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## Natural regeneration in exotic tree plantations in Hong Kong, China

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### Abstract

Tree plantations consisting mostly of a single exotic species have been established in Hong Kong, South China, for reforesting degraded lands since the 1950s. In this study, natural woody plant regeneration success under different types of closed-canopy plantations (*Acacia confusa*, *Lophostemon confertus*, *Melaleuca quinquenervia* and mixed-plantings) and natural secondary forests in the central New Territories were assessed. A total of 79 tree species, 64 shrubs and 23 woody climbers were recorded in 16 20 m × 20 m plantation plots. Stem density of woody plant regeneration was similar among all sites, ranging from 9031 to 10,950 stems > 0.5 m in height per hectare. Multivariate analysis of understorey species composition showed that there were consistent differences between plantation types. *Lophostemon* plantations generally had poor native plant colonization in comparison with natural secondary forests and other types of plantations. These differences between forest types can be at least partly attributed to pre-existing site conditions, since the tree species planted were matched to the site. Native woody plant colonization was poor on sites isolated from natural seed sources. Plantation understoreys were generally dominated by a few species of bird-dispersed shrubs, suggesting that enrichment planting with poorly dispersed shade-tolerant native tree species will be needed to facilitate regeneration in those plantations where natural regeneration is inadequate.

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**Keywords:** Plantations; Natural regeneration; Hong Kong; China; Succession

### 1. Introduction

Tree plantations are increasing throughout the world due to the demand for industrial timber and pulp. In Southeast Asia, plantations are established more for non-timber crops than timber, particularly coconuts, rubber, and oil palm (Corlett, 2005). There

were an estimated 187 million ha of forest plantation worldwide in 2001 and Asia had 62% of the world's total plantation area (FAO, 2001). Although around 50% of the plantations are established for timber, the many uses of plantations are being recognized, especially in the past 15 years, and more areas are planted with trees for environmental reasons.

Plantations have been suggested to promote woody understorey regeneration, and hence increase biodiversity (Haggard et al., 1997; Lamb, 1998; Lugo, 1997; Powers et al., 1997; Otsamo, 2000; Cusack and

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Montagnini, 2004). Plantations may promote regeneration in the understorey by shading out grasses, increasing soil nutrients (through uptake by deep roots and litter fall), improving micro-climate, and generally increasing the chance for seed germination and establishment, which is difficult in highly degraded sites (Parrotta, 1992; Kuusipalo et al., 1995; Parrotta et al., 1997). In addition, plantations can also protect sites from further degradation by preventing soil erosion and reducing fire hazard. For these reasons, trees of exotic or native origin are planted on degraded lands or pastures for rehabilitation, in the hope of preventing further site degradation and catalysing native plant colonization.

Plantations in the tropics can indeed promote understorey native plant regeneration in comparison with unproductive degraded lands or weed-dominated pastures where natural succession has been arrested (Parrotta and Knowles, 1999; Carnevale and Montagnini, 2002; Senbeta et al., 2002; Yirdaw and Luukkanen, 2003; Cusack and Montagnini, 2004). However, few studies have compared plantations with naturally regenerated forest of similar age. Natural succession with little or no intervention might have been a more effective rehabilitation method, as suggested by Fimbel and Fimbel (1996), Duncan and Chapman (2003) and Healey and Robert (2003). With plenty of 30–50-year closed-canopy plantations in Hong Kong, this study assessed native woody succession in exotic plantations. The understorey plant communities of natural secondary forests of similar ages were also studied for comparison. Hong Kong was probably the first area in the tropics where trees were planted purely for environmental reasons (Corlett, 1999), and the absence of logging pressure creates an unusual opportunity to study natural succession in mature plantations.

