

## Research Article

# Seed Rain in Abandoned Clearings in a Lowland Evergreen Rain Forest in Southern Thailand

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**Abstract:** Some forest restoration techniques treat remnant shrubs as competitors of newly planted tree seedlings, often clearing shrubs and weeds before trees are planted, but such plants may have significant value in attracting seed dispersers. In this study we examined the role of remnant trees and shrubs in grassland as a tool for passive and low cost ecological restoration. We determined the species density and abundance of both seed rain and its vertebrate dispersers in relation to different microhabitats (shrub-like vs. tree-like vegetation vs. grassland patches) in a 20-ha clearing of weeds mixed with early successional woody vegetation in a lowland evergreen forest in southern Thailand. We quantified seed rain from 60 seed traps placed in each microhabitat, and compared differences in seed abundance and species richness, while also examining the effect of distance from the forest edge. We found that seed rain abundance and seed species richness were significantly different among microhabitats. Seed rain was highest under shrubs, followed by under trees and then grassland, whereas seed species richness was highest under trees, followed by under shrubs, and grassland. Distance from the forest edge affected seed rain abundance under trees only. Birds (bulbuls and flowerpeckers) were the main dispersers of seeds at trees and shrubs respectively, while bats were the primary dispersers for the grassland patches. Different seed disperser groups appear to have complementary roles, such that sites containing a mixture of vegetation types including early successional vegetation may attract significantly more seed dispersers.

**Key words:** bats; birds; edge effects; forest restoration; seed dispersal

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## Introduction

Several factors can limit the rate of forest recovery, including lack of soil nutrients, competition with aggressive grasses, seasonal droughts, low rates of seed colonization, and predation on both seeds and seedlings [1- 2]. However, a major factor that often limits forest recovery is inadequate seed dispersal [2]. When seeds are dispersed by animals, different types of microhabitats within restoration areas are likely to attract (or discourage) different types of seed dispersers and thus generate seed rain with different characteristics. For example, seed rain under shrubs and trees that fruit year-round typically have a higher species richness and seed density than the seed rain in open, non-forest areas or beneath wind-dispersed trees [3-4, but see 5]. Thus, while seeds collected in open areas tend to be wind-dispersed species, most seeds deposited under woody plants are vertebrate-dispersed, because shrubs and trees provide perches and food for a variety of seed-dispersing animals [3-4, 6].

The more common animal seed dispersers in Old World tropical forests include birds and fruit bats [7]. Birds usually spend longer periods of time at fruiting trees and are more likely to defecate while perching on these trees or carry fruit to an adjacent perch before dropping or discarding the seeds, while bats are more likely to deposit seeds while flying over open areas [8 – 11]. Thus, seed rain in grassland microhabitats may result primarily from wind and fruit bat activity, while seed rain under shrubs and trees in grasslands may be brought mostly by birds. In addition, animal dispersed seeds may depend on distance from forest.

Distance from intact forest, which is typically the main source for seeds of late-successional plant species, has been shown to have a significant impact on the seed rain in deforested areas generated by seed-dispersing animals [12 – 14], although not always [6, 15 – 17]. Analysis of seed rain in relation to distance from forest edge can also provide information on the relative importance of different seed dispersal agents. Based on defecation behavior of bats and birds, some studies have suggested that bat-dispersed seed rain appears to decline less with distance from forest edge than bird-dispersed seed rain [9], while others suggest that seed rain from both species groups show a similar decline with distance from forest [13].

