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Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation

Abstract In the moist Neotropics, vertebrate frugivores have a much greater role in the dispersal of forest and successional woody plants than wind, and bats rather than birds play the dominant role in dispersing early successional species. I investigated whether these patterns also occurred in a Philippine montane rainforest and adjacent successional vegetation. I also asked whether seed mass was related to probability of dispersal between habitats. A greater number of woody species and stems in the forest produced vertebrate-dispersed seeds than wind-dispersed seeds. Although input of forest seeds into the successional area was dominated by vertebrate-dispersed seeds in terms of species richness, wind-dispersed seeds landed in densities 15 times higher. Frugivorous birds dispersed more forest seeds and species into the successional area than bats, and more successional seeds and species into the forest. As expected, seed input declined with distance from source habitat. Low input of forest seeds into the successional area at the farthest distance sampled, 40 m from forest edge, particularly for vertebrate-dispersed seeds, suggests very limited dispersal out of forest even into a habitat in which woody successional vegetation provides perches and fruit resources. For species of vertebrate-dispersed successional seeds, probability of dispersal into forest declined significantly with seed mass.

Keywords Distance from edge · Forest regeneration · Frugivores · Fruit · Seed mass

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Introduction

Due to deforestation and fragmentation, tropical forests are increasingly sharing edges with disturbed vegetation. Seed dispersal between these habitats has important implications for future vegetation composition and structure. Lack of input of forest seeds is one of the most intractable barriers to reestablishment of forest in cleared or degraded areas (Nepstad et al. 1991; Aide and Cavelier 1994; Da Silva et al. 1996; Nepstad et al. 1996; Holl 1999; Holl et al. 2000). Conversely, higher seed rain of successional species in treefall gaps close to forest edge than in those in pristine forest could increase degradation of forest (Janzen 1983).

As seeds are not in themselves mobile, their movement must be effected by dispersal vectors, whether abiotic (e.g., wind) or biotic (e.g., frugivorous vertebrates). Most woody species in tropical rain forests produce fleshy fruits that attract vertebrate seed dispersers (Howe and Smallwood 1982; Willson et al. 1989). Frugivorous birds and bats are the most important seed dispersal agents for tropical forest seeds into grasslands and early successional vegetation because the simple structure of these habitats poses less of a barrier to them than it does to other frugivorous vertebrates. In the moist Neotropics, fruit bats play the predominant role in the dispersal of early successional woody vegetation (Foster et al. 1986; Uhl 1987; Gorchov et al. 1993). In Southeast Asia, where the communities of frugivorous bats and birds are taxonomically distinct from those in the Neotropics (Fleming et al. 1987; Corlett 1998), seed dispersal studies have been largely anecdotal (Corlett 1998).

Spatial distributions of wind-dispersed seeds are relatively predictable, determined by seed production, seed morphology, and air currents (Augspurger 1986; Augspurger and Franson 1987; Greene and Johnson 1996). Distributions of vertebrate-dispersed seeds are much more variable, and depend not only on plant characteristics, but also on the identity and behavior of dispersers (Schupp 1993). For both wind- and vertebrate-dispersed seeds, an expected decrease in seed input with

distance from source vegetation has been documented (Willson and Crome 1989; Holl 1998; Martinez-Garza and Gonzalez-Montagut 1999, 2002). In clearcut strips in the Peruvian Amazon, input of bat-dispersed forest seeds declined less with distance from forest edge than input of bird-dispersed seeds (Gorchov et al. 1993), presumably because bats are more likely to defecate in flight rather than from perches (de Foresta et al. 1984).

Dispersal of seeds between habitats may also be influenced by seed size. Small-seeded species predominate in the seed rain of forest plants in successional areas adjacent to forest (Duncan and Chapman 1999; Harvey 2000), and large-seeded forest trees are thought to be dispersal limited in the colonization of successional habitats (Corlett 1991; Wunderle 1997). Larger-seeded plants produce proportionately fewer seeds than smaller-seeded plants per unit plant (Greene and Johnson 1994). Are larger seeds less likely than smaller seeds to be dispersed across habitats, or are they dispersed in relation to their abundance in the seed rain and simply produced in smaller numbers in the source habitat?

I studied seed input into Philippine montane rainforest and an adjoining patch of early successional vegetation. To compare bird and bat seed dispersal between these habitats I used seed traps that were open either during the night or the day. Because vertebrate-dispersed woody plants were much more common than wind-dispersed ones in the forest, I expected that among forest seeds dispersed into the successional area, vertebrate-dispersed seeds would predominate. Bats were expected to play the main dispersal role for successional seeds, as is the case in the Neotropics. A negative relationship between seed input and distance from source vegetation was expected. Smaller seeds were predicted to be more likely to be dispersed between habitats than larger seeds.

Materials and methods

Study site

The study was conducted within lower montane rainforest and an associated 1 ha area of successional vegetation (8°11'20"N, 124°55'20"E) at 1,450 m elevation on the northern slope of the Mt. Kitanglad range (peak 2,938 m elevation) on Mindanao, Philippines (Fig. 1). The forest was contiguous with the Mt. Kitanglad Range Nature Park, but was within 200 m of grassland to the north. The forest canopy was 25 m high and was dominated by *Lithocarpus* spp. (Fagaceae) and *Elaeocarpus* spp. (Elaeocarpaceae), comprising 32% and 22% of total basal area, respectively (Ingle 2001). Their seeds were not monitored as part of this study as *Lithocarpus* spp. produce acorns, which fall initially to the ground and are subsequently dispersed, presumably by rodents, and *Elaeocarpus* spp., which produces vertebrate-dispersed seeds, did not fruit during the study (August 1998–July 1999). In vegetation plots totalling 0.75 ha, a total of 80 species of vertebrate-dispersed woody plants ≥5 cm dbh were recorded, comprising 69% of stems and 51% of basal area (Ingle 2001). Ten wind-dispersed species were represented among woody plants ≥5 cm dbh, comprising 11% of stems and 12% of total basal area.