## 2. Methods

### 2.1. Study area

Hong Kong (22°08′–22°35′N; 113°49′–114°31′E) is situated to the east of the Pearl River (Zhujiang) Estuary on the South China Coast, and includes part of the Chinese mainland (Kowloon and the New Territories), and 235 outlying islands. Hong Kong

has a total land area of around 1102 km<sup>2</sup>, including approximately 66.4 km<sup>2</sup> of land reclaimed from the sea and all the offshore islands (HK Lands Department, 2004). Much of the territory has rugged topography. Most of the 6.8 million people reside in the lowland 20% of the total land area, and the remaining 80% of the land area is relatively undeveloped, and is mostly steep hillsides covered in secondary grasslands and shrublands. Hong Kong has a subtropical climate with a hot wet summer and cool dry winter (Dudgeon and Corlett, 2004). Mean annual rainfall in urban Kowloon is 2616 mm (1997–2003), the mean temperature of the coldest month is 16.9 °C, and the mean temperature of the warmest month is 28.8 °C. The original broad-leaved rainforest was cleared centuries ago, and most of the natural secondary forests have developed since 1945 (Dudgeon and Corlett, 2004). The canopy of these secondary forests, which cover around 16.3% of the total land area, is dominated by light-demanding *Machilus* spp. (Lauraceae), suggesting these forests are still in an early successional state (Zhuang and Corlett, 1997). About 23% of the territory is covered with grasslands maintained by frequent anthropogenic hill fires, which remain the main barrier to forest succession (Dudgeon and Corlett, 2004).

The principle aims of afforestation since the 1960s have been to: control soil erosion, protect water catchment areas, and conserve natural vegetation and wildlife (Corlett, 1999). A wide range of native and exotic tree species have been planted on sites with different levels of degradation; however, the foresters in Hong Kong depend mostly on a few easily propagated exotic tree species for afforestation, and the plantation area now covers around 5% of the territory (Ashworth et al., 1993). *Lophostemon confertus*, *Acacia confusa* and *Pinus elliottii* were the most common exotics planted, mostly on badly degraded sites. More recently, mixed plantings and native trees, including *Castanopsis fissa*, *Liquidambar formosana* and *Schima superba*, have been used to reforest areas with better soil conditions (Corlett, 1999).

### 2.2. Data collection and analysis

This study included natural regeneration surveys of plantations in the central New Territories, around the

134 highest hill Tai Mo Shan, at altitudes below 500 m.  
 135 Woody regeneration under four exotic plantation sites  
 136 of each of the four types (monocultures of *A. confusa*,  
 137 *L. confertus*, *Melaleuca quinquenervia*, and mixed-  
 138 species plantations), as well as four natural secondary  
 139 forests of similar age, were studied. To reduce the risk  
 140 of spatial autocorrelation the sites of each type were  
 141 interdispersed in the study area. At each site, the  
 142 abundance and species of understorey woody plants  
 143 were recorded in a 20 m × 20 m plot which was  
 144 haphazardly located at least 10 m from the plantation  
 145 edge. All woody species were counted and divided  
 146 into five height classes: <0.5, 0.5–1, 1–1.5, 1.5–2 and  
 147 >2 m. Nomenclature follows Corlett et al. (2000).  
 148 Diameter at breast height (dbh) of each planted exotic  
 149 tree within the plot was measured. Photosynthetically  
 150 active radiation (PAR) in the plantation understorey  
 151 was measured at breast height (ca. 1.3 m) by a Skye  
 152 PAR special sensor (SKP 210), and expressed as a

percentage of readings taken within the same hour in  
 an open area nearby. Canopy closure was measured in  
 four corners of the plot with a spherical crown  
 densiometer (Forestry Suppliers Ltd.) at breast height.  
 Stand characteristics, including canopy height, aspect,  
 slope and altitude, were also noted. If there was no  
 nearby seed source (secondary forest) within 500 m of  
 the plantation, the site was marked as isolated.  
 Plantation ages were determined by finding the  
 earliest aerial photographs in which the regular  
 planting pattern was visible. For natural secondary  
 forests, the ages were found by searching for the year  
 that showed the first signs of colonization by trees.  
 Stand characteristics of the 20 survey sites are  
 summarized in Table 1. The ages of the natural  
 secondary forests and plantations range from 25 to 50  
 and 15 to 50 years, respectively.

