



<b>Title</b>	<b>Seed rain into upland plant communities in Hong Kong, China</b>
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2 **Seed rain into upland plant communities in Hong Kong, China**

3

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11 **Key words:** Birds, Frugivory, Seed dispersal, Seed traps, Succession, Tropics12 **Abstract**

13 Hong Kong is an extreme example of tropical landscape degradation, with no substantial remnants of the  
 14 original forest cover and a highly impoverished disperser fauna. Seed availability is a potential limiting  
 15 factor in vegetation recovery in such landscapes. To assess the quantity and quality of the seed rain of  
 16 woody taxa, seed traps were placed in the major upland vegetation types: fire-maintained grassland,  
 17 shrubland, and secondary forest. Within the grassland site, traps were placed under isolated trees, isolated  
 18 male and female shrubs of *Eurya chinensis*, and in the open. Seeds were collected every 2 weeks for 2 years.  
 19 The seed rain was highest under female shrubs in grassland (6455 seeds m<sup>-2</sup> year<sup>-1</sup>), where it was almost  
 20 entirely confined to their fruiting period. Next highest were isolated trees (890 seeds), followed by male  
 21 isolated shrubs (611 seeds), shrubland (558 seeds), forest (129 seeds) and open grassland (47 seeds). The  
 22 number of seed taxa was highest in shrubland (59), followed by isolated trees (42), forest (42), female  
 23 isolated shrubs (28), male isolated shrubs (15), and open grassland (9). The seed rain differed in species  
 24 composition between the forest, shrubland, and grassland sites, while the differences within the grassland  
 25 site were largely in terms of quantity. Birds (particularly bulbuls, *Pycnonotus* spp.) are known or inferred to  
 26 be the major dispersal agents for 85% of the seed taxa trapped, 99% of the total number of seeds trapped,  
 27 and 99.8% of the seeds trapped in the grassland site. Few taxa and < 1% of the total seeds were dispersed  
 28 by wind and no seed taxa were definitely dispersed by fruit bats. The results suggest that even in the most  
 29 degraded landscape the seed rain is adequate for the development of woody vegetation cover, but that  
 30 human intervention will be needed for the restoration of plant diversity.

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32

33 **Introduction**

34 The spatial pattern of dispersed seeds forms the  
 35 template for the subsequent recruitment of new  
 36 individuals into the plant community. This pattern  
 37 may be greatly modified by post-dispersal seed and  
 38 seedling mortality, but even in intact ecosystems  
 39 the input of seeds can limit recruitment of partic-  
 40 ular species (Makana and Thomas 2004). In dis-  
 41 turbed, fragmented, and degraded tropical  
 42 landscapes, many studies have suggested that seed  
 43 availability is a major limiting factor in vegetation

recovery (e.g., Duncan and Chapman 1999; Holl 44  
 1999). The pattern and composition of the seed 45  
 rain in such landscapes is thus an indicator of the 46  
 regenerative potential. Factors that influence the 47  
 composition of the seed rain at a particular point 48  
 include the density, distribution, and fecundity of 49  
 the seed sources in the vicinity, the spatial pattern 50  
 of dispersal by the dispersal agent or agents 51  
 involved, and the landscape features (such as perch 52  
 availability for birds) that influence seed deposi- 53  
 tion. Some of these factors are potentially open to 54  
 manipulation and may therefore provide a means 55

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56 of accelerating landscape recovery (Howe and  
57 Miriti 2004).

58 Analysis of the seed rain in relation to the  
59 surrounding plant community can also provide  
60 information on the relative importance of dif-  
61 ferent seed dispersal agents in the landscape.  
62 Wind-dispersed seeds are usually easily recog-  
63 nized, while dispersal by frugivorous birds and  
64 bats can be distinguished where fruit preferences  
65 are known, or by comparing the diurnal and  
66 nocturnal seed rain where they are not. Fruit  
67 bats are major dispersal agents for Neotropical  
68 pioneer trees (e.g., Medellín and Gaona 1999),  
69 but their role in the old world tropics is less clear  
70 (Corlett 2002; Ingle 2003). Detection of dispersal  
71 by non-flying mammals usually relies on the  
72 characteristics of the faecal material in which  
73 they are deposited. None of this is possible,  
74 however, unless the seed trap design allows the  
75 capture of seeds dispersed by the full range of  
76 plant growth forms and dispersal mechanisms of  
77 interest (Page et al. 2002).

78 Prolonged human impact increases the impor-  
79 tance of the seed rain by exhausting alternative  
80 sources for regeneration, but may also reduce its  
81 quantity and diversity by eliminating seed dis-  
82 persal agents (Howe and Miriti 2004). Hong Kong  
83 has an unusual combination for the tropics of a  
84 highly degraded landscape, from which most large  
85 frugivores have been lost, and economic prosper-  
86 ity, which has reduced recent human impacts and  
87 allowed landscape recovery to begin (Dudgeon  
88 and Corlett 2004). The major aims of this study  
89 were, therefore, to describe the spatial pattern of  
90 seed input to the degraded upland landscape of  
91 Hong Kong, to identify the major seed dispersal  
92 agents involved, and to explore the consequences  
93 for landscape recovery. Finally, we hoped to  
94 derive general lessons from this 'worst case  
95 scenario' that can be applied to the increasing area  
96 of severely degraded landscapes in tropical East  
97 Asia.