The successional area was a 1-ha abandoned slash-and-burn farm that had first been cleared for cultivation during WWII. About 6 years prior to the study it was again cleared of woody vegetation
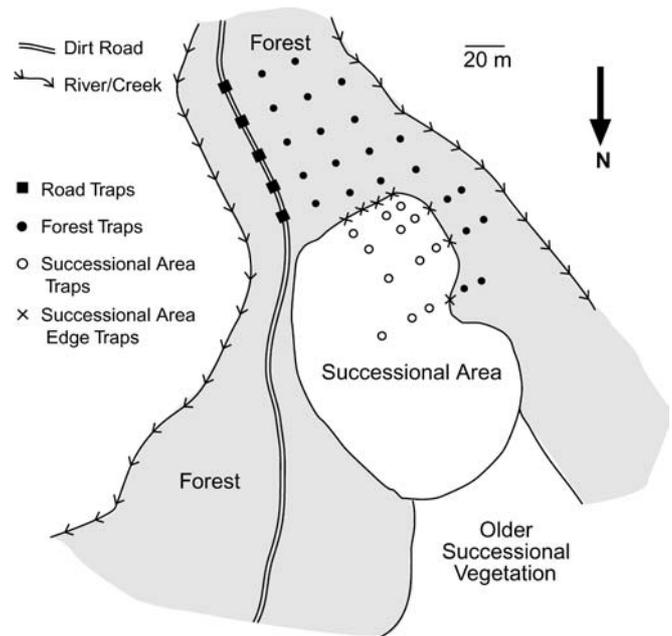

Fig. 1 Map of habitat types and location of seed traps

(then dominated by *Dodonaea angustifolia*, a wind-dispersed tree in the Sapindaceae), cropped for a year, and left to regenerate. At the time of the study most woody stems were <5 cm diameter and <5 m tall. *Cypholophus moluccanus* (Urticaceae), *Saurauia* spp. (Actinidiaceae), *Aralia bipinnata* (Araliaceae), and *Melastoma malabathricum* (Melastomataceae) each comprised over 10% of reproductive individuals, and *Mallotus ricinoides* (Euphorbiaceae) about 5%. All woody plant species of reproductive size recorded in the successional area produce vertebrate-dispersed seeds, with the exception of *C. moluccanus*, which produces seeds with no obvious dispersal adaptation. Along with *Melastoma malabathricum*, seedlings of *D. angustifolia* dominated the stems <10 mm diameter, but no *Dodonaea* of reproductive size were present. There was almost no overlap in species composition between the forest and the successional area.

An abandoned 6-m-wide road had been cut through the forest in 1992. Removal of trees from the road had resulted in an opening in the canopy, and some successional species, particularly *Aralia bipinnata*, *Melastoma malabathricum*, and *Rubus* spp., were present on the side of the road.

Seed rain measurement

I used night/day seed traps to sample seed rain. Bats were only netted or observed flying during the night, and birds only in the day. Vertebrate-dispersed seeds that landed in night traps and were not represented in the habitat (and therefore could not have come from vegetation above) were assumed to have been dispersed by frugivorous bats, and those that landed in day traps by frugivorous birds. Other vertebrates were unlikely to have contributed significantly to seeds of fleshy fruits that landed in traps. Monkeys *(Macaca fascicularis)* were only very occasionally heard or seen in or near the study area. Tree shrews, squirrels, and murid rodents, all of which have been recorded to include fleshy fruits in their diets (Corlett 1998), were present in the study area, but the raised seed traps would not have collected seeds dispersed by ground-dwelling small mammals. Seeds dropped by arboreal small mammals could have landed in forest seed traps, but any contributions were probably minor relative to those from birds and bats given the lower incidence of fruits in their diets, and because rodents are often seed predators. It is worth noting that the mammalian fauna of the

Philippine Islands, which are oceanic in origin, is strikingly different from mainland Southeast Asia and the Sunda Shelf in being depauperate in large mammals, including ungulates and primates, which in other areas have important roles in seed dispersal.

Some sampling error may have occurred if seeds dispersed during the night were intercepted by vegetation (especially in the forest) and landed into traps in the day, and vice versa, but any error is unlikely to have been biased towards either day or night traps. Wind and rain, which could bring seeds down from vegetation, occurred during both day and night. More leaves fell into traps in the day than in the night, but this is unlikely to have biased the seed rain appreciably because only a small proportion of leaves on trees are shed at any given time.

Each seed trap was 1 m^2 in area, and consisted of a shallow cone of fine nylon cloth attached by Velcro tabs to a frame of split bamboo supported by bamboo legs about 1 m off the ground. A string attached to the bottom of the cloth cone was tied to low vegetation or to a stake in the ground to hold the cone in place in case of wind. Traps were set in pairs of one day and one night trap. Circular covers of waterproof plastic sack material sewn to split bamboo circular frames slightly larger in diameter than the trap were used to close night traps during the day, and day traps during the night. The covers had drainage holes covered by nylon cloth.

After habitats were mapped, seed traps were located in predetermined arrays in areas designated as forest, successional area, successional area edge, and road (Fig. 1). Twelve pairs of traps were placed in the southern quarter of the successional area, at distances 10, 20, and 40 m from the border with forest to the southwest, and 10, 20, 40, and 65 m from forest to the southeast. Seven pairs of traps were placed along the edge of the successional area, just outside the crowns of forest trees. The vegetation around these traps was similar to that around the traps in the successional area. A total of 22 pairs of traps were placed in the forest on both sides of the successional area, at 10- or 20-m spacing. Forest traps were 10–60 m from successional vegetation, which occurred both in the successional area and along the road. Five pairs of traps were placed at 20-m intervals along the unused 6-m-wide dirt road cut through the forest in 1992, but data from these traps will not be presented here. Traps were positioned by locating the predetermined trapping points on the ground, and placing two adjacent traps in the nearest spot available that did not entail cutting stems of woody plants >2 cm diameter in the forest, and >2 cm diameter in the successional area. Vegetation overhanging traps was not cleared.

