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Seed rain into upland plant communities in Hong Kong, China

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Abstract

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

Introduction

The spatial pattern of dispersed seeds forms the template for the subsequent recruitment of new individuals into the plant community. This pattern may be greatly modified by post-dispersal seed and seedling mortality, but even in intact ecosystems the input of seeds can limit recruitment of particular species (Makana and Thomas 2004). In disturbed, fragmented, and degraded tropical landscapes, many studies have suggested that seed availability is a major limiting factor in vegetation recovery (e.g., Duncan and Chapman 1999; Holl 1999). The pattern and composition of the seed rain in such landscapes is thus an indicator of the regenerative potential. Factors that influence the composition of the seed rain at a particular point include the density, distribution, and fecundity of the seed sources in the vicinity, the spatial pattern of dispersal by the dispersal agent or agents involved, and the landscape features (such as perch availability for birds) that influence seed deposition. Some of these factors are potentially open to manipulation and may therefore provide a means

of accelerating landscape recovery (Howe and Miriti 2004).

Analysis of the seed rain in relation to the surrounding plant community can also provide information on the relative importance of different seed dispersal agents in the landscape. Wind-dispersed seeds are usually easily recognized, while dispersal by frugivorous birds and bats can be distinguished where fruit preferences are known, or by comparing the diurnal and nocturnal seed rain where they are not. Fruit bats are major dispersal agents for Neotropical pioneer trees (e.g., Medellin and Gaona 1999), but their role in the old world tropics is less clear (Corlett 2002; Ingle 2003). Detection of dispersal by non-flying mammals usually relies on the characteristics of the faecal material in which they are deposited. None of this is possible, however, unless the seed trap design allows the capture of seeds dispersed by the full range of plant growth forms and dispersal mechanisms of interest (Page et al. 2002).

Prolonged human impact increases the importance of the seed rain by exhausting alternative sources for regeneration, but may also reduce its quantity and diversity by eliminating seed dispersal agents (Howe and Miriti 2004). Hong Kong has an unusual combination for the tropics of a highly degraded landscape, from which most large frugivores have been lost, and economic prosperity, which has reduced recent human impacts and allowed landscape recovery to begin (Dudgeon and Corlett 2004). The major aims of this study were, therefore, to describe the spatial pattern of seed input to the degraded upland landscape of Hong Kong, to identify the major seed dispersal agents involved, and to explore the consequences for landscape recovery. Finally, we hoped to derive general lessons from this 'worst case scenario' that can be applied to the increasing area of severely degraded landscapes in tropical East Asia.

Methods

Study area

All seed traps were located between 170 and 700 m elevation on Hong Kong's tallest hill, Tai Mo Shan (22°25′, 14°07′ E), in the central New Territories, which forms part of the Chinese mainland. The topography of the site is rugged. Slopes and upper valleys are covered in fire-maintained grassland, shrubland, and isolated trees, with patches of secondary forest mostly along streams and at lower altitudes. The study area is on the northern and altitudinal limits of the climatic tropics, with hot wet summers and cool dry winters (Dudgeon and Corlett 2004). The temperature falls below zero several times a decade above 400 m elevation. Data from Hong Kong's dense network of rainfall stations suggests that there is a gradient of increasing mean annual rainfall in the study area from 2200 to 2400 mm at the lowest sites to more than 3000 mm at the highest (Hong Kong Observatory 2004).

Within the study area, seed traps were located at three sites representing the major upland vegetation types in Hong Kong: fire-maintained grassland, secondary shrubland, and 30–50 year old secondary forest (Dudgeon and Corlett 2004). The same three sites have been used for a variety of other ecological studies, so both their floras and faunas are well known. Of particular relevance to this study, bird community composition has been quantified at the forest (Kwok and Corlett 1999) and shrubland (Leven 2000) sites, and in shrubland within 200 m of the grassland site (Leven 2000). All the sites are within 6 km of each other. The grassland is dominated by the grasses *Eulalia quadrinervis* Kuntze and *Ischaemum aristatum* L., and there are scattered isolated trees (mostly *Machilus* spp.) and shrubs (mainly *Eurya* spp.). The shrubland dominants are *Litsea rotundifolia* (Nees) Hemsl., *Rhodomyrtus tomentosa* (Aiton) Hassk. and *Eurya* spp., with many other woody species present in smaller numbers. *Machilus* spp. dominate the forest canopy while *Psychotria asiatica* L. and *Ardisia quinquegona* Bl. dominate the understorey. Plant nomenclature follows Hong Kong Herbarium (2004).