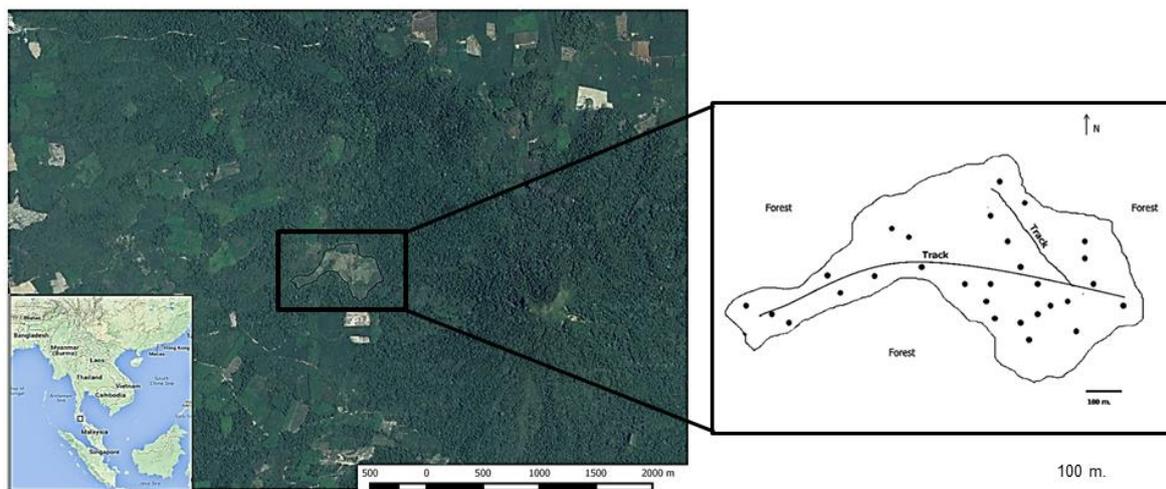
Only a few studies have examined the distribution of seed dispersers (bats and birds) and seed rain patterns relative to edge in SE Asian forest [13], which has the highest rate of deforestation in tropical regions [19]. Furthermore, no study in the region has looked in detail at how different plant growth forms attract particular dispersers, especially birds and bats. Currently, some forest restoration techniques treat remnant shrubs as competitors of newly planted tree seedlings; shrubs and weeds are often cleared before trees are planted [19 – 20]. In this study we determine the role of remnant trees and shrubs in grassland as a tool for passive and low cost ecological restoration. We examined the seed rain in a forest restoration area to answer the following questions: (1) Do seed rain abundance and richness vary with microhabitats within early successional microhabitats (woody shrubs, trees, and grassland patches)? (2) Does distance from the forest edge affect the pattern of seed rain and abundance of major seed dispersers?

We hypothesized that: (1) the abundance and species richness of seeds will be greater below shrubs and trees than in open areas, and seed rain under shrubs and trees will be mainly deposited by birds, while most of the seed rain in grassland patches will be dispersed by wind and fruit bats; and (2) the amount of seed rain in all microhabitats will decline with distance from the forest edge as well as the abundance of bulbuls (family Pycnonotidae) (likely the most important seed-dispersing family of birds in the region) [11, 32] . However, seed rain dispersed by bats may not be strongly related to distance from forest edge because at least some bats may be less sensitive to edge effects than birds [9,21] .

## Methods

### Study site

This study was carried out from November 2009 to October 2010 in the Khao Pra Bang Kham Wildlife Sanctuary, Krabi province, southern Thailand (8° 10' 20" N, 98° 80' 15" E, 16,800 ha). Krabi province has a distinct dry season from December to March, when the combined rainfall is less than 150 mm. The rainy season starts mid-April, peaking in September (419 mm) (Krabi meteorological station). The annual rainfall in 2010 was >2,000 mm (Krabi meteorological station). On average, the warmest month is March (average 33°C), and the coolest month is January (average 31°C). The Khao Pra Bang Kham Wildlife Sanctuary covers remnants of lowland evergreen rain forest which have largely disappeared from peninsular Thailand due to conversion to oil palm and rubber plantations [22] (Fig. 1). After the area was established as a wildlife sanctuary, 19 rubber and oil palm plantations within the new sanctuary were cleared of their crops, resulting in patches of grassland. The present study was carried out in a 20-ha weedy grassland containing a mix of early successional woody vegetation. The plot was surrounded by a mix of secondary (~25%) and primary (~75%) lowland evergreen rain forest.



**Fig. 1** Map of the study site within the Khao Pra Bang Kham Wildlife Sanctuary (Krabi, Thailand). Seed rain samples were taken from 30 trios of 6 traps per trio (black dots). Bird observations were conducted along the track.

A permanent stream runs at the west edge of this grassland, and on the east a strip of forest 200 m wide separates this grassland from oil palm plantations outside the sanctuary. The study site is mostly covered (~80%) by the grass *Imperata cylindrica*, with the remainder covered by a mix of woody plants including *Callicarpa arborea* (Beauty Berry), *Antidesma ghaesembilla* (Black Currant), *Melastoma malabathricum* (Indian Rhododendron), *Ziziphus oenopolia*, and *Dillenia spp.*, as well as herbaceous species such as *Ageratum conyzoides* and *Eupatorium odoratum*. *Callicarpa arborea* and *Melastoma malabathricum* are the most common woody species.

In 2009, this grassland was planted with saplings as part of a restoration program led by the Forest Restoration Unit of Chiang Mai University. Restoration plantings consisted of several native species including *Garcinia merguensis*, *Vatica odorata*, *Eugenia grandis*, and *Madhuca malaccensis*. Saplings were 0.5-1.0 m tall, and planted at a density of 3,000 trees per hectare over an area of 0.32 ha on the eastern edge of the grassland. The remaining grassland area was replanted with a mixture of exotic (*Acacia mangium*, *Acacia auriculiformis*) and native species (*Parkia speciosa*) by the wildlife sanctuary,

but most (>80%) of the seedlings planted by the wildlife sanctuary died during a prolonged drought period in 2010.