Species richness (number of woody species),  
 Simpson's evenness and regeneration stem density

Table 1  
 Characteristics of the sites sampled for the vegetation survey

Vegetation type	Site no.	Aspect	Slope (°)	Altitude (m)	Basal area (m <sup>2</sup> /ha)	Tree density (stem/ha)	PAR (%) <sup>a</sup>	Canopy closure (%) <sup>a</sup>	Canopy height (m)	Age
<i>A. confusa</i>	AC1	S	30	330	12.0	350	9.3 (8.7)	99.2 (0.4)	12	35
	AC2	SW	30	240	31.4	1400	4.8 (2.2)	97.1 (1.3)	15	15
	AC3	NE	15	140	18.3	500	4.7 (3.4)	98.0 (0.8)	20	35
	AC4	SW	15	190	11.5	375	7.6 (3.5)	97.6 (0.8)	20	15
<i>L. confertus</i>	LC1	NW	10	310	21.4	800	12.9 (1.3)	94.7 (1.3)	17	35
	LC2	SE	30	320	18.9	3075	16.0 (11.5)	91.4 (5.4)	10	25
	LC3	SW	10	240	28.9	1025	8.2 (3.5)	90.4 (5.0)	13	30
	LC4	NW	10	160	30.3	1275	5.9 (2.5)	94.8 (1.8)	20	35
<i>A. auriculiformis</i> , <i>A. confusa</i> , <i>A. mangium</i> , <i>L. confertus</i> , <i>Eucalyptus citriodora</i> , <i>Cunninghamia lanceolata</i>	M1	SE	20	200	28.7	2700	17.8 (1.5)	92.0 (0.4)	15	25
	M2	SW	30	100	21.6	1325	37.0 (6.1)	85.3 (4.0)	15	20
	M3	SW	30	271	31.3	1425	5.7 (1.9)	97.5 (0.7)	20	15
	M4	S	10	400	25.7	850	4.9 (3.9)	94.0 (2.5)	20	35
<i>M. quinquenervia</i>	MQ1	S	10	210	41.8	465	5.3 (0.2)	92.8 (1.8)	23	45
	MQ2	NW	10	120	31.5	650	2.9 (1.5)	96.8 (0.5)	30	35
	MQ3	E	10	220	69.4	525	4.3 (2.0)	97.3 (0.8)	30	45
	MQ4	W	20	200	102.1	625	4.0 (1.4)	97.4 (0.6)	30	50
Natural secondary forests	N1	SW	15	290	–	–	–	96.5 (0.9)	15	50
	N2	N	15	170	–	–	–	99.3 (0.2)	20	50
	N3	N	15	290	–	–	–	98.1 (1.0)	10	30
	N4	NE	20	410	–	–	–	96.8 (1.4)	15	25

<sup>a</sup> Means with standard deviations in parentheses.