Assessment of seed rain

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

the holes and for easy collection of the seeds. The trays were covered by wire mesh (mesh size 1.5×1.5 cm) to exclude rodents, which are the major seed predators in the study area and quickly consume or remove seeds placed at ground level (K.P.S. Chung, personal communication). The design was tested using a variety of non-local seeds and plastic beads, with losses always less than 5%. However, small wind-dispersed seeds – produced only by herbaceous plants and a few woody vines in the study area – could potentially be blown out of the traps at exposed sites.

Many studies assess seed rain on a transect across vegetation boundaries, usually from primary forest to non-forest (e.g., Cubina and Aide 2001; Ingle 2003). In our study area, however, the vegetation consists of a complex mosaic of secondary vegetation types of various ages, all of which may act as seed sources, and there are no substantial primary forest remnants. The seed traps in this study were therefore located in relatively uniform tracts of vegetation at least 20 m away from vegetation boundaries. Twenty traps each were haphazardly distributed in the shrubland and forest sites with each trap at least 5 m apart. In the grassland site, 20 traps were placed under isolated trees (all *Machilus* spp., which did not fruit during the study period), 20 under isolated shrubs (all *Eurya chinensis* R. Br., 10 male and 10 female), and 20 in open grassland. While there is replication within habitats, the spatial separation need for true independence made it logistically impossible to have independent replicates of each vegetation type.

The traps were visited every 14(±3) days for 2 years, from April 2002 to March 2004, except for the traps under isolated shrubs, which were visited from August 2002 to July 2004. At each visit, the cloths were collected and replaced, and seeds were separated, counted, and identified in the laboratory with the aid of a large reference collection. All seeds and fruits in the traps were counted, but intact fleshy fruits were excluded from further analysis, as they are likely to have fallen directly from above, and only seeds from woody plants are considered in this paper. The remote locations of the study sites made the twice-daily visits needed to distinguish diurnal and nocturnal seed rain impractical, but seed dispersal agents are known, or can be reliably inferred, for almost all common woody species in Hong Kong, as well many less common species (Corlett 1996, 2002; Au et al. unpublished).

Data analysis

Seed counts from each trap were standardized to number of seeds m^{-2} $year^{-1}$ for data analysis. The wide variation in the number of seeds per fruit means that the seed numbers in traps give a misleading picture of the number of frugivory events needed to get them there. Most fleshy fruits in the study area are swallowed whole by most frugivores, so converting the seed rain into 'fruit equivalents', by dividing the number of seeds of each species by the mean number of seeds per fruit, gives a rough estimate of the number of frugivory events involved. Patterns in the species composition of the seed rain were analysed by non-metric multidimensional scaling (MDS) using the PRIMER software package (Clarke and Warwick 1994). The standardized data were square-root transformed to down-weight the effect of the most abundant seed species. Traps that collected no seeds during the study period (six grassland traps) were omitted from the analyses. The Bray–Curtis coefficient was used as a similarity measure.

Results

A total of 37,002 seeds of 86 woody plant taxa were collected in 2 years in the 100 seed traps (total trap area = 18 m^2) (Appendix 1). The mean seed rain was highest under female isolated shrubs in grassland (6455 seeds m^{-2} $year^{-1}$), followed by isolated trees (890 seeds m^{-2} $year^{-1}$), male isolated shrubs (611 seeds m^{-2} $year^{-1}$), shrubland (558 seeds m^{-2} $year^{-1}$), forest (129 seeds m^{-2} $year^{-1}$), and open grassland (47 seeds m^{-2} $year^{-1}$) (Table 1). There was considerable variation between traps in each habitat, particularly for isolated shrubs (Figure 1). Six of the 20 open grassland traps collected no seeds in 2 years, while one trap under a female isolated shrub collected 5711 seeds $year^{-1}$. The total number of seed taxa collected was highest in shrubland (59), followed by isolated trees (42), forest (42), female isolated shrubs (28), male isolated shrubs (15), and open grassland (9). Seed diversity (as seed taxa per 100 seeds) was highest in forest and

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[a] (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