Seed traps were run for 2 weeks each month over 12 lunar months, from 21 August 1998 to 25 July 1999. As bat activity may differ between lunar phases (Morrison 1978), each trapping period was started within 3 days of the New Moon so that the 2-week sampling period included both new and full lunar phases. For each trapping period, one trap within each pair was randomly designated the "day" trap, the other the "night" trap. For each trap pair the covers were switched between day and night traps at dawn and at dusk within a 30-min period. The times when the covers were moved (between 0445 and 0555 hours and 1715 and 1830 hours) were determined by local light conditions.

Seed loss from the traps due to predation was assumed to be minimal on the basis of observations and seed predation experiments. Arthropods capable of eating or carrying seeds were rarely observed in the traps and were never observed carrying or feeding on seeds. Birds and rodents were never observed on or in the traps during the twice-daily checks and at other times when we were in the trapping areas. To assess predation on larger seeds, four kidney bean seeds (*Phaseolus vulgaris*, 13 mm long) were placed in each trap 4 days before the end of the July 1999 trapping period. All kidney bean seeds were recovered intact when the traps were collected.

The nylon trap cones and contents were air-dried. Larger seeds and fruits were separated. Debris remaining in traps after removal of leaves and twigs was transferred to a small cloth bag, which was agitated in a detergent solution and air-dried. The contents were examined for smaller seeds using magnifying lenses. For each trap,

seeds were sorted by morphotype and apparently full and undamaged seeds were counted; for species in which seed counts exceeded 200 seeds per trap, number were estimated by using subsamples. Seed viability was not assessed. Seeds in fruits were tallied separately.

The possibility of undercounting small seeds because they were discarded with debris or overlooked during tallying was assessed by placing a random number (0–14, mean = 7) of *Ficus* seeds (ca. 0.8 mm long) that had been dyed brown in traps the day before the end of the January 1999 trapping period. Seeds were recovered from 81 out of 87 traps (93%) in which seeds were placed. Of the 647 seeds placed in traps, 72% were recovered.

Insofar as possible, morphotypes were identified to species by comparison with a reference collection assembled while monitoring tree phenology, or by comparison with herbarium specimens of taxa encountered in the study area. Seed length and weight were measured on air-dried seeds. Fibrous structures derived from the fruit wall and closely associated with the seed coat were included in the measurements.

Each seed morphotype was assumed to correspond to a single plant species, with the following exceptions. For the genera *Medinilla, Freycinetia, Schefflera,* and *Eurya,* two or more species are thought to be represented, based on species presence in the vegetation or differences in seed morphology. Separating seeds of the genus *Ficus* into species is difficult or impossible (Thomas 1982; Duncan and Chapman 1999). I grouped *Ficus* seeds into five morphotypes, but the variation within some morphotypes suggests that some groups include more than one species. For simplicity, seed morphotypes are referred to as species in the results.

Based on morphology, seeds were categorized into the following dispersal modes: wind, vertebrate (endozoochory), and no special device, following Willson et al. (1990). The traps were not effective at sampling seeds of grasses and of herbs and shrubs in the Asteraceae because the trap height was higher than some fruiting plants, so their seeds are not reported here.

Seed species were classified as to source habitat based on representation in the vegetation. Successional species were those represented by reproductive individuals in the successional area. Forest species were reproductive in forest but not in the successional area. For seed morphotypes that were not identified to plant species, if most seeds trapped fell in forest traps they were assumed to have come from forest plants. Two of the five morphotypes of *Ficus* could not be assigned to a regeneration strategy as appreciable numbers of seeds landed in both successional area and forest traps, and species of *Ficus* were present in both habitats.

Netting and observations of bats and birds

To record the composition of the fruit bat community, fruit bats were netted each month from August 1998 to August 1999. Bats were identified following Ingle and Heaney (1992). Birds were observed opportunistically, and Dale Clayton and Sarah Al-Tamimi of the University of Utah captured birds with mist nets set in the forest within the study area in April 1999, depositing voucher specimens in The Field Museum, Chicago.

Data analyses

ANOVAs were used to determine whether seed input into traps (measured as seed density and number of species per trap) differed significantly among dispersal agents (bird, bat, wind) and with distance to source habitat of seeds. As the dependent variables were not normally distributed, number of seed species was transformed by taking the square root, and seed density (seeds m^{-2}year^{-1}) was transformed as ln (seed density +0.01). Separate analyses were performed for input of seeds from forest plants into the successional area (including the successional area edge), and that from successional plants into forest. For successional seeds trapped in forest, distance to source habitat was to the abandoned farm or the road, whichever was closer. For each dispersal agent, the two

measures of seed input were regressed separately on distance from source habitat.

To examine the relationship between seed mass and the probability of dispersal from source to destination habitats, two ratios of representation in seed traps in the two habitats were used to estimate probability of dispersal. For each seed species I calculated the ratio between destination and source habitats of: (1) the 75th percentiles of the number of "free" seeds (excluding those in fruits) per trap in each habitat; and (2) the proportion of traps in each habitat in which the species was represented. The 75th percentile was used instead of the mean or the median because the means were highly influenced by traps with the most seeds, and for most species the median number of seeds in a trap in the destination habitat was zero. Both ratios were regressed against seed mass for (1) wind-dispersed species from forest to the successional area, (2) vertebrate-dispersed species from forest to the successional area, and (3) vertebrate-dispersed species from the successional area to forest. Species with zero values for median number of seeds per trap in the source habitat were excluded from the analysis, with the exception of vertebrate-dispersed successional seeds as only three species fit this criterion, so for this group the analysis was performed on species with 75th percentiles in the source habitat >0.

As successional edge traps were surrounded by successional vegetation they were pooled with successional area traps as the source habitat for successional seeds. Seed mass was $\log_{10}$ transformed. Analyses were performed using SAS System for Windows release 8.2 (SAS Institute 1999). Tests were considered significant if $P<0.05$.