## 98 Methods

### 99 Study area

100 All seed traps were located between 170 and 700 m  
101 elevation on Hong Kong's tallest hill, Tai Mo Shan  
102 (22°25', 14°07' E), in the central New Territories,

which forms part of the Chinese mainland. The 103  
topography of the site is rugged. Slopes and upper 104  
valleys are covered in fire-maintained grassland, 105  
shrubland, and isolated trees, with patches of sec- 106  
ondary forest mostly along streams and at lower 107  
altitudes. The study area is on the northern and 108  
altitudinal limits of the climatic tropics, with hot 109  
wet summers and cool dry winters (Dudgeon and 110  
Corlett 2004). The temperature falls below zero 111  
several times a decade above 400 m elevation. Data 112  
from Hong Kong's dense network of rainfall sta- 113  
tions suggests that there is a gradient of increasing 114  
mean annual rainfall in the study area from 2200 to 115  
2400 mm at the lowest sites to more than 3000 mm 116  
at the highest (Hong Kong Observatory 2004). 117

118 Within the study area, seed traps were located at  
119 three sites representing the major upland vegeta-  
120 tion types in Hong Kong: fire-maintained grass-  
121 land, secondary shrubland, and 30–50 year old  
122 secondary forest (Dudgeon and Corlett 2004). The  
123 same three sites have been used for a variety of  
124 other ecological studies, so both their floras and  
125 faunas are well known. Of particular relevance to  
126 this study, bird community composition has been  
127 quantified at the forest (Kwok and Corlett 1999)  
128 and shrubland (Leven 2000) sites, and in shrub-  
129 land within 200 m of the grassland site (Leven  
130 2000). All the sites are within 6 km of each other.  
131 The grassland is dominated by the grasses *Eulalia*  
132 *quadrinervis* Kuntze and *Ischaemum aristatum* L.,  
133 and there are scattered isolated trees (mostly  
134 *Machilus* spp.) and shrubs (mainly *Eurya* spp.).  
135 The shrubland dominants are *Litsea rotundifolia*  
136 (Nees) Hemsl., *Rhodomyrtus tomentosa* (Aiton)  
137 Hassk. and *Eurya* spp., with many other woody  
138 species present in smaller numbers. *Machilus* spp.  
139 dominate the forest canopy while *Psychotria asi-*  
140 *atica* L. and *Ardisia quinqueгона* Bl. dominate the  
141 understorey. Plant nomenclature follows Hong  
142 Kong Herbarium (2004).

### 143 Assessment of seed rain

144 Seed traps were placed on the ground in order to  
145 sample the seed rain from all vegetation layers,  
146 including low-growing shrubs. Each seed trap  
147 consisted of a plastic tray of surface area 0.18 m<sup>2</sup>  
148 (52×34 cm), with holes drilled in the base to drain  
149 out rainwater. The trays were lined with a brown  
150 cloth to prevent small seeds being washed out from