### Seed rain

Seed rain was collected with seed traps set within 200 m of the track (~2 km long) running through the grassland. Each seed trap consisted of a 1 m<sup>2</sup> wooden frame covered with a plastic sheet and supported by wooden legs that raised the frame 0.5 m above the ground to prevent seed removal by most seed predators. The corners of the plastic sheets were tied down to hold them against wind and rain. Each plastic sheet was pierced in the middle and these holes were covered with a polyester cloth that allowed rainwater to drain, but retained any seeds in the trap. Pairs of seed traps were placed in trios (traps < 10 m apart formed a trio), with one pair in each trio placed in a grassy patch (no woody vegetation), one pair set under a fruiting tree (*Callicarpa arborea*), and one pair set under a shrub (*Melastoma malabathricum*) (Fig. 1). We placed 30 pairs of seed traps in each microhabitat, for a total of 180 seed traps. A pair of traps in a given microhabitat was considered a replicate. In the present study, *C. arborea* is classified as a tree because it is a woody perennial plant, with a single main stem, and has a definite crown [23]. *C. arborea* trees in our study area were 8-10 m tall; this species is typically found in open habitats and mixed forests. *M. malabathricum* is a shrub, defined as a woody perennial plant, often without a definite crown [23], and generally between 0.5 and 5 m high in our study area. This species is mostly found in abandoned agricultural areas and disturbed or deforested sites. Both plant species produce fruit all year but peak from June to November. During the first month of the study, we checked traps every morning (when traps contained seeds left by bats during the night) and every evening (when traps contained seeds left by birds during the day) to learn how to identify seeds dispersed by birds, bats, and civets. The defecations from birds are solid and coarse-textured while bat feces resemble a single gelatinous cluster, rather than being deposited in separate pieces. The defecations from civets are distinctively bigger than bird and bat defecations. We identified bat and squirrel ejectives from the size of visible teeth marks on the remaining flesh. After the first month, seeds were only collected once a day. Trapped seeds were collected and cleaned every morning for 10-15 days each month ( $10.8 \pm 1.9$  days).

All fecal seeds and pulp lacking seeds were classified as being dispersed by bird, bat, or small mammal. Whole fruits of *C. arborea* found under trees, and of *M. malabathricum* found under shrubs, were assumed to have fallen from plants overhanging the seed traps and were not included in the analyses. However, seeds of *Callicarpa arborea* and *Melastoma malabathricum* which were contained in fecal material and/or had otherwise shown clear indications of being ingested by a bird or mammal, were not excluded from analysis because these two species were the dominant seeds in the traps (72%). Furthermore, it was likely that >90% of the *Callicarpa arborea* and *Melastoma malabathricum* seed observed in traps under the same species were dispersed from elsewhere, because bulbuls, which were responsible for a large majority of the feeding observations (see below), spend only a mean of 2.5 minutes feeding in one location before moving to another tree or shrub (Kerdkeaw, unpublished data). Bulbuls have gut retention times >20 minutes (mean gut passage time of *Pycnonotus brunneus* and *P. goiavier* for seeds of *C. arborea* are 22.9 and 23.2 minutes, respectively [Kerdkeaw, unpublished data]) and therefore would have a low probability of digesting and depositing seeds without dispersal (6-10%, Kerdkeaw, unpublished data). This is also likely true of other dispersers in our study area, such as flowerpeckers; Ward and Paton (2007) showed that the seed shadow of mistletoe from movements of the flowerpecker *Dicaeum hirundinaceum* had only a 12% chance of being deposited under the same host tree.

All visible seed samples were identified by comparison to the reference collection obtained from a nearby area, and also from the Prince of Songkla University herbarium. Most seeds were identified to

species, but some seeds could be identified only to genus, namely, *Ficus* and *Ixora*. Tiny (<1 mm) seeds, such as from an unidentified *Ficus*, were germinated in a nursery and seedlings were recorded as species present but were not analyzed quantitatively. At each fruiting tree of *C. arborea*, we measured distance from the forest edge with a range finder.

### *Animal observations*

Bird surveys were conducted by walking along the existing tracks and among isolated trees in the grassland (Fig. 1). When birds were encountered, we stopped and counted the number of birds and noted the plant used for perching or otherwise using. Surveys were conducted from 7:30-10:00 a.m. for 10-15 days per month (total of 360 hours) on the same days that seeds were collected. Birds were identified by using *A Guide to Birds of Thailand* [24]. Bats were surveyed by netting in both the wet and the dry season. Mist nets were set in various locations near forest edge in the early evening (5:00 p.m.) for 10 days between May and August 2010 for a total of 150 net hours. Since bat flights tended to be high in open areas, only a few mist nets were set in the open microhabitats. Bats were identified following *The Mammals of Thailand and South-East Asia* [25]. To observe terrestrial mammals, five camera traps were set randomly near the track focusing on the animals that were likely to walk along the track. Camera traps were set for 36 days (180 total trap nights). The photos were taken 10 minutes apart to reduce counting multiple detections of the same individual.