Results

Frugivorous bats and birds

A total of 16 bird species whose diets include fruits were recorded at the study area (Table 1). As observations and netting were opportunistic, this list probably represents only a subset of the avian frugivores. Passerines comprised ten species, ranging in mass from 7 to 60 g. Doves and parrots, represented by four species, weighed 100–200 g, and the two species of hornbills ranged from 450 to

Table 1 Species of frugivorous birds and bats recorded in the study area. Body weights are from captured individuals, museum specimens, or the literature

Scientific name	Common name	Body wt. (g)
Columbidae		
Ptilinopus occipitalis	Yellow-breasted Fruit Dove	170–210
Phapitreron amethystina	Amethyst Brown-Dove	100–130
Phapitreron leucotis	White-eared Brown-Dove	75–105
Psittacidae		
*Prioniturus montanus**	Montane Raquet-tail	100
Bucerotidae		
Buceros hydrocorax	Rufous Hornbill	1300–1600
Penelopides panini	Mindanao Tarictic Hornbill	450
Campephagidae		
Lalage nigra	Pied Triller	24–30
Pycnonotidae		
Hypsipetes philippinus	Philippine Bulbul	35–40
Pycnonotus goiavier	Yellow-vented Bulbul	25
Timaliidae		
Macronous striaticeps	Brown Tit-Babbler	15–18
Turdidae		
Turdus sp.	Thrush	60
Sturnidae		
Basilornis miranda	Apo Myna	105–115
Zosteropidae		
Zosterops montanus	Mountain White-eye	7–9
Lophozosterops goodfellowi	Black-masked White-eye	17–19
Dicaeidae		
Dicaeum ignipectus	Fire-breasted Flowerpecker	7–9
Dicaeum nigrilore	Olive-capped Flowerpecker	10
Pteropodidae		
Alionycteris paucidentata	Mindanao pygmy fruit bat	14–18
Cynopterus brachyotis	Common short-nosed fruit bat	30–40
Dyacopterus spadiceus	Dayak fruit bat	85–95
Haplonycteris fischeri	Philippine pygmy fruit bat	16–20
Harpyionycteris whiteheadi	Harpy fruit bat	90–110
Ptenochirus jagori	Musky fruit bat	70–90
Ptenochirus minor	Lesser musky fruit bat	55–70
Pteropus vampyrus	Golden-backed flying fox	750–800
Rousettus amplexicaudatus	Common rousette	65–75

* Seed predator

1,600 g. Most of the frugivorous bird species recorded include insects and other invertebrates in their diets, but doves, thrushes, mynas, bulbuls, and white-eyes were frequently observed feeding on fruits.

Eight species of frugivorous bats were netted (Table 1), ranging in body weight from 14 to 110 g. *Ptenochirus jagori* and *P. minor* comprised 76% of total captures, whereas *Alionycteris paucidentata*, *Dyacopterus spadiceus*, and *Rousettus amplexicaudatus* were represented by one or two captures. On several nights in November and December 1998 up to 500 flying foxes, which include fruit in their diet, were observed flying over the study area at dusk. These were probably from a day roost of 750 g *Pteropus vampyrus* about 7 km SW of the study area.

Overall composition of the seed rain

A total of 136,480 seeds was collected in seed traps in all habitats. Most seeds were collected "free"; <1% was in fruits that landed in traps. The seeds represented 92 morphotypes, of which 66 were vertebrate-dispersed, eight were wind-dispersed, and 18 had no obvious dispersal device. Of the 66 vertebrate-dispersed species, 38 were classified as coming from forest plants and six from successional plants. Seventeen of the 21 vertebrate-dispersed species that were not classified to source habitat were represented by ≤10 seeds. Of the eight wind–dispersed species, seven were forest trees and one occurred in older successional vegetation.

Dispersal of forest seeds into the abandoned farm: dispersal agent and distance

For input of forest seeds into the successional area, both seed density and number of species were significantly affected by distance from forest (0–40 m), dispersal agent (wind, birds, bats), and the interaction between distance and dispersal agent (Table 2 a). For all dispersal agents, seed input tended to decrease with distance from source vegetation (Fig. 2). This relationship was strongest for bat-dispersed seeds.

Wind-dispersed forest seeds outnumbered vertebrate-dispersed forest seeds by a factor of 15 in the successional area. Density of wind-dispersed seeds averaged 4,294±2,159 seeds $m^{-2}year^{-1}$ (n=7) at forest edge (just outside the crowns of forest trees, of which some produced wind-dispersed seeds), and 102±78 seeds $m^{-2}year^{-1}$ (n=2) in traps 40 m from forest edge. Densities of bird-dispersed seeds ranged from an average of 129.1±69.0 seeds $m^{-2}year^{-1}$ (n=6) at 10 m from forest edge to 6.5±4.3 seeds $m^{-2}year^{-1}$ (n=2) at 40 m from forest, and those of bat-dispersed forest seeds from 56.1±15.6 seeds $m^{-2}year^{-1}$ (n=7) at the forest edge and 1.1±1.1 seeds $m^{-2}year^{-1}$ (n=2) at 40 m.

The top four wind-dispersed species were recorded in at least 8 of the 12 traps in the successional area (Table 3). In contrast, of the top four vertebrate-dispersed forest species represented in the day seed rain in the successional area, only one was trapped in over half the traps; of the top four species in the night seed rain, all were caught in less than half the traps (Table 4 a).

Table 2 Results of ANOVA analyses on predictor variables on seed density (log–transformed) and number of species per trap (square root transformed) of (*a*) seed input of forest seeds into the successional area, and (*b*) seed input of successional seeds into forest

Effect	df	Seed density F	No. of species F
(a)			
Distance	1	25.45****	23.12****
Dispersal agent (wind, birds, bats)	2	13.12****	12.57****
Distance × Dispersal agent	1	3.57*	3.29*
Total	56		
(b)			
Distance	1	22.38****	17.35***
Dispersal agent (birds, bats)	1	0.34	0.23
Distance × Dispersal agent	1	6.79*	5.53*
Total	43		

*<0.05; **<0.01; *** <0.001; **** <0.0001

Table 3 Wind-dispersed forest species trapped in the successional area: densities, numbers of traps with seeds (of 12), and seed measurements, for species represented by ≥20 seeds