151	the holes and for easy collection of the seeds. The	common species (Corlett 1996, 2002; Au et al.	202
152	trays were covered by wire mesh (mesh size	unpublished).	203
153	1.5×1.5 cm) to exclude rodents, which are the		
154	major seed predators in the study area and quickly		
155	consume or remove seeds placed at ground level		
156	(K.P.S. Chung, personal communication). The	<i>Data analysis</i>	204
157	design was tested using a variety of non-local seeds	Seed counts from each trap were standardized to	205
158	and plastic beads, with losses always less than 5%.	number of seeds m <sup>-2</sup> year <sup>-1</sup> for data analysis. The	206
159	However, small wind-dispersed seeds – produced	wide variation in the number of seeds per fruit	207
160	only by herbaceous plants and a few woody vines	means that the seed numbers in traps give a mis-	208
161	in the study area – could potentially be blown out	leading picture of the number of frugivory events	209
162	of the traps at exposed sites.	needed to get them there. Most fleshy fruits in the	210
163	Many studies assess seed rain on a transect	study area are swallowed whole by most frugi-	211
164	across vegetation boundaries, usually from pri-	vores, so converting the seed rain into ‘fruit	212
165	mary forest to non-forest (e.g., Cubina and Aide	equivalents’, by dividing the number of seeds of	213
166	2001; Ingle 2003). In our study area, however, the	each species by the mean number of seeds per fruit,	214
167	vegetation consists of a complex mosaic of sec-	gives a rough estimate of the number of frugivory	215
168	ondary vegetation types of various ages, all of	events involved. Patterns in the species composi-	216
169	which may act as seed sources, and there are no	tion of the seed rain were analysed by non-metric	217
170	substantial primary forest remnants. The seed	multidimensional scaling (MDS) using the PRI-	218
171	traps in this study were therefore located in rela-	MER software package (Clarke and Warwick	219
172	tively uniform tracts of vegetation at least 20 m	1994). The standardized data were square-root	220
173	away from vegetation boundaries. Twenty traps	transformed to down-weight the effect of the most	221
174	each were haphazardly distributed in the shrub-	abundant seed species. Traps that collected no	222
175	land and forest sites with each trap at least 5 m	seeds during the study period (six grassland traps)	223
176	apart. In the grassland site, 20 traps were placed	were omitted from the analyses. The Bray–Curtis	224
177	under isolated trees (all <i>Machilus</i> spp., which did	coefficient was used as a similarity measure.	225
178	not fruit during the study period), 20 under iso-		
179	lated shrubs (all <i>Eurya chinensis</i> R. Br., 10 male	<b>Results</b>	226
180	and 10 female), and 20 in open grassland. While	A total of 37,002 seeds of 86 woody plant	227
181	there is replication within habitats, the spatial	taxa were collected in 2 years in the 100 seed	228
182	separation need for true independence made it	traps (total trap area = 18 m <sup>2</sup> ) (Appendix 1). The	229
183	logistically impossible to have independent repli-	mean seed rain was highest under female isolated	230
184	cates of each vegetation type.	shrubs in grassland (6455 seeds m <sup>-2</sup> year <sup>-1</sup> ), fol-	231
185	The traps were visited every 14(±3) days for	lowed by isolated trees (890 seeds m <sup>-2</sup> year <sup>-1</sup> ),	232
186	2 years, from April 2002 to March 2004, except for	male isolated shrubs (611 seeds m <sup>-2</sup> year <sup>-1</sup> ),	233
187	the traps under isolated shrubs, which were visited	shrubland (558 seeds m <sup>-2</sup> year <sup>-1</sup> ), forest (129	234
188	from August 2002 to July 2004. At each visit, the	seeds m <sup>-2</sup> year <sup>-1</sup> ), and open grassland (47	235
189	cloths were collected and replaced, and seeds were	seeds m <sup>-2</sup> year <sup>-1</sup> ) (Table 1). There was consider-	236
190	separated, counted, and identified in the labora-	able variation between traps in each habitat, par-	237
191	tory with the aid of a large reference collection. All	ticularly for isolated shrubs (Figure 1). Six of the	238
192	seeds and fruits in the traps were counted, but	20 open grassland traps collected no seeds in	239
193	intact fleshy fruits were excluded from further	2 years, while one trap under a female isolated	240
194	analysis, as they are likely to have fallen directly	shrub collected 5711 seeds year <sup>-1</sup> . The total num-	241
195	from above, and only seeds from woody plants are	ber of seed taxa collected was highest in shrubland	242
196	considered in this paper. The remote locations of	(59), followed by isolated trees (42), forest (42),	243
197	the study sites made the twice-daily visits needed	female isolated shrubs (28), male isolated shrubs	244
198	to distinguish diurnal and nocturnal seed rain	(15), and open grassland (9). Seed diversity (as	245
199	impractical, but seed dispersal agents are known,	seed taxa per 100 seeds) was highest in forest and	246
200	or can be reliably inferred, for almost all common		
201	woody species in Hong Kong, as well many less		

Table 1. Seed rain of woody taxa into seed traps placed in six habitats in upland Hong Kong.

Sites	Seed number (seeds $m^{-2} yr^{-1}$ )	Fruit equivalents <sup>a</sup> (fruits $m^{-2} yr^{-1}$ )	Seed taxa	Taxa per 100 seeds
Grassland: open	47	5	9	19.2
Grassland: isolated trees	890	90	42	4.7
Grassland: female shrubs	6455	733	28	0.4
Grassland: male shrubs	611	52	15	2.5
Shrubland	558	213	59	10.6
Forest	129	59	42	32.6

<sup>a</sup> Number of seeds of each species in the seed rain divided by the mean number of seeds per fruit. Fleshy fruited species only.

lowest under isolated trees and shrubs in grassland (Table 1). The number of seed taxa collected was positively correlated with the number of seeds across habitats, but this relationship was not significant (Spearman's Rank Correlation  $r_s = 0.70$ ,  $p = 0.14$ ).

*Eurya* (probably two shrub species) was the only seed taxon found in all habitats and it dominated the seed rain in grassland, particularly under the

isolated female shrubs of *Eurya chinensis* (Appendix 1; Figure 2). The pioneer tree *Schefflera heptaphylla* (L.) Frodin dominated the seed rain at the shrubland site, while there was no clear dominant in the forest. Sixteen taxa were represented only by a single seed in a single trap at one site. Potential forest canopy trees contributed < 0.1% of the seed rain at the grassland site, while light-demanding non-forest shrubs and small trees contributed < 10% of the seed rain at the forest site. The two-dimensional MDS plot (Figure 3) of seed species composition has a stress value of 0.13, suggesting it is a good representation of the similarities between traps (Clarke and Warwick 1994). The forest and shrubland traps form largely distinct groups, while the isolated tree, female shrub, male shrub, and open grassland traps form overlapping groups, with some of the open grassland traps as outliers. The major differences in species composition are thus between the forest, shrubland, and grassland sites, while the differences between the various habitats at the grassland site are largely a matter of seed quantity.