[a] 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
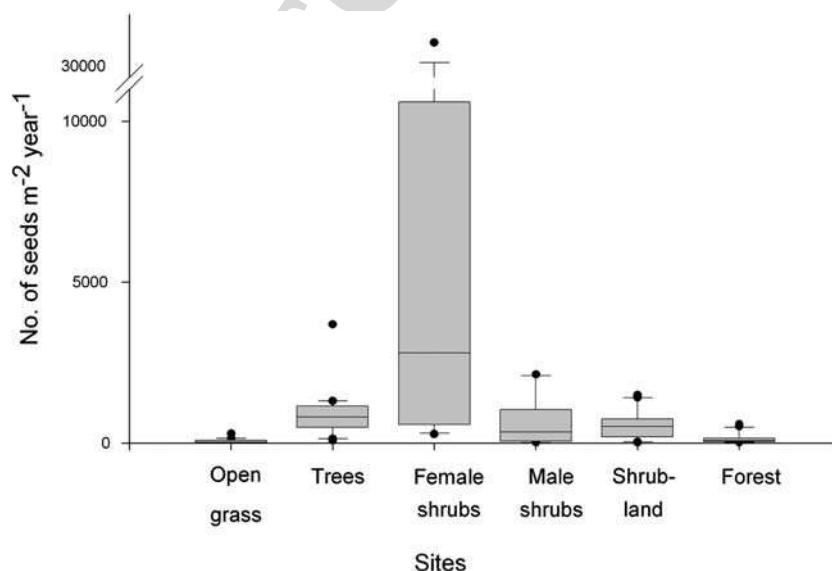

Figure 1. Box plots of numbers of seeds m^{-2} $year^{-1}$ arriving in individual seed traps in six habitats in upland Hong Kong: open grassland, isolated trees in grassland, female and male isolated shrubs (*Eurya chinensis*) in grassland, shrubland, and forest. The box indicates the 25th and 75th percentiles, 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.
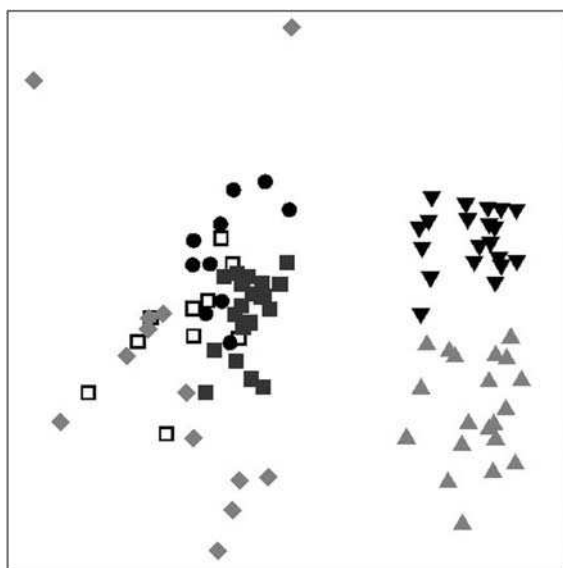
Figure 2. The seasonal pattern of seed rain (seeds m^{-2} per 2 weeks) in six habitats in upland Hong Kong. The shaded bar indicates the fruiting period of *Eurya chinensis*, under which the 'isolated shrub' seed traps were placed, and the dotted lines indicate the numbers of *Eurya* seeds in these traps. 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 by comparison with taxa with known dispersal
296 agents (Corlett 1996; Au et al. unpublished). Some
297 of these bird-dispersed taxa are known to also be
298 dispersed by fruit bats (2 taxa), civets (7 taxa),
299 and/or macaques (at least 2 taxa). However, no
300 civet or macaque faeces were found in the seed
301 traps and, although macaques usually spit out
302 large (>4 mm diameter) seeds singly (Lucas and
303 Corlett 1998) they were only present at the forest
304 site. No exclusively mammal-dispersed taxa were
305 found in the traps, although some exclusively bat-
306 dispersed fig species (*Ficus fistulosa* Bl., *F. hispida*
307 L.f., and *F. variegata* Bl.) are present in the study

308 area and may have been included among the '*Ficus*
309 spp.' that could not be identified to the species
310 level. In terms of numbers of seeds, 99% were
311 from taxa known or inferred to be dispersed by
312 birds and 0.8% (largely *Cratoxylum cochinchinense*
313 (Lour.) Bl. at the shrubland site) were dispersed by
314 wind. Taxa known to be at least occasionally dis-
315 persed by fruit bats made up 3.2% of the seeds,
316 but most of these were from *Schefflera heptaphy-*
317 *lla*, which is predominantly dispersed by birds, and
318 only 0.4% were from taxa (mostly *Ficus* spp.) that
319 may have been dispersed largely by bats. Most of
320 the seeds dispersed by wind, unknown agents, or,
321 potentially, bats were found in traps at the
322 shrubland and forest sites, while 99.8% of seeds at
323 the grassland site came from taxa that are known
324 or inferred to be dispersed by birds.
325 Conversion of seed numbers into fruit equiva-
326 lents reduces the contrast between sites (Table 1)
327 because the seed rain at the grassland site is domi-
328 nated by species with many-seeded fruits (mean 9.4
329 seeds fruit^{-1}), while species with few-seeded fruits
330 dominate the seed rain in shrubland (mean 2.6
331 fruit^{-1}) and forest (mean 2.2 fruit^{-1}). The median
332 seed size at the grassland site (1.5 mm diameter) was
333 also significantly smaller than that in both
334 shrubland (3.2 mm) and forest (4.1 mm)
335 (Kruskal–Wallace test, $p < 0.001$, Dunn's method
336 of multiple comparisons, $p < 0.05$ for all pairwise
337 comparisons). All seeds from fleshy fruits came
338 from taxa with mean fruit diameters ≤ 14.2 mm,
339 except for several larger-fruited species of *Ficus*,
340 which are either soft enough for birds to peck out
341 seed-containing pieces or known to be dispersed by
342 bats.