### *Statistical analyses*

The number of seeds from each pair of seed traps was combined into one number for the whole year. One trap below a *Callicarpa arborea* contained more than 2,000 seeds, nearly double that of other traps beneath *Callicarpa* and thus this replicate was excluded from the statistical analyses below (N = 174). We examined the effects of distance to forest and microhabitat in each trio using multiple regression with dummy variables. For example, the dummy for trees was assigned a value of 1 if the seeds were collected from under a tree and 0 otherwise. As there were possible issues of spatial autocorrelation due to the relatively close proximity of each trap within a trio, trio was identified as a block. To test effects of microhabitat on the abundance of seed dispersers, Chi-square tests were applied to investigate the number of each bird species group spotted at shrubs versus trees. Thirteen bird groups were classified based on taxonomy, body size and behavior, including barbets, bulbuls, flowerpeckers, pigeons, white-eyes, leafbirds, parrots, flycatchers, orioles, monarch, ioras, babblers, and broadbills. Since bulbuls were by far the most abundant, we tested the effect of distance from the forest edge on the number of bulbuls using regression analysis. A Mann-Whitney U Test was conducted to examine the effect of microhabitats on seed rain dispersed by bats, since the amount of seed rain into grassland patches was not normally distributed and could not be transformed. All statistical analyses were conducted in R for Windows (version 13; R Development Core Team).

## **Results**

### *Seed rain*

A total of 64,021 seeds of 40 plant taxa were recorded in one year from 180, 1 m<sup>2</sup> seed traps (total trap effort 561,600 hours). The large majority of seed species were dispersed by birds (29 taxa); the remainder were dispersed by wind (7 taxa), bats (4 taxa), squirrels (1 taxa), and civets (2 taxa) (Appendix 1). The seeds of *Callicarpa arborea* and *Melastoma malabathricum* were the dominant seed species in the traps (72%), presumably due to their dominance in the study area. Most of the seed rain (77%) was collected from June to November with a peak (50% of collected seed) during August to October (Fig. 2). For seed species richness, there was no significant interaction between microhabitat and distance from the forest edge. Seed species richness was, however, affected by microhabitat. Seed species richness under *C. arborea* trees was the highest, followed by under *M. malabathricum* shrubs and grassland respectively (Table 1). The number of seeds (mean  $\pm$  SD) was highest under *M.*

*malabathricum* shrubs ( $1,237.6 \text{ seeds} \pm 175.1$ ,  $N = 29$ ), followed by under *C. arborea* trees ( $806.2 \pm 154.8$ ,  $N = 29$ ) and in grassy microsites ( $163.8 \pm 140.3$ ,  $N = 29$ ). There were strong positive microhabitat effects on the number of seeds, and there was a significant interaction between microhabitat and distance from the forest. Seed rain deposited under trees was significantly negatively correlated with distance from the forest. The correlation between the number of seeds and distance from the forest edge was not significant for shrub or grass microhabitats (Table1).

Table 1. Summary of multiple regressions to detect the effects of distance to forest and microhabitats on A) number of seeds dispersed, and B) seed species richness ( $N = 29$ ).

	Estimate	SE	t-value	p-value
A) Number of seeds				
Intercept	61.345	53.855	1.139	0.258
Distance to forest	4.087	1.886	2.167	0.033 *
Microhabitat (shrub)	1159.078	77.907	14.878	<0.001***
Microhabitat (tree)	1027.286	84.770	12.119	<0.001***
Distance to forest: Microhabitat (shrub)	-3.299	2.971	-1.110	0.270
Distance to forest: Microhabitat (tree)	-15.050	3.002	-5.013	<0.001***
B) Seed species richness				
Intercept	1.521	0.755	2.016	0.047*
Distance to forest	0.018	0.026	0.670	0.505
Microhabitat (shrub)	2.610	1.092	2.391	0.019*
Microhabitat (tree)	5.891	1.188	4.960	<0.001***
Distance to forest: Microhabitat (shrub)	0.006	0.042	0.152	0.879
Distance to forest: Microhabitat (tree)	-0.043	0.042	-1.024	0.309

