A., 2004. Effects of forest fragmentation on the granivory of differently sized seeds. Biol. Conserv. 115 (1), 63–70.

Dylewski, Ł., Ortega, Y.K., Bogdziewicz, M., Pearson, D.E., 2020. Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecol. Lett. 23 (6), 1024–1033.

Farwig, N., Bleher, B., von der Gönna, S., Böhning-Gaese, K., 2008. Does forest fragmentation and selective logging affect seed predators and seed predation rates of *Prunus africana* (Rosaceae)? Biotropica 40 (2), 218–224.

Ganesh, T., Davidar, P., 2005. Fruiting Phenology and Pre-dispersal Seed Predation in a Rainforest in Southern Western Ghats, IndiaDew, J.L., Boubli, J.P. (Eds.), In: Tropical Fruits and Frugivores: the Search for Strong Interactors. Springer, Dordrecht, pp. 139–154.

Germain, R.M., Johnson, L., Schneider, S., Cottenie, K., Gillis, E.A., MacDougall, A.S., 2013. Spatial variability in plant predation determines the strength of stochastic community assembly. Am. Nat. 182 (2), 169–179.

Gopal, A., Mudappa, D., Raman, T.R.S., Naniwadekar, R., 2020a. Forest cover and fruit crop size differentially influence frugivory of select rainforest tree species in Western Ghats, India. Biotropica 52 (5), 871–883.

Gopal, A., Mudappa, D., Raman, T.R.S., Naniwadekar, R., 2020b. Seed fates of four rainforest tree species in the fragmented forests of Anamalais in the southern Western Ghats, India. Dryad Digital Repository. https://doi.org/10.5061/dryad.qv9s4mwd5.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1 (2), e1500052.

Hanson, T., Brunsfeld, S., Finegan, B., 2006. Variation in seedling density and seed predation indicators for the emergent tree *Dipteryx panamensis* in continuous and fragmented rain forests. Biotropica 38 (6), 770–774.

Jansen, P.A., Hirsch, B.T., Emsens, W.J., Zamora-Gutierrez, V., Wikelski, M., Kays, R., 2012. Thieving rodents as substitute dispersers of megafaunal seeds. Proc. Natl. Acad. Sci. 109 (31), 12610–12615.

Janzen, D.H., 1971. Seed predation by animals. Annu. Rev. Ecol. Systemat. 2 (1), 465–492.

Jha, C.S., Dutt, C.B.S., Bawa, K.S., 2000. Deforestation and land use changes in Western Ghats, India. Curr. Sci. 79, 231–238.

Jayson, E.A., 2006. Status, Distribution, Food and Feeding of Malabar Spiny Dormouse (*Platacanthomys lasiurus* Blyth) in the Western Ghats of Kerala. Kerala Forest Research Institute, Peechi. Final Report of the Research Project KFRI/378/02. KFRI Research Report No. 293.

Krishnadas, M., Agarwala, M., Sridhara, S., Eastwood, E., 2018. Parks protect forest cover in a tropical biodiversity hotspot, but high human population densities can limit success. Biol. Conserv. 223, 147–155.

Kumar, A., Chellam, R., Choudhury, B.C., Mudappa, D., Vasudevan, K., Ishwar, N.M., Noon, B.R., 2002. Impact of Rainforest Fragmentation on Small Mammals and Herpetofauna in the Western Ghats, South India. Wildlife Institute of India, Dehradun, vii+, p. 146. WII-USFWS Collaborative Project Final Report.

Kumar, A., Pethiyagoda, R., Mudappa, D., 2004. Western Ghats and Sri Lanka. Hotspots revisited — Earth's biologically richest and most endangered ecoregions. CEMEX, Mexico 152–157.

Larios, L., Pearson, D.E., Maron, J.L., 2017. Incorporating the effects of generalist seed predators into plant community theory. Funct. Ecol. 31 (10), 1856–1867.

Laurance, W.F., Camargo, J.L., Luizão, R.C., Laurance, S.G., Pimm, S.L., Bruna, E.M., Stouffer, P.C., Williamson, G.B., Benítez-Malvido, J., Vasconcelos, H.L., Van Houtan, K.S., Zartman, C.E., Boyle, S.A., Didham, R.K., Andrade, A., Lovejoy, T.E., 2011. The fate of Amazonian forest fragments: a 32-year investigation. Biol. Conserv. 144 (1), 56–67.

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science 349 (6250), 827–832.

Lichti, N.I., Steele, M.A., Swihart, R.K., 2017. Seed fate and decision-making processes in scatter-hoarding rodents. Biol. Rev. 92 (1), 474–504.

Mendes, C.P., Ribeiro, M.C., Galetti, M., 2016. Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic forest. Ecography 39 (5), 465–475.

Mudappa, D., Raman, T.R.S., 2007. Rainforest Restoration and Wildlife Conservation on Private Lands in the Western Ghats. In: Shahabuddin, G., Rangarajan, M. (Eds.), Making conservation work. Ranikhet. Permanent Black, Uttaranchal, pp. 210–240.

Mudappa, D., Kumar, A., Chellam, R., 2001. Abundance and habitat selection of the Malabar spiny dormouse in the rainforests of the southern Western Ghats, India. Curr. Sci. 80 (3), 424–429.