Table 2  
Species occurring in over half of the plantation sites

Species	Frequency in plantations	Mean density (stems/ha) <sup>a</sup>	Growth habit <sup>b</sup>	Dispersal agent <sup>c</sup>
Annonaceae				
<i>Desmos chinensis</i> Lour.	13	1356 (1472)	C	Bird and bat
Aquifoliaceae				
<i>I. asprella</i> Champ.	14	373 (353)	S	Bird
Araliaceae				
<i>S. heptaphylla</i> (L.) D.G. Frodin	15	895 (1036)	T	Bird
Asclepiadaceae				
<i>Gynemna sylvestre</i> (Retz.) Schult.	8	–	W	Bird
Caprifoliaceae				
<i>Viburnum odoratissimum</i> Ker-Gawl.	8	88 (104)	T	Bird
Chloranthaceae				
<i>Sarcandra glabra</i> (Thunb.) Nakai	12	3073 (3761)	S	Bird
Daphniphyllaceae				
<i>Daphniphyllum calycinum</i> Benth.	10	645 (896)	S/T	Bird and civet
Euphorbiaceae				
<i>M. paniculatus</i> (Lam.) Muell. Arg.	8	122 (179)	T	Bird
Guttiferae				
<i>Cratoxylum cochinchinense</i> (Lour.) Blume	8	94 (97)	T	Wind
Lauraceae				
<i>L. rotundifolia</i> var. <i>oblongifolia</i> (Nees) Allen	15	3037 (4665)	S	Bird
<i>M. pauhoi</i> Kanehira	11	661 (611)	T	Bird
Mimosaceae				
<i>A. lucidum</i> (Benth.) Nielsen	8	2063 (1941)	T	?
Moraceae				
<i>Ficus hirta</i> Vahl.	12	133 (145)	S	Bird
Myrsinaceae				
<i>A. crenata</i> Sims	11	377 (711)	S	Bird
<i>Embelia ribes</i> Burm. f.	9	–	W	Bird
Myrtaceae				
<i>S. jambos</i> (L.) Alston*	10	240 (307)	T	Bat
Phyllanthaceae				
<i>A. dioica</i> (Roxb.) Muell. Arg.	16	2295 (4380)	T	Bird
<i>Breynia fruticosa</i> (L.) Hook. f.	14	100 (69)	S	Bird
<i>B. tomentosa</i> Blume	8	269 (346)	S	Bird
<i>Glochidion eriocarpum</i> Champ. ex. Benth.	12	248 (267)	S	Bird
Rosaceae				
<i>R. indica</i> (L.) Lindl.	12	1429 (2061)	S	Bird
<i>Rubus reflexus</i> Ker	9	617 (1321)	C	Bird
Rubiaceae				
<i>Mussaenda pubescens</i> Ait f.	10	78 (53)	C	Bird
<i>P. asiatica</i> L.	16	9550 (9731)	S	Bird
Rutaceae				
<i>M. pteleifolia</i> (Champ. ex Benth.) T. Hartley	14	364 (438)	S/T	Bird
<i>Zanthoxylum avicennae</i> (Lam.) DC	12	117 (109)	T	Bird

Table 2 (Continued)

Species	Frequency in plantations	Mean density (stems/ha) <sup>a</sup>	Growth habit <sup>b</sup>	Dispersal agent <sup>c</sup>
<i>Zanthoxylum nitidum</i> (Roxb.) DC	11	–	W	Bird
Smilacaceae				
<i>Smilax china</i> (L.)	8	138 (166)	C	Bird

<sup>a</sup> Frequency of plants is out of 16 plantation vegetation survey sites. Standard deviation of density is in parentheses.

<sup>b</sup> Growth habit: C, climbing shrub; S, shrub; T, tree; and W, woody climber. (\*) exotic or naturalised plant.

<sup>c</sup> Dispersal agent: source from Corlett (1996).

were found for all sites. Stems shorter than 0.5 m were not included in the regenerated stem density calculation since they often have high mortality (Otsamo, 2000). Simpson’s evenness ( $E_{1/D}$ ) was calculated as:

$$\frac{1/\sum p_i^2}{S}$$

where  $p_i$  is the proportion of individuals in the  $i$ th species, and  $S$  is the number of species (Magurran, 2004).

The abundance data was log transformed and a species composition matrix for the sites was calculated by Bray–Curtis similarity (Clarke and Warwick, 2001). The log transform down-weights the importance of the highly abundant species so that less common species are also reflected in the Bray–Curtis similarity. The non-metric multidimensional scaling (MDS) ordination was used to create a graphical representation of similarities between sites. This is an iterative procedure whereby the MDS plot is constructed by successively refining the positions of the points until they satisfy as closely as possible the dissimilarity (or similarity) relations between samples. Analysis of similarity (ANOSIM) was used to check for differences in species composition between vegetation types. A separate matrix was created using stand characteristics (which were square-root transformed to reduce right-skewness and stabilize