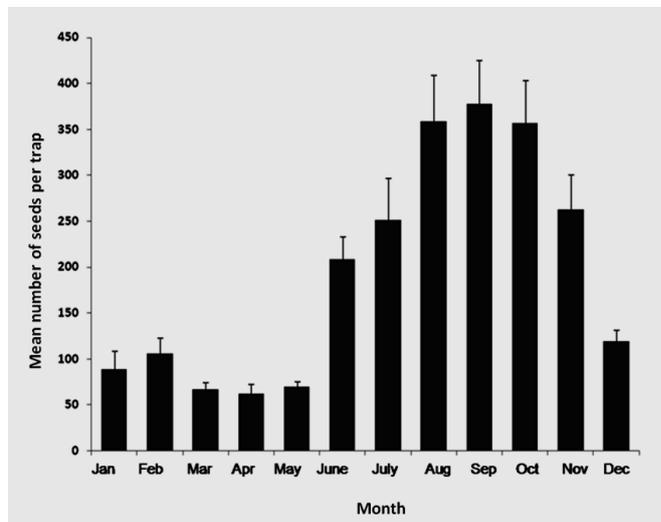
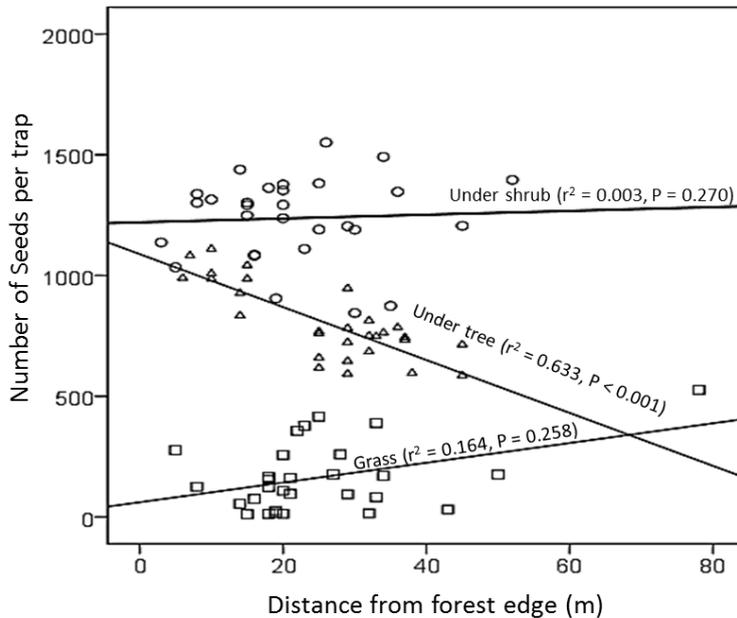


Fig. 2 Pattern of monthly seed rain at the study site within the Khao Pra Bang Kram Wildlife Sanctuary (Krabi, Thailand) from November 2009 to October 2010. The lines above the bars represent SD.

### Seed dispersers

Twenty-three species of birds from 13 families were observed. The most abundant taxa were the bulbuls (*Pycnonotus goiavier*, *P. atriceps*, and *P. blanfordi*), distantly followed by flowerpeckers and barbets (Table 2). Vegetation preference differed among these groups. Significantly more individuals were seen at trees than shrubs for both bulbuls (chi-square = 383.0,  $P < 0.001$ ,  $df = 1$ ) and barbets (chi-square = 26.5,  $P < 0.001$ ,  $df = 1$ ). However, flowerpeckers preferred shrubs over trees (chi-square = 20.0,  $P < 0.001$ ,  $df = 1$ ). The frequency of bulbuls at trees did not significantly decrease with increasing

distance from forest ( $r^2 = 0.04$ ,  $P = 0.34$ ,  $N = 29$ ). For other seed dispersers observed during the study, 19 individuals of two fruit bat species (*Cynopterus sphinx* (15) and *Megaerops ecaudatus* (4)) were netted, and 25 pictures of Large Indian Civets (*Viverra zibetha*) were recorded from camera traps. The correlation between seed rain dispersed by bats and distance from the forest was not significant ( $r^2 = 0.01$ ,  $P = 0.43$ ,  $N = 29$ ).



**Fig. 3** The number of seeds plotted against distance from the forest edge for the three microhabitat types (trees, shrubs, grassland). Each point represents the number of seeds collected from a pair of seed traps at a given location.

We found that seeds deposited under the *C. arborea* trees and *M. malabathricum* shrubs (mean  $\pm$ SD) were mainly dispersed by birds ( $747.2 \pm 127.7$ , 92.3%) and ( $1176.8 \pm 172.7$ , 95.25%) respectively; followed by bats ( $61.3 \pm 64.3$ , 7.58%) and ( $57.9 \pm 70.0$ , 4.69%) respectively; and wind ( $0.7 \pm 2.0$ , 0.09%) and ( $0.8 \pm 2.4$ , 0.06%) respectively; whereas in grassy areas the majority of seeds (97.29%) were dispersed by bats ( $155.3 \pm 143.5$ ) followed by wind ( $4.3 \pm 5.0$ , 2.71%) (Fig. 4). The number of seeds dispersed by bats into the grass was significantly higher than under shrubs and trees (data from shrubs and trees were pooled, Mann-Whitney  $U(59) = 608.5$ ,  $Z = -2.42$ ,  $P = 0.01$ ). The number of seeds dispersed by birds under *M. malabathricum* shrubs was significantly higher than under the *C. arborea* trees, while the traps from the grass patches contained no bird dispersed seed (Mann-Whitney  $U(59) = 24.0$ ,  $Z = -63$ ,  $P < 0.001$ ). Wind dispersed seeds deposited in the grass patches were significantly higher than under shrubs and under trees, but there was no significant difference in the number of wind dispersed seeds between shrubs and trees (Kruskal-Wallis  $H(2) = 31.83$ ,  $P < 0.001$ ).