Species	Family	Seed mass (mg)	Seed length (mm)	Seed density (seeds $m^{-2}year^{-1}$)	Traps with seeds
Spiraeopsis celebica	Cunoniac.	0.041	1.8	1,333	12
Weinmannia hutchinsonii	Cunoniac.	0.065	1	56	12
Alstonia cf. *macrophylla*	Apocynac.	1.6	5	11	9
Vernonia arborea	Asterac.	0.46	4	4	8
All seeds				1,405	

256

Fig. 2 Input of forest seeds (seed density, number of species per trap) into the successional area versus distance from forest by **a** wind, **b** birds, and **c** bats. Seed density is plotted on a log scale; 1 was added to values so that zeros would not be excluded. Note differences in scale on y-axis. Some points in the plots of numbers of species represent more than one observation. P and adjusted R^2 values are for the regressions on distance of seed density (transformed by taking the natural log of $0.01 +$ seeds m^{-2}year^{-1}) and of number of seed species per trap (square root transformation)
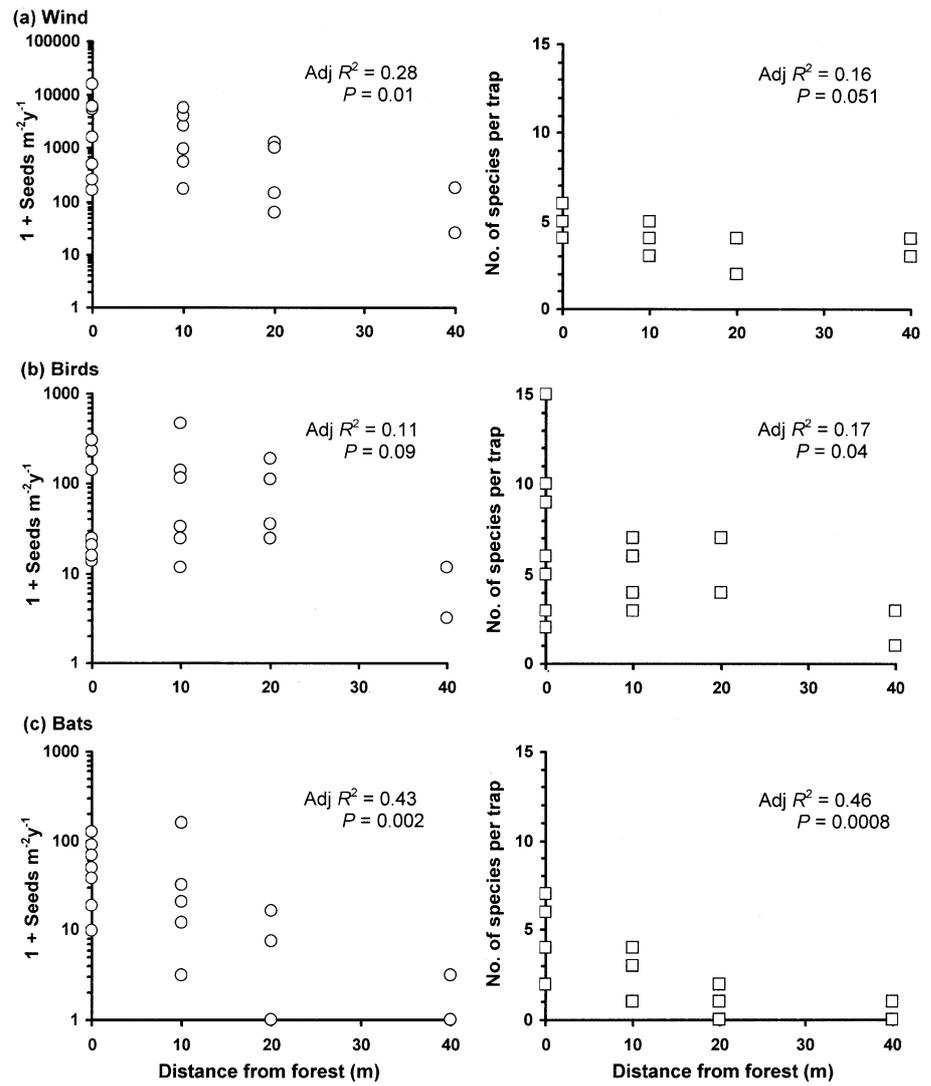
Table 4 Day and night seed densities (seeds m^{-2}year^{-1}), numbers of traps with seeds, and seed measurements, for species represented by =20 seeds for (*a*) vertebrate-dispersed forest species trapped in the successional area (12 traps), and (*b*) vertebrate-dispersed successional species trapped in forest (22 traps)

Species	Family	Habit	Seed mass (mg)	Seed length (mm)	Day		Night	
					Density	Traps	Density	Traps
(a)								
Freycinetia spp.	Pandanac.	Vine	0.077	1	37.8	5	3.8	4
Eurya spp.	Theac.	Tree	0.35	1	13.0	9	3.1	5
Schefflera spp.	Araliac.	Vine	2.5	4.5	13.7	5	0.2	1
Unidentified sp. A			0.13	1.1	0.4	2	12.7	3
Vaccinium elegans	Ericac.	Tree	0.12	1.3	7.6	1	0.2	1
Urophyllum sp.	Rubiac.	Treelet	0.15	0.8	7.2	1		
Ficus sp. 1	Morac.		0.23	1.5	5.2	7	1.3	3
All Forest Seeds					95.1		22.1	
(b)								
Aralia bipinnata	Araliac.	Treelet	0.37	2.2	34.33	21	4.06	11
Rubus sp.	Rosac.	Shrub	0.33	1.4	17.29	16	2.09	10
Melastoma malabathricum	Melastom.	Shrub	0.055	0.7	16.39	20	2.35	8
Saurauia spp.	Actinidiac.	Treelet	0.092	0.9	4.55	10	0.89	5
All successional seeds					74.4		9.7	