the variance of the data), including the variables: age, %PAR, canopy closure, tree density, planted basal area, altitude, canopy height, and isolation. For plantation sites only, the BIO-ENV procedure was used to link these abiotic site variables to the species composition using Spearman’s rank correlation coefficient ( $\rho_s$ ). This exploratory procedure can determine the suite of environmental variables that is most likely to have shaped the MDS ordination of the understorey community. Thus, it enables further studies to be planned on how this suite of variables shapes the community. All of the multivariate tests above were conducted using PRIMER v5 (Primer-E Ltd., 6 Hedingham Gardens, Roborough, Plymouth PL6 7DX, UK, <http://www.primer-e.com>). Finally, we plotted the  $k$ -dominance curves for abundance of all four types of plantations and natural secondary forests in order to compare species dominance in the understorey communities of these sites.

### 3. Results

#### 3.1. Stand characteristics and species richness

A total of 165 native or naturalised woody species, including 79 trees, 45 shrubs, 23 woody climbers, and

Table 3

Mean values of woody species richness, tree species richness, Simpson’s evenness, and regeneration stem density of woody species regeneration under four types of plantation and spontaneous secondary forests

Plantation species	No. of all woody plant species	No. of tree species	Simpson’s evenness ( $E_{1/D}$ )	Regeneration stem density (stems/ha)
<i>A. confusa</i> ( $n = 4$ )	38 (2.8)	15.3 (3.6)	0.114 (0.036)	9031 (3503)
<i>Losphostemon confertus</i> ( $n = 4$ )	35 (7.0)	10.8 (4.6)	0.153 (0.117)	9094 (6375)
Mixed-plantation ( $n = 4$ )	41 (5.4)	15.5 (2.1)	0.131 (0.048)	10000 (4967)
<i>M. quinquenervia</i> ( $n = 4$ )	50 (6.9)	25.3 (8.7)	0.120 (0.042)	10950 (4934)
Natural secondary forest ( $n = 4$ )	62 (16.8)	28.3 (7.8)	0.191 (0.050)	15531 (4808)

Standard deviations are in parentheses.

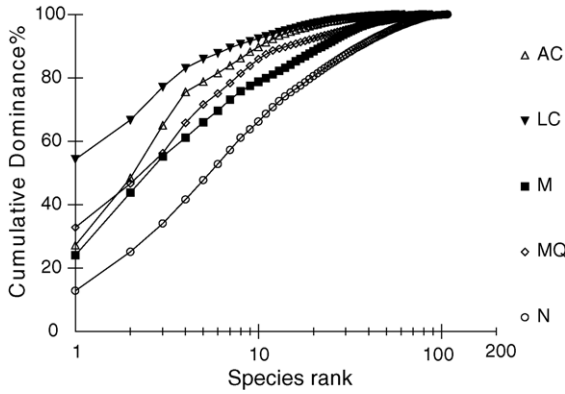


Fig. 1. *k*-Dominance plot of woody plants regeneration under plantations and natural secondary forests (AC: *A. confusa*; LC: *L. confertus*; M: mixed-planting; MQ: *M. quinquenervia*; N: natural secondary forest).

221 19 climbing shrubs, from 59 families were recorded in  
 222 plantations. Phyllanthaceae, Lauraceae and Rubiaceae  
 223 were the most common families of plants found under  
 224 the plantations. Table 2 lists the 28 species occurring  
 225 in over half of the sites surveyed. *Aporosa dioica* and  
 226 *Psychotria asiatica* were found in all plantation and  
 227 secondary forest sites. *Litsea rotundifolia*, *Schefflera*  
 228 *heptaphylla*, *Ilex asprella* and *Melicope pteleifolia*  
 229 were also very common. The mean values of woody  
 230 species richness, number of tree species, Simpson’s  
 231 evenness and regeneration stem density are shown in