Discussion

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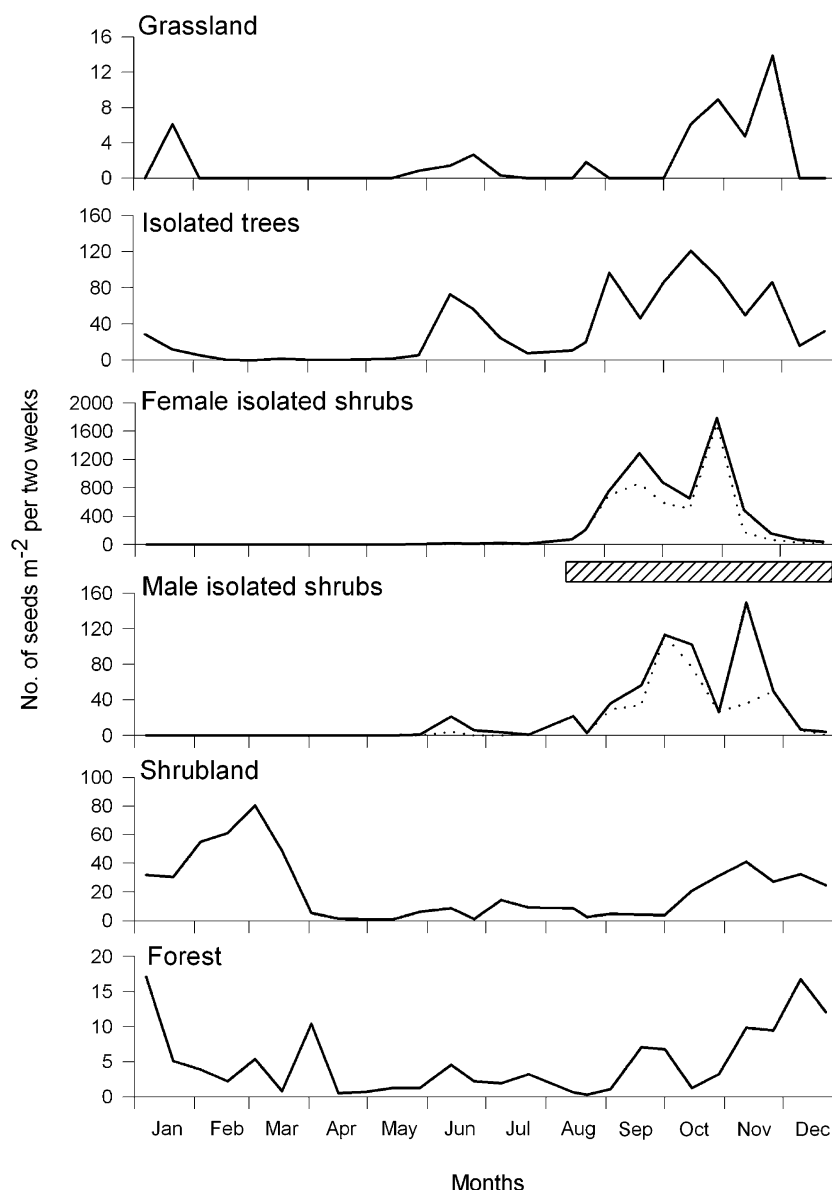355 Neotropics can be explained by the completely

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.

different lineages of plants and animals involved, including a different suborder of bats, largely endemic families of frugivorous birds, and unrelated genera of woody pioneers (Primack and Corlett 2005). However, *Cynopterus* fruit bats are the sole dispersal agent for the dominant pioneer on highly degraded sites in Singapore and the southern Malay Peninsula, *Adinandra dumosa* (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).