Fig. 3 Input of successional seeds (seed density, number of species per trap) into forest versus distance from source habitat by **a** birds, and **b** bats. Seed density is plotted on a log scale; 1 was added to values so that zeros would not be excluded. Note differences in scale on *Y-axis*. Some points in the plots of numbers of species represent more than one observation. *P* and adjusted R^2 values are for the regressions on distance of seed density (transformed by taking the natural log of seeds m^{-2}year^{-1}+0.01) and of number of seed species per trap (square root transformation)
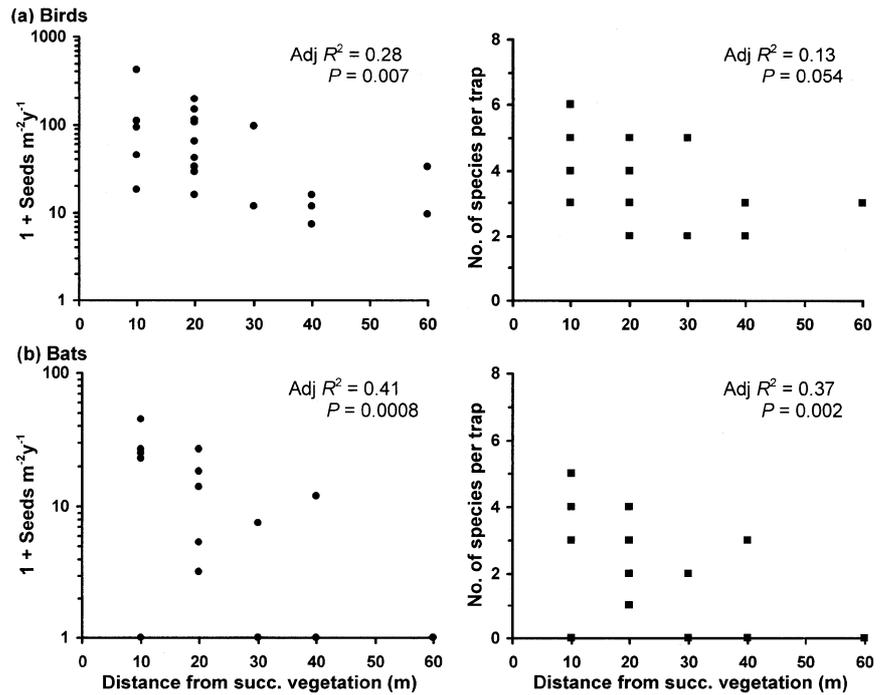
Spiraeopsis celebica, which accounted for 95% of the wind-dispersed forest seeds trapped in the successional area at least 10 m from the forest (Table 3), establishes in openings and persists in the forest canopy. Most seeds trapped probably came from two fruiting trees in the forest on the west edge of the successional area.

Six of the seven most common species of vertebrate-dispersed forest seeds represented in the seed rain in the successional area were found in higher densities and in higher numbers of traps in day than night, with the exception having higher densities in the night than the day due to a large number of seeds in one trap (Table 4 a). Most seeds were small, ≤0.35 mg mass and =1.5 mm long. *Freycinetia* spp., a minute-seeded climber in the Pandanaceae, dominated the forest seeds trapped in the successional area. Although *Vaccinium elegans* and *Urophyllum* sp. were trapped at relatively high densities (>7 seeds m^{-2}year^{-1}), they were recovered in only 1 or 2 of the 12 traps in the successional area.

Dispersal of successional plant seeds into the forest: dispersal agent and distance

Input of vertebrate-dispersed successional seeds into forest was significantly affected by distance from source habitat (0–60 m), and the interaction between distance and dispersal agent (birds, bats) (Table 2 b). Input of both bird- and bat-dispersed successional seeds declined with distance from source vegetation, with a stronger relationship for bat-dispersed seeds (Fig. 3).

Aralia bipinnata was the most abundantly represented successional species in forest traps (Table 4 b). Other well-represented species were *Melastoma malabathricum, Ru-*
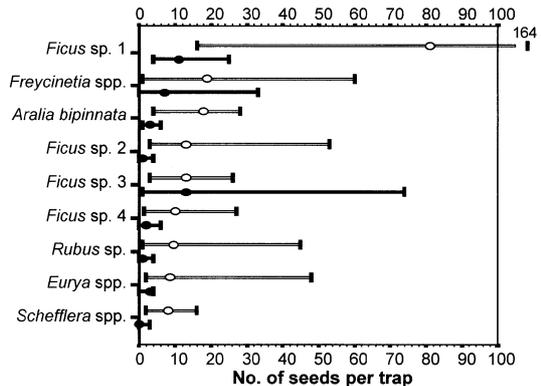
Fig. 4 Day (*open circles*) and night (*filled circles*) trap data for seed species with a 75th percentile of ≥5 seeds per trap. *Circles* are 75th percentiles of number of seeds per trap; *bars* to left and right indicate medians and 90th percentiles, respectively

bus sp., and *Saurauia* spp. None of these species, all with seeds <4 mg, were observed in the area in which forest traps were set, yet all but *Saurauia* spp. were trapped in over half of forest traps. All were trapped in greater densities and numbers of traps in the day than in the night.