The seasonal pattern of seed rain differed little between the 2 years of study so the data have been combined (Figure 2). Most seed rain occurred between September and January, with

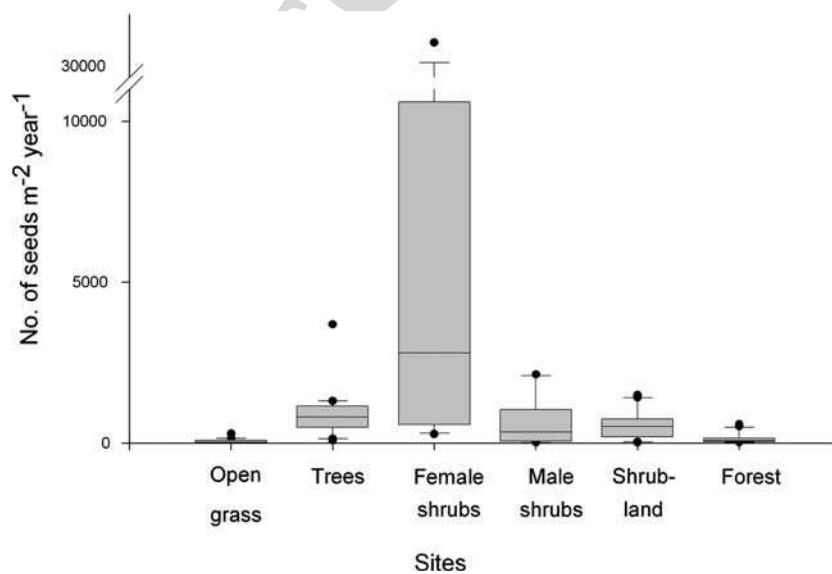


Figure 1. Box plots of numbers of seeds  $m^{-2} year^{-1}$  arriving in individual seed traps in six habitats in upland Hong Kong: open grassland, isolated trees in grassland, female and male isolated shrubs (*Eurya chinensis*) in grassland, shrubland, and forest. The box indicates the 25th and 75th percentiles, the line inside the box is the median, the capped bars indicate the 10th and 90th percentiles, and the outlying symbols are the extreme values.

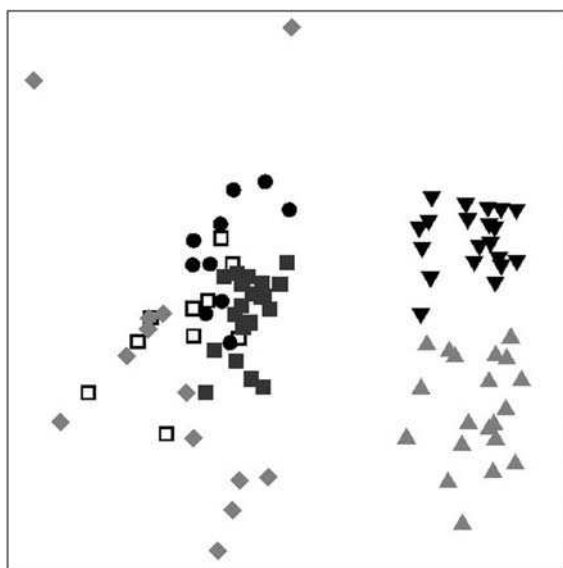


Figure 2. The seasonal pattern of seed rain (seeds  $m^{-2}$  per 2 weeks) in six habitats in upland Hong Kong. The shaded bar indicates the fruiting period of *Eurya chinensis*, under which the 'isolated shrub' seed traps were placed, and the dotted lines indicate the numbers of *Eurya* seeds in these traps. Note the different scales of the y-axes.

283 peaks for individual taxa outside this period.  
 284 Within the grassland site, the traps in open  
 285 grassland and under isolated trees showed a  
 286 similar temporal pattern, but almost all seed  
 287 dispersal to the male and female isolated *Eurya*  
 288 *chinensis* shrubs occurred while the female shrubs  
 289 were in fruit.

290 A total of 86 woody plant taxa were found in the  
 291 seed rain, of which six are wind-dispersed, and  
 292 seven have unknown dispersal agents (Appendix  
 293 1). The remaining 73 taxa are all known to be  
 294 dispersed by birds or, in a few cases, inferred to be  
 295 dispersed by birds or, in a few cases, inferred to be  
 296 dispersed by birds or, in a few cases, inferred to be  
 297 dispersed by fruit bats (2 taxa), civets (7 taxa),  
 298 and/or macaques (at least 2 taxa). However, no  
 299 civet or macaque faeces were found in the seed  
 300 traps and, although macaques usually spit out  
 301 large (>4 mm diameter) seeds singly (Lucas and  
 302 Corlett 1998) they were only present at the forest  
 303 site. No exclusively mammal-dispersed taxa were  
 304 found in the traps, although some exclusively bat-  
 305 dispersed fig species (*Ficus fistulosa* Bl., *F. hispida*  
 306 L.f., and *F. variegata* Bl.) are present in the study  
 307

area and may have been included among the '*Ficus*  
 spp.' that could not be identified to the species  
 level. In terms of numbers of seeds, 99% were  
 from taxa known or inferred to be dispersed by  
 birds and 0.8% (largely *Cratoxylum cochinchinense*  
 (Lour.) Bl. at the shrubland site) were dispersed by  
 wind. Taxa known to be at least occasionally dis-  
 persed by fruit bats made up 3.2% of the seeds,  
 but most of these were from *Schefflera heptaphy-*  
*lla*, which is predominantly dispersed by birds, and  
 only 0.4% were from taxa (mostly *Ficus* spp.) that  
 may have been dispersed largely by bats. Most of  
 the seeds dispersed by wind, unknown agents, or,  
 potentially, bats were found in traps at the  
 shrubland and forest sites, while 99.8% of seeds at  
 the grassland site came from taxa that are known  
 or inferred to be dispersed by birds.