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

The absence of independent replicates for each vegetation type means that comparisons between the grassland, shrubland, and forest sites should be treated with caution. However, knowledge of the plant and vertebrate communities at each site, and on the relationships between them, gives us the confidence to extrapolate the major results to other sites in upland Hong Kong with similar biotas. The effectiveness of grassland perches in attracting frugivorous birds is highlighted by the higher seed rain under isolated shrubs and trees than under continuous shrubland and forest, presumably because perches in grassland act as bottlenecks in bird movements across the open area. Many other studies have shown that isolated trees and shrubs act as foci for seed rain (e.g., Toh et al. 1999; Guevara et al. 2004), but their function is likely to depend strongly on the behavioural characteristics of the principle seed dispersal agents involved. Larger-gaped birds, such as *Garrulax* species, were rarely seen to visit isolated perches in the study area (Weir 2004), so perches may be ineffective in attracting seeds from fruits that bulbuls avoid because of their size or other reasons. Seed diversity (as seed taxa per 100 seeds) was strikingly lower under perches in grassland than in shrubland and forest, with grassland perches attracting many small seeds but few species (Table 1). The shrubland 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 limitation of this study is that seeds dispersed by terrestrial 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 common 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.) Burtt & 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*, *Elaeocarpus*, *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-generalist 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 communication), 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 subsequent 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.

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

A variety of interventions have been suggested to accelerate the recovery of deforested tropical landscapes (Howe and Miriti 2004). The provision of artificial perches in open areas (e.g., Holl 1998) 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 Corlett 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 reintroduction will be facilitated if mature food plants are widely available.

Appendix 1. Woody seed rain (m^{-2} $year^{-1}$) into six habitats in upland Hong Kong. Only taxa contributing 5 seeds m^{-2} $year^{-1}$ in one or more habitats are included in the main table: less common taxa are listed in the footnote[1]. 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	*Desmos chinensis*	Climber	B	–	0.1	–	–	0.4	17.2
Aquifoliaceae	*Ilex asprella*	Shrub	B	0.1	5.8	–	–	9.0	0.1
	Ilex pubescens	Shrub	B	–	6.8	2.5	–	0.7	1.9
	Ilex rotunda	Tree	B	–	2.4	0.6	0.3	3.6	10.0
Araliaceae	*Schefflera heptaphylla*	Tree	BF	–	0.4	–	–	238.9	2.9
Clusiaceae	*Cratoxylum cochinchinense*	Tree	Wind	–	–	–	–	62.4	–
Euphorbiaceae	*Mallotus paniculatus*	Tree	B	–	3.8	11.9	–	7.6	–
Fabaceae	*Acacia confusa*[2]	Tree	?	–	–	–	–	12.3	–
Lauraceae	*Litsea cubeba*	Small tree	B	–	1.3	25.2	–	0.3	0.3
	Litsea rotundifolia	Tree	B	–	0.4	–	–	27.5	0.1
	Machilus spp.	Tree	B	–	1.8	0.3	1.1	0.6	7.5
Melastomataceae	*Melastoma* spp.	Shrub	B	–	118.6	168.7	119.3	4.2	6.2
Moraceae	*Ficus* spp.	Shrub/tree	BCMF	–	5.4	13.0	–	–	19.0
	Ficus variolosa	Shrub	B	–	0.6	20.3	0.3	0.1	–
Myrsinaceae	*Embelia ribes*	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	*Rhodomyrtus tomentosa*	Shrub	BCM	14.3	1.7	78.8	24.3	6.5	–
Phyllanthaceae	*Aporosa dioica*	Tree	B	–	–	–	–	22.1	0.3
	Bridelia tomentosa	Tree	B	–	–	–	–	17.6	0.7
	Glochidion sp.	Shrub	B	–	–	–	–	7.8	–
Rosaceae	*Rubus reflexus*	Shrub	BC	5.1	158.5	36.1	28.3	1.1	–
Rubiaceae	*Psychotria asiatica*	Shrub	B	–	0.3	2.2	–	56.6	22.8
	Psychotria serpens	Climber	B	–	4.1	4.4	0.6	14.6	10.5
Rutaceae	*Melicope pteleifolia*	Small tree	B	–	–	–	–	17.3	0.4
Theaceae	*Eurya* spp.	Shrub	B	20.1	556.0	6066.0	433.8	4.2	0.8
	Schima superba	Tree	wind	–	–	–	–	0.3	8.2
Verbenaceae	*Callicarpa* sp.	Shrub/tree	B	6.0	2.8	19.4	0.3	–	–
Vitaceae	*Ampelopsis cantoniensis*	Climber	B	–	0.1	0.3	–	1.7	9.7

[1] Additional seed taxa found in traps but not contributing > 5 seeds m^{-2} year^{-1} 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*[2] (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). [2] Planted exotic species.

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