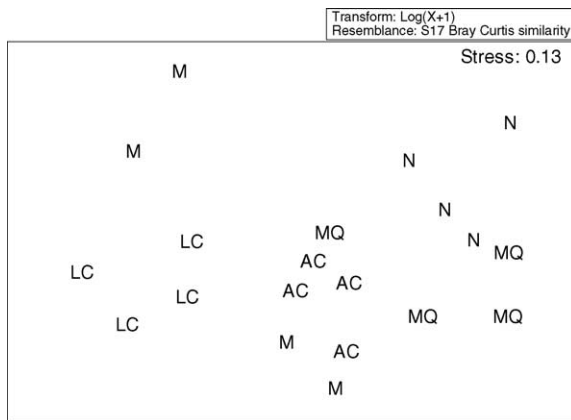


Fig. 2. Multidimensional scaling (MDS) ordinations of species composition of woody regeneration (AC: *A. confusa*; LC: *L. confertus*; M: mixed-planting; MQ: *M. quinquenervia*; N: natural secondary forests).

Table 4  
 Analysis of similarity between the species composition of different types of plantations and natural secondary forests

Types	<i>R</i> statistic	<i>p</i>
AC, LC	0.74	0.029**
AC, M	0.115	0.286
AC, MQ	0.26	0.114
AC, N	0.771	0.029**
LC, M	0.323	0.057
LC, MQ	0.917	0.029**
LC, N	1	0.029**
M, MQ	0.469	0.029**
M, N	0.656	0.029**
MQ, N	0.26	0.086

\*\* *p* < 0.05.

Table 3. Fig. 1 shows the *k*-dominance plot of four types of plantations and natural secondary forests. *Lophostemon* plantations clearly show high dominance by a single species in their understorey (*P. asiatica*), while mixed-plantings have a species accumulation pattern closer to natural regeneration.

3.2. Species composition

The MDS ordination (Fig. 2) shows the relative similarity between sites. The low stress level (0.13) shows that this is a relatively good two-dimensional representation with no real prospect of a misleading interpretation (Clarke and Warwick, 2001). *L. confertus* (LC) plantation sites form a group away from other types of plantation, and are the furthest away from natural secondary forests (N). *A. confusa* (AC) plantation sites form a closer group and are rather dissimilar to LC and N, while mixed-plantings (M) and *M. quinquenervia* (MQ) sites show a wide variation. The results of the one-way ANOSIM agree well with the pattern on the MDS (Table 4). BIO-ENV identified %PAR, canopy closure, tree density, planted basal area, and isolation as the most important variables controlling understorey species composition in plantations.

4. Discussion and conclusions

Many woody species occur in both plantations and natural secondary forests, but are often more abundant and older in the latter. Among the species shown in

260 Table 2, trees like *A. dioica*, *S. heptaphylla*, *M.*  
 261 *pteleifolia* and *Machilus pauhoi* are present in both  
 262 plantations and secondary forests of similar age, but are  
 263 often much larger in secondary forests. Better  
 264 regeneration in natural secondary forests is very  
 265 probably a reflection of better site conditions for plant  
 266 growth, as most of the sites selected for afforestation  
 267 with exotic tree species were severely degraded (with  
 268 serious surface soil erosion after prolonged disturbance  
 269 by cutting and then fire), while natural forest succession  
 270 is concentrated on the least degraded sites (Corlett,  
 271 1999). Three species were found only in the plantation  
 272 sites: *Ardisia crenata*, *Bridelia tomentosa* and *Mallotus*  
 273 *paniculatus*. These are light-demanding early succes-  
 274 sion species that are common in shrublands (Hau and  
 275 Corlett, 2002), and their presence presumably reflects  
 276 the generally lower degree of canopy closure in  
 277 plantations. On the other hand, some very common  
 278 secondary forest species, including *Garcinia oblongi-*  
 279 *folia*, *Syzygium hancei*, *Wikstroemia nutans* and *Ardisia*  
 280 *quinquegona*, were rare in plantations, being confined  
 281 to sites with good soil conditions and near to natural  
 282 seed sources. Finally, *Syzygium jambos*, a bat-dispersed  
 283 exotic tree which has established self-sustaining wild  
 284 populations in Hong Kong (Corlett, 1999), was only  
 285 found in plantations. Although none of the exotic tree  
 286 species used in Hong Kong's plantation is locally  
 287 invasive, some signs of natural regeneration of *M.*  
 288 *quinquenervia* in Hong Kong have been detected in  
 289 recent years (Hau, 2001). *M. quinquenervia* is a well-  
 290 known invasive tree in Florida (Turner et al., 1998) and  
 291 elsewhere, and both *L. confertus* and *A. confusa* are  
 292 locally naturalised in Hawaii (Wagner et al., 1990), so  
 293 exotic plantations should be monitored to prevent them  
 294 from becoming invasion foci for exotic trees in Hong  
 295 Kong.