Conversion of seed numbers into fruit equiva-  
 lents reduces the contrast between sites (Table 1)  
 because the seed rain at the grassland site is domi-  
 nated by species with many-seeded fruits (mean 9.4  
 seeds fruit<sup>-1</sup>), while species with few-seeded fruits  
 dominate the seed rain in shrubland (mean 2.6  
 fruit<sup>-1</sup>) and forest (mean 2.2 fruit<sup>-1</sup>). The median  
 seed size at the grassland site (1.5 mm diameter) was  
 also significantly smaller than that in both  
 shrubland (3.2 mm) and forest (4.1 mm)  
 (Kruskal–Wallace test,  $p < 0.001$ , Dunn's method  
 of multiple comparisons,  $p < 0.05$  for all pairwise  
 comparisons). All seeds from fleshy fruits came  
 from taxa with mean fruit diameters  $\leq 14.2$  mm,  
 except for several larger-fruited species of *Ficus*,  
 which are either soft enough for birds to peck out  
 seed-containing pieces or known to be dispersed by  
 bats.

## Discussion

The most striking result of this study is the over-  
 whelming dominance of bird-dispersed seeds and  
 taxa in the seed rain, particularly in the grassland  
 site. This contrasts not only with the typically  
 dominant role of fruit bats in similar situations in  
 the Neotropics (e.g., Uhl 1987; Medellin and  
 Gaona 1999), but also with the only other detailed  
 tropical Asian study, in the Philippines, where  
 birds were more important than bats, but wind  
 dispersed the majority of seeds into successional  
 vegetation (Ingle 2003). The contrast with the  
 Neotropics can be explained by the completely

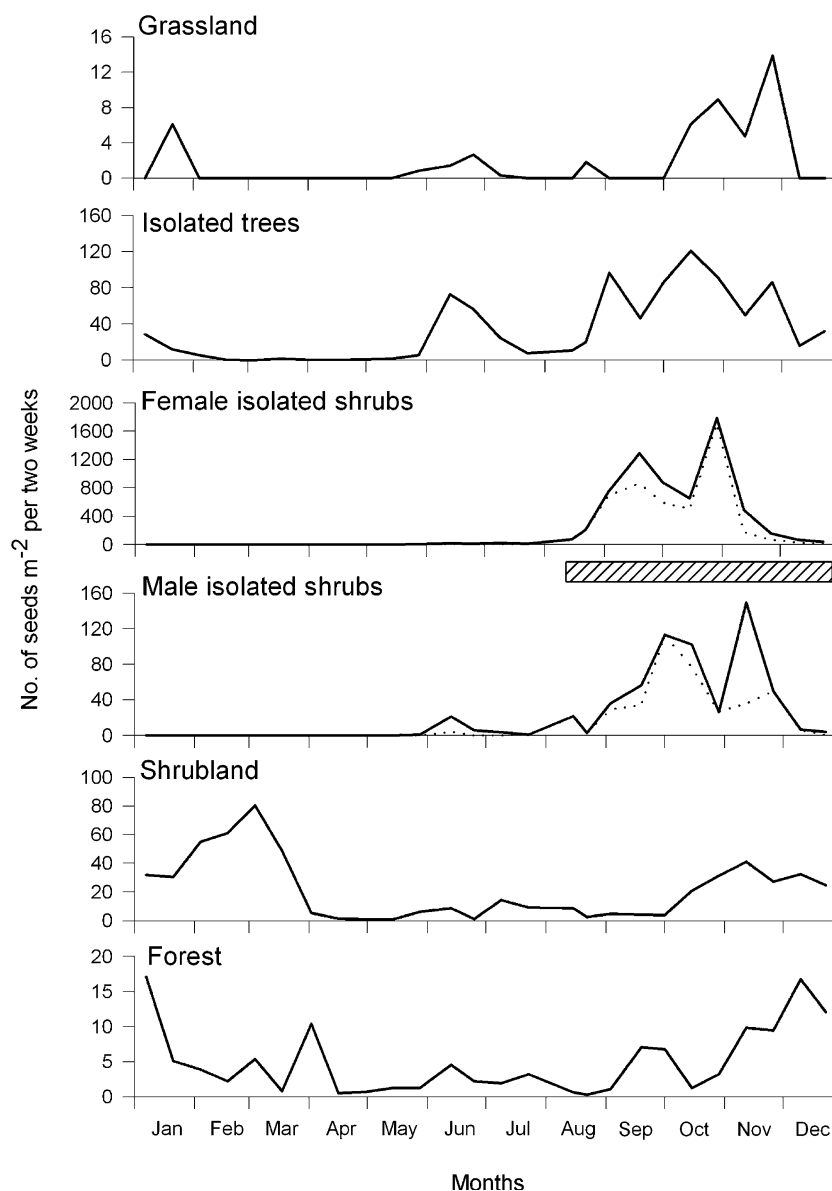


Figure 3. Two-dimensional MDS plot of the seed species composition in 94 individual seed traps in upland Hong Kong. Rhombus (fx): open grassland; square (■): isolated trees; circle (●): female isolated shrubs; open square (□): male isolated shrubs; inverted triangle (▼): shrubland; triangle (▲): forest.