Muthuramkumar, S., Ayyappan, N., Parthasarathy, N., Mudappa, D., Raman, T.R.S., Selwyn, M.A., Pragasan, L.A., 2006. Plant community structure in tropical rain forest fragments of the Western Ghats, India. Biotropica 38 (2), 143–160.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4 (2), 133–142.

Naniwadekar, R., Chaplod, S., Datta, A., Rathore, A., Sridhar, H., 2019. Large frugivores matter: insights from network and seed dispersal effectiveness approaches. J. Anim. Ecol. 88, 1250–1262.

Nayak, R., Karanth, K.K., Dutta, T., Defries, R., Karanth, K.U., Vaidyanathan, S., 2020. Bits and Pieces: Forest Fragmentation by Linear Intrusions in India, 99. Land Use Policy, 104619.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Vegan: Community Ecology Package. R Package Version. https://CRAN.R-project.org/package=vegan.

Osuri, A.M., Chakravarthy, D., Mudappa, D., Raman, T.S., Ayyappan, N., Muthuramkumar, S., Parthasarathy, N., 2017. Successional status, seed dispersal mode and overstorey species influence tree regeneration in tropical rain-forest fragments in Western Ghats, India. J. Trop. Ecol. 33 (4), 270–284.

Paine, C.T., Beck, H., Terborgh, J., 2016. How mammalian predation contributes to tropical tree community structure. Ecology 97 (12), 3326–3336.

Palmer, G.J., Catterall, C.P., 2018. Impacts of rainforest fragmentation on the composition of ground-active vertebrate communities and their patterns of seed consumption. PloS One 13 (9), e0202870.

Pascal, J.P., Ramesh, B.R., Franceschi, D.D., 2004. Wet evergreen forest types of the southern Western Ghats, India. J. Trop. Ecol. 45 (2), 281–292.

Prasad, S., Chellam, R., Krishnaswamy, J., Goyal, S.P., 2004. Frugivory of *Phyllanthus emblica* at Rajaji National Park, northwest India. Curr. Sci. 87 (9), 1188–1190.

Raman, T.R.S., 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. Biodivers. Conserv. 15, 1577–1607.

Rathod, I.M., Aruchamy, S., 2010. Spatial analysis of rainfall variation in Coimbatore district Tami Nadu using GIS. Int. J. Geomatics Geosci. 1 (2), 106–118.

R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. https://www.R-project.org/.

Sidhu, S., Datta, A., 2015. Tracking seed fates of tropical tree species: evidence for seed caching in a tropical forest in north-east India. PloS One 10 (8), e0134658.

Sinu, P.A., 2012. Seed predators of an old-world tropical deciduous tree (*Terminalia bellirica*: Combretaceae) in wet habitats of the Western Ghats, India. Curr. Sci. 103 (3), 309–314.

Soares, L.A.S., Faria, D., Vélez-Garcia, F., Vieira, E.M., Talora, D.C., Cazetta, E., 2015. Implications of habitat loss on seed predation and early recruitment of a keystone palm in anthropogenic landscapes in the Brazilian Atlantic rainforest. PloS One 10 (7), e0133540.

Sridhar, H., Raman, T.S., Mudappa, D., 2008. Mammal persistence and abundance in tropical rainforest remnants in the southern Western Ghats, India. Curr. Sci. 748–757.

Terborgh, J., 2012. Enemies maintain hyperdiverse tropical forests. Am. Nat. 179 (3), 303–314.

Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends Ecol. Evol. 11 (8), 330–333.

Vander Wall, S.B., 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. Philos. Trans. R. Soc 365 (1542), 989–997.

Wang, B., Chen, J., 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. Ecology 90 (11), 3023–3032.

Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. Trends Ecol. Evol. 17 (8), 379–384.

Wang, B., Ye, C.X., Cannon, C.H., Chen, J., 2013. Dissecting the decision making process of scatter-hoarding rodents. Oikos 122 (7), 1027–1034.

Wright, S.J., Duber, H.C., 2001. Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the Palm *Attalea butyraceae*, with implications for tropical tree diversity. Biotropica 33 (4), 583–595.

Wickham, H., 2017. Tidyverse: Easily Install and Load the 'Tidyverse'. R Package version 1.2.1. https://CRAN.R-project.org/package=tidyverse.

Xiao, Z., Chang, G., Zhang, Z., 2008. Testing the high-tannin hypothesis with scatter-hoarding rodents: experimental and field evidence. Anim. Behav. 75 (4), 1235–1241.

Zambrano, J., Coates, R., Howe, H.F., 2015. Seed predation in a human-modified tropical landscape. J. Trop. Ecol. 31, 379–383.

Zhang, H., Zhang, Z., 2008. Endocarp thickness affects seed removal speed by small rodents in a warm-temperate broad-leafed deciduous forest, China. Acta Oecol. 34 (3), 285–293.

Zhang, Z., Wang, Z., Chang, G., Yi, X., Lu, J., Xiao, Z., Zang, H., Cao, L., Wang, F., Li, H., Yan, C., 2016. Trade-off between seed defensive traits and impacts on interaction patterns between seeds and rodents in forest ecosystems. Plant Ecol. 217, 253–265.