Table 2. The number and proportion of each bird taxa observed at shrubs and trees in Khao Pra Bang Khram Wildlife Sanctuary

Bird group	Tree	Shrub	Proportion
Megalaimidae (Barbet)	32	2	0.0083
Pycnonotidae (Bulbul)	2569	1345	0.9558
Dicaeidae (Flowerpecker)	20	60	0.0195
Columbidae (Pigeon)	12	9	0.0021
Zosteropidae (White-eye)	4	1	0.0012
Chloropseidae (Leafbird)	2	0	0.0005
Psittaculidae (Parrot)	4	5	0.0022
Muscicapidae (Flycatcher)	7	3	0.0024
Oriolidae (Oriole)	3	0	0.0007
Monarchidae (Monarch)	3	0	0.0007
Aegithinidae (Iora)	9	12	0.0051
Timaliidae (Babbler)	4	1	0.0012
Eurylaimidae (Broadbill)	1	0	0.0003
Proportion	0.65	0.35	

## Discussion

Our study found that both seed species richness and the number of seeds beneath shrubs and trees were significantly different from the grassy areas. This is similar to a study of upland plant communities in Hong Kong [4], and to studies in other regions which show that isolated trees [6, 15], and shrubs [2-3, 26-27] are crucial for tropical tree seedling recruitment due to their ability to attract seed dispersers. Moreover, this spatial pattern of seed rain matches other studies indicating that isolated shrubs and trees play a major role in facilitating bird movements across open habitats [4-5, 15].

Although seed rain under shrubs was greater than under trees, birds were observed at trees more frequently than at shrubs. This is probably because most seeds found under the *Melastoma malabathricum* shrubs were also from *M. malabathricum*, which have seeds that are far smaller and more numerous than seed species deposited under trees. One fruit of this plant contains approximately 1,245 seeds (SD = 127.3, N = 16); therefore, the number of seeds under a plant is not necessarily indicative of the number of birds that have visited.

Different seed dispersers commonly provide distinct, and often complementary, contributions to community succession. These differences have particular value during habitat restoration, when areas with limited seed banks rely almost exclusively on dispersers to bring in seeds. Previously, birds were thought to contribute much more seed dispersal to the early stages of succession than bats [28-29]. However, the results from this study indicate that birds play almost no role in open grassy habitat, as even our small areas of grassland contained no bird-dispersed seed. However, birds are likely to have a larger impact in areas that have already started to recover (e.g. some shrubs and trees present), whereas bats are potentially more influential seed dispersers in open areas. Our result is consistent with a study in Peruvian lowland forest [29], which also found that bats were the primary disperser

into treeless/shrubless habitats. This difference in seed rain patterns can be explained by different defecation behaviors, as bats typically defecate during flight [11, 30-31], whereas birds usually defecate while perched [30-31]. However, to examine the efficiency of bird versus bat dispersal, seed germination and seedling survival experiments are needed.

In addition, as expected, bird species varied with microhabitats. Bulbuls, which were the most abundant avian taxa (approximately 95% of observed birds), have been shown to be effective dispersers because they deposit most seeds away from parent plants [32-33], and their diet is highly frugivorous. For example the diet of *Pycnonotus brunneus*, which was sampled in the same study area, consisted of 92.2% fruit [34]. Furthermore, a study in Hong Kong reported that bulbuls move from the forest to isolated trees close to the forest edge, but less commonly to shrubs [33]. Barbets were observed at trees significantly more frequently than at shrubs. On the other hand, flowerpeckers were observed at shrubs significantly more often than at trees. This may be due to the small size of flowerpeckers (4-8 g), which allows them to access and utilize frail shrub branches that cannot support the weight of larger, less maneuverable birds such as bulbuls and barbets.