356 different lineages of plants and animals involved,  
 357 including a different suborder of bats, largely  
 358 endemic families of frugivorous birds, and unre-  
 359 lated genera of woody pioneers (Primack and  
 360 Corlett 2005). However, *Cynopterus* fruit bats are  
 361 the sole dispersal agent for the dominant pioneer  
 362 on highly degraded sites in Singapore and the  
 363 southern Malay Peninsula, *Adinandra dumosa*  
 364 (Phua and Corlett 1989; Corlett 1991). The con-

trast with the Philippines seems to reflect simply  
 the absence from Hong Kong of the tiny-seeded,  
 wind-dispersed tree genera involved. Indeed, 99%  
 of the wind-dispersed seeds in the successional area  
 in the Philippines came from two species in the  
 family Cunoniaceae, which is absent from Hong  
 Kong (Ingle 2003). Wind-dispersed taxa were also  
 a very minor component in the woody succession  
 in Singapore (Corlett 1991).

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374 The light-vented bulbul, *Pycnonotus sinensis*  
 375 (mass 32 g) is the commonest frugivorous bird  
 376 across the entire habitat mosaic, followed by the  
 377 Japanese white-eye, *Zosterops japonicus* (10 g)  
 378 (Corlett 2002; Dudgeon and Corlett 2004). Other  
 379 similar-sized bulbuls, babblers (particularly *Garrulax*  
 380 spp.; 50–130 g), and – in winter – thrushes  
 381 (*Turdus*, *Zoothera*; 50–150 g) are important in  
 382 some of the habitats. The common bulbuls have a  
 383 gape limit for swallowing fruits of 13–14 mm  
 384 and are probable dispersal agents for all the bird-  
 385 dispersed taxa found. The spatial pattern of seed  
 386 dispersal generally matches the observed behav-  
 387 iour of the common bulbuls, including their will-  
 388 ingness to cross open areas to isolated perches  
 389 (Weir 2004). Although they clearly prefer tall  
 390 perches, such as isolated trees, they readily visit  
 391 smaller fruiting plants, which accounts for both  
 392 the concentration of seed rain under shrubs dur-  
 393 ing the fruiting period and the elevenfold disparity  
 394 in the number of seeds dispersed to female over  
 395 male shrubs, which otherwise appear identical.

396 The absence of independent replicates for each  
 397 vegetation type means that comparisons between  
 398 the grassland, shrubland, and forest sites should be  
 399 treated with caution. However, knowledge of the  
 400 plant and vertebrate communities at each site, and  
 401 on the relationships between them, gives us the  
 402 confidence to extrapolate the major results to other  
 403 sites in upland Hong Kong with similar biotas. The  
 404 effectiveness of grassland perches in attracting  
 405 frugivorous birds is highlighted by the higher seed  
 406 rain under isolated shrubs and trees than under  
 407 continuous shrubland and forest, presumably be-  
 408 cause perches in grassland act as bottlenecks in bird  
 409 movements across the open area. Many other  
 410 studies have shown that isolated trees and shrubs  
 411 act as foci for seed rain (e.g., Toh et al. 1999;  
 412 Guevara et al. 2004), but their function is likely to  
 413 depend strongly on the behavioural characteristics  
 414 of the principle seed dispersal agents involved.  
 415 Larger-gaped birds, such as *Garrulax* species, were  
 416 rarely seen to visit isolated perches in the study area  
 417 (Weir 2004), so perches may be ineffective in  
 418 attracting seeds from fruits that bulbuls avoid be-  
 419 cause of their size or other reasons. Seed diversity  
 420 (as seed taxa per 100 seeds) was strikingly lower  
 421 under perches in grassland than in shrubland and  
 422 forest, with grassland perches attracting many  
 423 small seeds but few species (Table 1). The shrub-  
 424 land and forest sites support a similar frugivore

fauna, more diverse than that in grassland, but the  
 mean total density of frugivorous birds is at least  
 five times higher in the forest than the shrubland  
 (Kwok and Corlett 1999; Leven 2000). This makes  
 the lower seed rain in forest, and lower number of  
 frugivory events needed to account for it (Table 1),  
 difficult to explain.