Species representation in day and night seed rain

Excluding trap-seed species combinations in which fruiting conspecifics occurred above traps or were suspected to do so, only 9 of the 66 vertebrate-dispersed seed species were represented by ≥5 seeds in at least a quarter of either day traps or night traps (i.e., 75th percentiles ≥5) (Fig. 4). Typical of seed trap data, the high
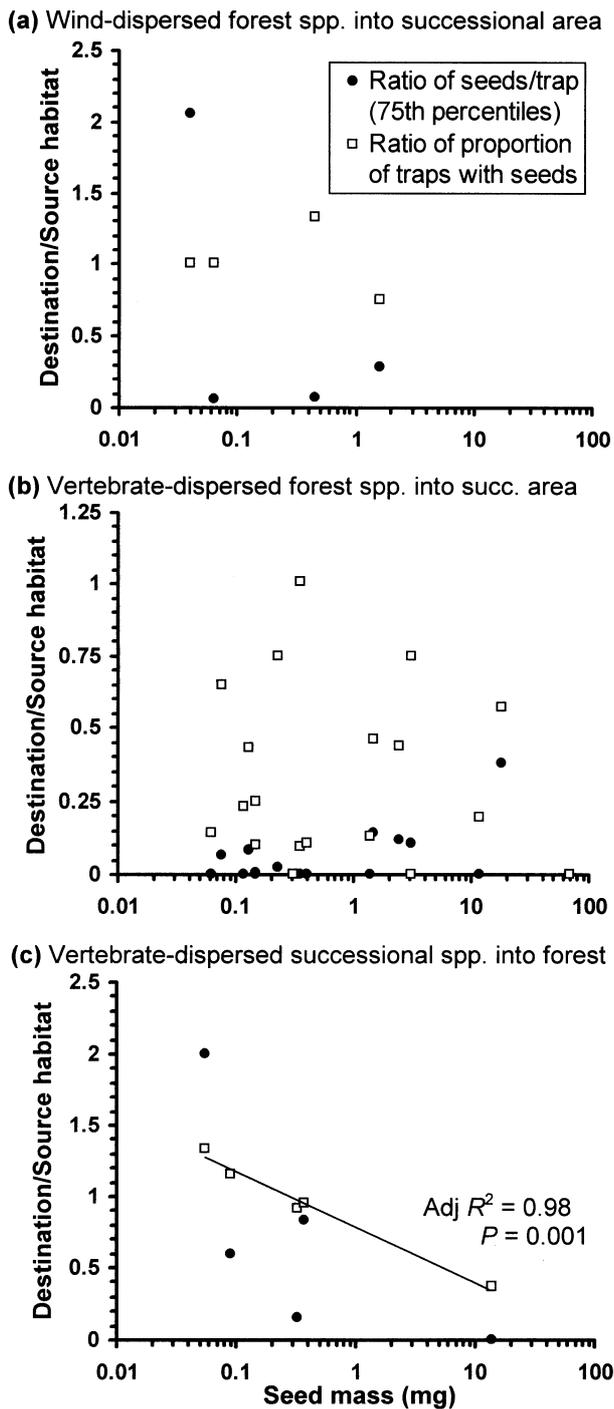
258

(a) Wind-dispersed forest spp. into successional area

- Ratio of seeds/trap (75th percentiles)
- Ratio of proportion of traps with seeds

(b) Vertebrate-dispersed forest spp. into succ. area

(c) Vertebrate-dispersed successional spp. into forest

Adj R^2 = 0.98
P = 0.001

Seed mass (mg)

Fig. 5a, b Ratios of representation of seed species in destination and source habitats plotted against seed mass. *Filled circles* are destination/source habitat ratios of 75th percentiles of number of seeds per trap; *open squares* are ratios of the proportions of traps with seeds. Plots are of **a** wind-dispersed species from forest to the successional area, **b** vertebrate-dispersed species from forest to the successional area, and **c** vertebrate-dispersed species from the successional area to forest. Note differences in the scales of the *y*-axis. Significant *P* values for the regression of ratios on log seed mass and corresponding adjusted R^2 values are indicated

values of the 90th percentiles relative to the 75th percentiles show that a few traps collected most seeds. For all nine species, median numbers of seeds per trap were higher for day traps, and both the 75th and 90th percentiles were higher in day traps than night traps for all but one species, indicating a greater overall dispersal role by birds, with bat dispersal negligible for five of the nine species.

Seed dispersal between habitats: relationship with seed mass

For both wind-dispersed and vertebrate-dispersed species of forest seeds, no relationship was detected between seed mass and either of the two measures of the probability of dispersal into the successional area (Fig. 5a, b). For species of vertebrate-dispersed successional seeds, seed mass was strongly negatively related to the ratio of the proportion of traps with seeds in forest and the successional area (Fig. 5c). The two successional species with the smallest seeds, *Melastoma malabathricum* and *Saurauia* spp., had higher probabilities of landing in seed traps in the forest than in those in the successional area (Fig. 5c).

Discussion

Input of forest seeds into the successional area was dominated by wind-dispersed seeds

The numerical preponderance of wind-dispersal among forest seeds trapped in the successional area was unexpected because vertebrate-dispersed woody plants exceeded wind-dispersed plants by a factor of over three for basal area and over six for stem density and number of species. In other forest and successional vegetation sites in the tropics, densities of vertebrate-dispersed seeds at least twice those of wind-dispersed seeds were recorded (Young et al. 1987 – Costa Rican secondary forest and successional vegetation; Martinez-Ramos and Soto-Castro 1993 – Mexican rainforest; Loiselle et al. 1996 – Costa Rican rainforest). But differences in methods among these studies and mine make comparisons problematic. Most of the wind-dispersed seeds in my study were <1 mm wide and <0.01 mg. The Mexican study excluded seeds <1 mm, and the Costa Rican studies counted germinants from soil trays instead of trapped seeds. Because germination of very small seeds can be inhibited by even low levels of soil or litter (Molofsky and Augspurger 1992; Metcalfe and Grubb 1995; Dalling et al. 1998), germination trays are likely to underestimate the smallest seeds.

The wind-dispersed species common in seed traps, *Spiraeopsis celebica*, *Weinmannia hutchinsonii*, *Alstonia macrophylla*, and *Vernonia arborea* are small to minute-seeded early seral species that establish on poor or mineral soils (van Steenis 1972). Small wind-dispersed seeds appear to be an effective strategy for pioneer

canopy species to distribute their seeds widely. On Barro Colorado Island in Panama, the small wind-dispersed seeds of *Jacaranda copaia*, *Terminalia amazonica*, and *Luehea seemanii* were trapped in all or all but one of 200 seed traps, despite being relatively rare trees in the forest (Harms 1997).

Although wind-dispersed seeds landed in high densities, very few seedlings were observed in both the forest and the successional area. Seed size is negatively correlated with establishment (Silman 1996; Dalling et al. 1998), and the litter-free sites that small seeds often require to establish were rare or absent in the successional area. Management to modify microsites may enhance their regeneration; in Thailand, cutting grasses and ferns before seed fall of *Engelhartia spicata* was recommended (Hardwick et al. 1997).

Seed input declined with distance from source habitat

The observed decrease in seed input with distance from source habitat for both forest and successional seeds was expected, and has been documented elsewhere in the tropics for dispersal of both wind and vertebrate-dispersed seeds between early successional vegetation and forest (Willson and Crome 1989; Martinez-Garza and Gonzalez-Montagut 1999, 2002).