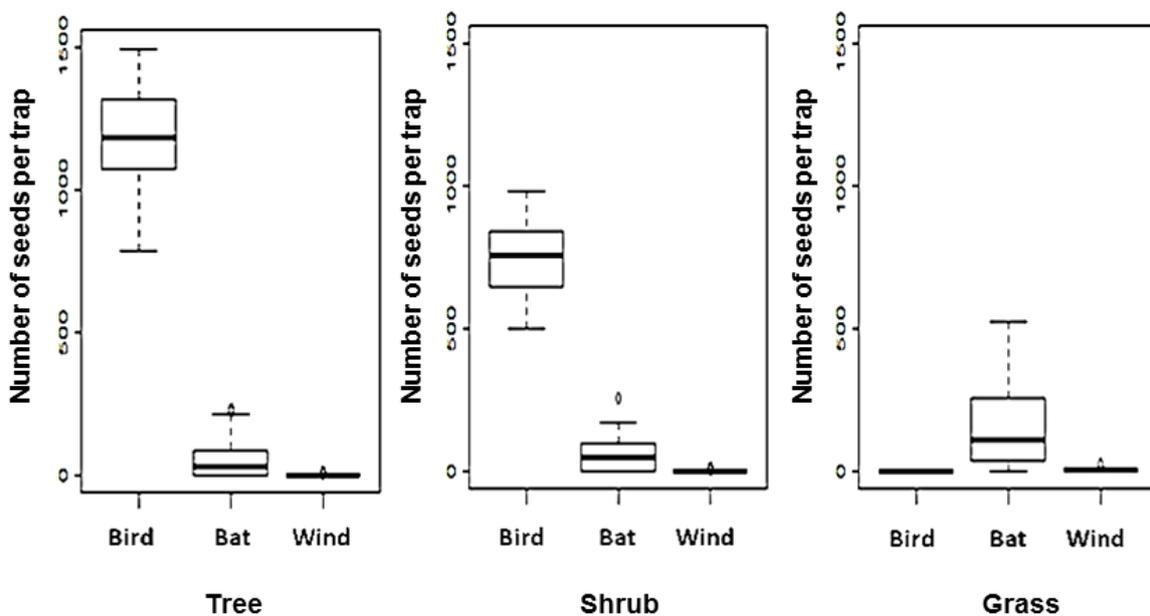


Fig. 4 Number of seeds dispersed by birds, bats, and wind for each vegetation structure type at the Kram Wildlife Sanctuary (Krabi, Thailand) from November 2009 to October 2010.

The amount of seed rain declined with distance from the forest edge for bird-dispersed seeds beneath trees, but there was no significant correlation between the number of bat-dispersed seeds and distance from the forest edge. Similar patterns, in which seed rain dispersed by birds shows a greater decline with distance from the forest edge than bat-dispersed seeds, have been found in other studies [9, but see 13]. A likely explanation for this pattern is that many frugivorous birds avoid large treeless areas that could expose them to predators [35], which probably limits the ability of most forest-associated birds to disperse seeds into large deforested areas. In this study, bulbuls (namely, *P. atriceps*, *P. goiavier*, and *P. finlaysoni*) were the major bird species observed. Contrary to our predictions, we did not detect a significant decrease in bulbul abundance with increasing distance

from the forest edge. This may be because we examined all bulbul species as one group, but major feeding habitats vary among species (Kerdkeaw, unpublished data). For example, *P. finlaysoni*, *P. brunneus*, and *P. atriceps* are usually found near the forest edge, while *P. goiavier* is more active in younger successional vegetation farther from the forest edge [Kerdkeaw, unpublished data]. Thus, greater resolution of how distance from the forest edge affects bulbul abundance may be gained by incorporating species into the analysis.

### Implications for conservation

Previous studies indicate that frugivorous birds in early successional forests prefer perches that are taller than the surrounding vegetation while searching for food [36, 37]. Maintaining fruiting trees and shrubs in forest restoration areas may provide “stepping stones” for birds within fragmented forest ecosystems and can potentially attract greater numbers of dispersers, particularly bulbuls. Bulbuls were by far the most numerous (>95%) disperser in our study area; they are also abundant, are potentially keystone dispersers in Southeast Asia, and at least some species appear to breed readily in disturbed forest habitats such as ours [11, 32]. In addition, at least some bulbul species in our study area spend significant amounts of time in intact forest as well as in open, non-forest habitat [34,] making them potentially ideal for dispersing seeds of forest trees into deforested habitats [11].

Our results also strongly suggest that different microhabitats (e.g., trees, shrubs) can attract different groups of avian seed dispersers, such as flowerpeckers, in addition to bulbuls. At least some species of flowerpeckers are also considered effective dispersers [11]. On the other hand, there were few forest birds from other families sighted (only 2.5% of all observations) in the open habitats of our study area, indicating that without bulbuls and flowerpeckers, dispersal of forest plants into such open areas would likely be much rarer. Given these disperser patterns, for landscape planning, isolated remnant trees and shrubs, in addition to well preserved forest patches, should be considered key to maintaining ecosystem resilience [38]. Finally, because bats were the primary dispersers for grassland patches in our study area and elsewhere [13, 29], protecting fruit bat populations may be crucial for securing the future of plant communities in tropical forest regions, particularly where treeless grassland patches are in need of reforestation. However, as restoration studies of lowland evergreen rain forest in this region are not yet common, and this study was conducted in only one 20-hectare site and focused on one species of shrub and one species of tree, the results may not necessarily be representative of such regenerating clearings in general.