No seed trap design functions equally well for  
 all components of the seed rain and a major limi-  
 tation of this study is that seeds dispersed by ter-  
 restrial mammals were unlikely to be caught.  
 Within the study area, the masked palm civet  
 (*Paguma larvata*), small Indian civet (*Viverricula*  
*indica*), and a muntjac (*Muntiacus* sp.) are com-  
 mon and known to disperse seeds, including large  
 seeds from fruits too big for the common avian  
 frugivores to swallow (Corlett 1996; Dudgeon and  
 Corlett 2004). Muntjacs appear to deposit seeds  
 (such as *Choerospondias axillaries* (Roxb.) Burt &  
 Hill) only under a woody canopy, but both civets  
 frequently defecate in open areas, particularly on  
 paths or rocks. Taxa for which civets are known to  
 be important dispersal agents (*Diospyros*, *Elaeo-*  
*carpus*, *Gnetum*, *Syzygium*) are present, but not  
 common, in the study area, so the omission of this  
 component from the measured seed rain is unlikely  
 to change the overall picture much. Habitat-gen-  
 eralist rats (*Niviventer fulvescens* and *Rattus*  
*sikkimensis*) also disperse some very small seeds,  
 including those of the common pioneer shrubs,  
*Rhodomyrtus tomentosa* and *Melastoma* spp., but  
 their significance is unknown.

The seed template defines what is possible for  
 plant recruitment (Howe and Miriti 2004). What  
 actually happens depends also on post-dispersal  
 processes that result in seed and seedling mortality.  
 Rats are the major seed predators in the study area  
 (Hau 1997; K.P.S.Chung, personal communica-  
 tion), while anthropogenic fires are probably the  
 major cause of seedling and sapling mortality  
 (Dudgeon and Corlett 2004). Grazing by feral  
 cattle is also an increasing, selective, cause of  
 mortality. Seasonal drought, low soil nutrients,  
 and competition with grasses all reduce the sub-  
 sequent growth rate of established tree seedlings  
 (Hau and Corlett 2003). However, previous studies  
 in Hong Kong have shown that if grassland is  
 protected from fire for 10–15 years, colonization  
 by shrubs and trees suppresses the grasses and  
 greatly reduces fire susceptibility, suggesting that  
 fires are the major barrier to woody succession.



476 This study has shown that light-demanding  
477 shrubs and trees with small, small-seeded, fruits  
478 are well-dispersed in one of the most highly  
479 degraded of tropical landscapes. This means that  
480 the development of a woody plant cover is unlikely  
481 to be prevented by limited seed dispersal. There is  
482 a risk, however, that under-dispersal of the  
483 majority of the forest flora will lead to a low-  
484 diversity landscape, which may then persist indef-  
485 initely. There are indications of this in many parts  
486 of Hong Kong, where the relatively low-diversity  
487 secondary forests that have grown up in the last  
488 30–50 years contain pockets of high floristic  
489 diversity along streams and in other sites where  
490 woody species have persisted through the period of  
491 minimum forest cover, but have not yet spread out  
492 into the new forest areas (Zhuang and Corlett  
493 1997; Dudgeon and Corlett 2004). The close match  
494 between the dominant seed dispersal agents and  
495 the dominant fleshy fruited plants in the modern  
496 landscape is probably the result of multiple cycles  
497 of frugivory, seed dispersal, and plant growth,  
498 which will have tended to favour habitat-generalist  
499 frugivores and the fruit species they prefer.

500 A variety of interventions have been suggested  
501 to accelerate the recovery of deforested tropical  
502 landscapes (Howe and Miriti 2004). The provision  
503 of artificial perches in open areas (e.g., Holl 1998)  
504 or the planting of pioneer trees and shrubs may

accelerate the development of a woody plant  
cover, but will not increase its diversity. In view of  
Hong Kong's high labour costs, the prevention of  
anthropogenic fires is the most cost-effective tool  
for accelerating woody succession (Hau and Cor-  
lett 2003). Any funds available for tree planting  
could then be used to plant underrepresented late-  
successional woody species (Tucker and Murphy  
1997), either directly into the non-forest matrix for  
species that can tolerate such conditions, or under  
the canopy of Hong Kong's extensive secondary  
forests and exotic plantations (Lee et al. 2005). In  
the longer term, the loss of dispersal agents will  
have to be addressed, but their successful reintro-  
duction will be facilitated if mature food plants are  
widely available.

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*Appendix 1.* Woody seed rain ( $\text{m}^{-2} \text{year}^{-1}$ ) into six habitats in upland Hong Kong. Only taxa contributing 5 seeds  $\text{m}^{-2} \text{year}^{-1}$  in one or more habitats are included in the main table; less common taxa are listed in the footnote<sup>1</sup>. Plant species names follow Hong Kong Herbarium (2004). Dispersal agent(s): upper case – observed, lower case – inferred; B, b = bird, C, c = civet, F, f = fruit bat, M, m = macaque, wind = wind dispersed.