The negative relationship with distance for dispersal of forest seeds into the successional area was stronger for bats than for birds. In contrast, seed input into a 25-m-wide strip clearcut in Amazonian rainforest showed a more pronounced decline with distance from edge for bird-dispersed seeds than for bat-dispersed seeds (Gorchov et al. 1993). The availability of perching structures in the successional area may have diminished the effect of distance from source habitat on seed input from birds.

Bird-dispersed seeds predominated over bat-dispersed seeds

In the moist Neotropics, the early successional species that commonly establish in gaps and open areas in or adjacent to forests (e.g., *Piper* spp., *Solanum* spp., *Vismia* spp., and *Cecropia* spp.) are primarily (but not exclusively) bat-dispersed (Foster et al. 1986; Uhl 1987; Gorchov et al. 1993, 1995; Medellin and Gaona 1999). But in my study, birds dispersed more seeds and species of successional plants into forest than bats.

Neotropical and Asian fruit bats are commonly considered ecological equivalents, but Asian fruit bats belong to a separate suborder and cannot echolocate. The frugivorous bird communities of Asia and the Neotropics are also taxonomically distinct; of the 15 bird families in Asia in which frugivory has been consistently observed, only 3 also occur in the New World (Corlett 1998).

Seeds of successional plants in Southeast Asia tend to be larger than their counterparts in the Neotropics (Putz and Appanah 1987), and Grubb (1998) suggested that

their size precludes them from bat dispersal. A detailed study in Amazonian forest found the a combination of fruit length, type, and color best separated bird fruits from bat fruits, but no association between seed size and frugivore group was detected (Gorchov et al. 1995). Fruit morphology rather than seed size may be the more important factor in determining the dispersers of Southeast Asian successional species, many of which have arillate seeds (e.g., various Euphorbiaceae, *Alphitonia* spp., and *Clerodendrum* spp.), a character associated with bird dispersal (Gorchov et al. 1995). The fruits of successional species in my study area also appear to be more accessible and attractive to birds than to bats, but the diversity of plant and disperser communities represented in Southeast Asia caution against generalizing from one or a few studies. A variety of patterns is likely. For example, the dominant pioneer on degraded land in Singapore, *Adinandra dumosa* (Theaceae), is dispersed primarily by the fruit bat *Cynopterus brachyotis* (Phua and Corlett 1989; Corlett 1991).

Smaller successional seeds had higher probability of dispersal to forest

Among vertebrate-dispersed successional seeds, smaller seeds were more likely to be dispersed into the adjacent forest. For fruits that are swallowed whole, larger fruits (which often have larger seeds) have fewer avian disperser species because gape width constrains the upper size limit of available fruits (Wheelwright 1985; Dowsett-Lemaire 1988). But the smallest frugivores observed, Mountain White-eyes (8 g body weight), were seen feeding upon the compound fruits of the largest-seeded successional species, *Mallotus ricinoides* (14 mg, 4.5 mm diameter), and all other successional species common in the seed rain had seeds small enough (0.7–1.5 mm long) to pass through the guts of even small frugivorous birds and bats (Levey 1986; Corlett 1998). Nonetheless, not all seeds small enough to pass through a frugivore gut are necessarily processed in this way: in feeding trials with captive frugivorous birds, the proportion of seeds that were spat out or regurgitated increased with seed size (Levey 1987). Ingested seeds tend to be moved farther than those that are spat out or regurgitated, often while feeding in the fruiting plant.

Community-level studies of seed production and dispersal have largely ignored seed size (an exception is Jackson 1981), and commonly express seed input as counts or densities that lump together species that differ in seed mass by orders of magnitude. While convenient, such summary numbers implicitly weight seeds of different sizes equally, an assumption that may not be appropriate given that relationship of seed size with seed production (Greene and Johnson 1994), seedling establishment (Silman 1996; Dalling et al. 1998), and, as shown by my study, probability of dispersal.

Seeds of the smallest-seeded successional species were more evenly distributed in the forest than in the source

habitat, landing in a higher proportion of traps. This may be because perching sites and food resources were more likely to be found above traps in the forest than in the successional area, where not all traps were under woody vegetation. Other studies have found higher seed rain under trees or artificial perches than in open areas (Guevara et al. 1986; Holl 1998; Duncan and Chapman 1999) and under trees that produce vertebrate-dispersed fruits compared to those that do not (Slocum and Horvitz 2000).

It is worth noting that the size range of vertebrate-dispersed forest seeds collected in traps was much smaller than that represented in the vegetation. Larger seeds are produced in smaller numbers and were therefore not sampled effectively with the limited number of seed traps. In the successional vegetation a feeding roost of *Ptenochirus* fruit bats under an abaca (*Musa textilis*) plant accumulated seeds of *Prunus* spp. and *Syzygium* spp. (both =1 cm diameter), and a variety of bird species were observed feeding on *Cinnamomum* spp. and *Syzygium* spp., indicating that larger seeds are being dispersed by both birds and bats.

Implications for forest restoration

Much of the impetus for studies of seed dispersal comes from an interest in the re-establishment of forest on deforested sites. Most vertebrate- and wind-dispersed seeds will land within 100 m or less of a fruiting tree (Greene and Johnson 1996; Laman 1996), so planting forest trees that themselves produce seeds into degraded areas will be necessary to expedite regeneration. In my study, birds dispersed more seeds than bats, and wind-dispersed forest seeds were most abundant in the seed rain in successional vegetation within 40 m of forest. Therefore, woody plants producing relatively small, wind- and bird-dispersed seeds hold promise for initial colonization of cleared areas on Mt. Kitanglad, provided that obstacles to establishment can be addressed. Large-seeded trees will require planting in subsequent efforts, as these can be severely limited by dispersal (Corlett 1991; Wunderle 1997), and are depended upon by hornbills and other strict forest frugivores, of which most are endemic (Hamann and Curio 1999). The remaining tropical forest fragments are reservoirs of forest plant and animal populations and nuclei from which regeneration can take place (Turner and Corlett 1996); the importance of their conservation cannot be overemphasized.

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