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Appendix 1. Species that were found in seed rain at Khao Pra Bang Khram Wildlife Sanctuary (Krabi, Thailand). Seed dispersing animals were identified from fecal samples. SQ = squirrel; BD = bird; WD = wind; BT = bat; CV = civet. The habitat association of each plant species is also indicated (grassland [GS] or forest [FT]).

Family	Species	Dispersal agents	Number of seeds	Habitat	Number of traps
Arecaceae	<i>Elaeis guineensis</i> Jacq.	SQ	25	GS	10
Annonaceae	<i>Unona hahnii</i> Finet & Gagnep.	BD	31	FT	15
Arecaceae	<i>Calamus javensis</i> Blume	BD	79	GS,FT	18
Bignoniaceae	<i>Pajanelia longifolia</i> (Willd.) K.Schum.	WD	12	FT	9
Bignoniaceae	<i>Oroxylum indicum</i> (L.) Kurz	WD	54	GS	5
Cannabaceae	<i>Trema orientalis</i> (L.) Blume.	BD	139	GS	50
Chrysobalanaceae	<i>Parinari anamense</i> Hance.	BD	42	FT	16
Compositae	<i>Eupatorium odoratum</i> L.	WD	101	GS	25
Dipterocarpaceae	<i>Shorea gratissima</i> Dyer	WD	9	FT	7
Dipterocarpaceae	<i>Hopea odorata</i> Roxb.	WD	13	FT	9
Euphorbiaceae	<i>Antidesma ghaesembilla</i> Gaertn.	BD	95	GS,FT	43
Flagellariaceae	<i>Flagellaria indica</i> L.	BD	72	GS	32
Labiatae	<i>Callicarpa arborea</i> Roxb.	BD	3,219	GS	120
Lamiaceae	<i>Vitex</i> sp.	BD	230	GS,FT	46
Lythraceae	<i>Lagerstroemia floribunda</i> Jack.	WD	76	GS,FT	17
Malvaceae	<i>Grewia nervosa</i> (Lour.) Panigrahi	BD	84	GS	19
Melastomataceae	<i>Memecylon corticosum</i> Ridl.	BD	92	FT	17
Melastomataceae	<i>Melastoma malabathricum</i> L.	BD, CV	42,988	GS	125
Moraceae	<i>Streblus ilicifolius</i> (Vidal) Corner.	BD	98	GS,FT	19
Moraceae	<i>Ficus</i> sp1	BD, BT	8,721	NA	125
Moraceae	<i>Ficus</i> sp2	BD, BT	9,562	NA	98
Myrtaceae	<i>Syzygium pyriform</i> (Blume) DC.	BD	12	FT	6
Myrtaceae	<i>Syzygium antisepticum</i> (Blume) Merr. & L. M. Perry	BD	21	FT	8
Myrtaceae	<i>Eugenia</i> sp.	BD	37	NA	14
Myrtaceae	<i>Psidium guajava</i> L.	BD	84	GS	12
Myrtaceae	<i>Rhodomyrtus tomentosa</i> (Aiton) Hassk.	BD	92	GS	24
Passifloraceae	<i>Passiflora foetida</i> L.	BD	104	GS	19
Rhamnaceae	<i>Ziziphus oenopolia</i> (L.) Mill.	BD	211	GS	43
Rubiaceae	<i>Morinda citrifolia</i> L.	BD	14	GS,FT	9
Rubiaceae	<i>Psychotria angulata</i> Korth.	BD	18	GS	5

Rubiaceae	<i>Rennellia speciosa</i> (Wall. ex Kurz) Hook. f.	WD	31	FT	10
Rubiaceae	<i>Ixora cibdela</i> Craib	BD	35	FT	7
Rubiaceae	<i>Lasianthus chrysoneurus</i> (Korth.) Miq.	BD	43	FT	19
Rutaceae	<i>Acronychia pedunculata</i> (L.) Miq.	BT	21	FT	9
Sapindaceae	<i>Allophyllus cobbe</i> (L.) Raeusch.	BD	38	FT	10
Sapotaceae	<i>Madhucamalaccensis</i> (C.B.Clarke) H.J.Lam	CV	21	GS	1
Solanaceae	<i>Capsicum frutescens</i> L.	BD	102	GS	20
Solanaceae	<i>Solanum torvum</i> Sw.	BT	392	GS	3
Vitaceae	<i>Leea indica</i> (Burm. f.) Merr.	BD	11	GS	2
Zingiberaceae	<i>Cheilocostus speciosus</i> (J.Koenig) C.D.Specht	BD	211	GS	19