Family	Species	Growth forms	Dispersal agent(s)	Grassland				Shrubland	Forest
				Open	Trees	Female shrubs	Male shrubs		
Annonaceae	<i>Desmos chinensis</i>	Climber	B	–	0.1	–	–	0.4	17.2
Aquifoliaceae	<i>Ilex asprella</i>	Shrub	B	0.1	5.8	–	–	9.0	0.1
	<i>Ilex pubescens</i>	Shrub	B	–	6.8	2.5	–	0.7	1.9
	<i>Ilex rotunda</i>	Tree	B	–	2.4	0.6	0.3	3.6	10.0
Araliaceae	<i>Schefflera heptaphylla</i>	Tree	BF	–	0.4	–	–	238.9	2.9
Clusiaceae	<i>Cratoxylum cochinchinense</i>	Tree	Wind	–	–	–	–	62.4	–
Euphorbiaceae	<i>Mallotus paniculatus</i>	Tree	B	–	3.8	11.9	–	7.6	–
Fabaceae	<i>Acacia confusa</i> <sup>2</sup>	Tree	?	–	–	–	–	12.3	–
Lauraceae	<i>Litsea cubeba</i>	Small tree	B	–	1.3	25.2	–	0.3	0.3
	<i>Litsea rotundifolia</i>	Tree	B	–	0.4	–	–	27.5	0.1
	<i>Machilus</i> spp.	Tree	B	–	1.8	0.3	1.1	0.6	7.5
Melastomataceae	<i>Melastoma</i> spp.	Shrub	B	–	118.6	168.7	119.3	4.2	6.2
Moraceae	<i>Ficus</i> spp.	Shrub/tree	BCMF	–	5.4	13.0	–	–	19.0
	<i>Ficus variolosa</i>	Shrub	B	–	0.6	20.3	0.3	0.1	–
Myrsinaceae	<i>Embelia ribes</i>	Climber	B	–	1.0	–	–	6.2	1.1

## Appendix 1. (Continued)

Family	Species	Growth forms	Dispersal agent(s)	Grassland				Shrubland	Forest
				Open	Trees	Female shrubs	Male shrubs		
Myrtaceae	<i>Rhodomyrtus tomentosa</i>	Shrub	BCM	14.3	1.7	78.8	24.3	6.5	–
Phyllanthaceae	<i>Aporosa dioica</i>	Tree	B	–	–	–	–	22.1	0.3
	<i>Bridelia tomentosa</i>	Tree	B	–	–	–	–	17.6	0.7
	<i>Glochidion</i> sp.	Shrub	B	–	–	–	–	7.8	–
Rosaceae	<i>Rubus reflexus</i>	Shrub	BC	5.1	158.5	36.1	28.3	1.1	–
Rubiaceae	<i>Psychotria asiatica</i>	Shrub	B	–	0.3	2.2	–	56.6	22.8
	<i>Psychotria serpens</i>	Climber	B	–	4.1	4.4	0.6	14.6	10.5
Rutaceae	<i>Melicope pteleifolia</i>	Small tree	B	–	–	–	–	17.3	0.4
Theaceae	<i>Eurya</i> spp.	Shrub	B	20.1	556.0	6066.0	433.8	4.2	0.8
	<i>Schima superba</i>	Tree	wind	–	–	–	–	0.3	8.2
Verbenaceae	<i>Callicarpa</i> sp.	Shrub/tree	B	6.0	2.8	19.4	0.3	–	–
Vitaceae	<i>Ampelopsis cantoniensis</i>	Climber	B	–	0.1	0.3	–	1.7	9.7

<sup>1</sup> Additional seed taxa found in traps but not contributing  $> 5$  seeds  $m^{-2}$  year<sup>-1</sup> in any one habitat: *Acer sino-oblongum* (wind), *Adinandra millettii* (?), *Alangium chinense* (B), *Alyxia sinensis* (B), *Antidesma venosum* (b), *Antirhea chinensis* (B), *Aquilaria sinensis* (?), *Aralia armada* (B), *Ardisia crenata* (B), *A. quinquegona* (B), *Asparagus cochinchinensis* (B), *Berchemia floribunda* (B), *Breynia fruticosa* (B), *Bridelia insulana* (B), *Caesalpinia* sp. (wind), *Cassytha filiformis* (B), *Casuarina equisetifolia*<sup>2</sup> (wind), *Cayratia corniculata* (B), *Celtis sinensis* (B), *Cinnamomum parthenoxylon* (B), *Clerodendrum canescens* (b), *Daphniphyllum calycinum* (B), *D. oldhamii* (B), *Dendrotrophe frutescens* (bC), *Dioscorea* sp. (wind), *Diploclisia glaucescens* (?), *Diplospora dubia* (B), *Elaeagnus* sp. (b), *Embelia laeta* (bC), *Ficus hirta* (B), *F. vasculosa* (B), *Gardenia jasminoides* (B), *Lantana camara* (B), *Litsea glutinosa* (B), *Microcos nervosa* (BC), *Morinda umbellata* (B), *Osmanthus marginatus* (?), *Rhaphiolepis indica* (B), *Rhus chinensis* (B), *R. hypoleuca* (B), *R. succedanea* (B), *Sapium discolor* (B), *Sarcandra glabra* (B), *Sarcoperma laurinum* (B), *Sloanea sinensis* (?), *Smilax china* (B), *Syzygium hancei* (BC), *Symplocos lancifolia* (B), *Tetracera asiatica* (B), *Trema tomentosa* (B), *Trichosanthes* sp. (?), *Viburnum odoratissimum* (B), *V. sempervirens* (B), *Viscum* sp. (B), *Wikstroemia indica* (B), *W. nutans* (b), *Zanthoxylum avicennae* (B), *Z. scandens* (B), *Z. sp.* (B).<sup>2</sup> Planted exotic species.

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