296 Other studies on natural regeneration under  
 297 plantations have shown that the canopy characteristic  
 298 of the planted species is a possible influence on the  
 299 understory communities (e.g. Lugo, 1992; Parrotta,  
 300 1995). However, species effect cannot be recognized  
 301 in this study because comparisons between the  
 302 different forest types are confounded by pre-existing  
 303 site differences as the species planted were matched to  
 304 the site conditions. *M. quinquenervia* was mostly  
 305 planted on abandoned paddy fields and other areas  
 306 subject to flooding (Corlett, 1999), *L. confertus* was  
 307 largely planted on sites with poor soil, as it is believed

308 to be tolerant of drought, while natural secondary  
 309 forests always occupy the best sites. A controlled  
 310 experiment in which plantation species are randomly  
 311 assigned to sites is theoretically possible, but is  
 312 unlikely to be carried out in practice. Cautious  
 313 interpretation of observational studies, such as this  
 314 one, is therefore the only practical approach. Both the  
 315 MDS and ANOSIM show that the species composition  
 316 in natural secondary forests is significantly different  
 317 from the plantations, with the exception of the *M.*  
 318 *quinquenervia* sites. *Lophostemon* plantation sites  
 319 differ significantly from other types of plantation. The  
 320 fact that only four species, *P. asiatica*, *Archidendron*  
 321 *lucidum*, *L. rotundifolia* and *Rhaphiolepis indica*,  
 322 accounted for 83% of the total woody stems found in  
 323 the *Lophostemon* plantations understory (Fig. 1), and  
 324 the low number of woody species found, shows that  
 325 the woody plant invasion is poor under *Lophostemon*  
 326 plantations. All *A. confusa* plantation sites show  
 327 similar species composition, as seen in the MDS  
 328 ordination and a lower dispersion of species richness,  
 329 Simpson's evenness value and regeneration stem  
 330 density (Table 3). Mixed-plantings and *M. quinqu-*  
 331 *nervia* plantation sites, however, show a wider range of  
 332 variation. The understory of *Melaleuca* plantations  
 333 had more abundant natural regeneration, similar to  
 334 that of natural secondary forests, as shown by the  
 335 closer distances in the MDS ordination and the  
 336 ANOSIM results. Moreover, *M. quinquenervia* grows  
 337 very well at the studied sites, reaching a canopy height  
 338 of around 30 m, and basal area up to 100 m<sup>2</sup>/ha. The  
 339 good performance of both the planted trees and the  
 340 subsequent native plant regeneration probably reflect  
 341 the deeper, moister soils of these sites. The BIO-ENV  
 342 results show that understory light availability, tree  
 343 density, planted basal area, and isolation are good  
 344 predictors of the species composition in the under-  
 345 storey. Again, this result is at least partly confounded  
 346 by pre-existing site conditions, since these factors will  
 347 be influenced by site quality and location.

348 A previous study by Zhuang (1997) also showed  
 349 that the understory in eight plantation sites had lower  
 350 species diversity than secondary forests. This suggests  
 351 that simply reforesting hillsides with trees – at least  
 352 with the exotic monocultures studied here – is not  
 353 sufficient to restore natural forest diversity in Hong  
 354 Kong. Other factors, for example the seed dispersal  
 355 ability of colonizing plants, should be considered in

the planning stage of plantation establishment. Seed dispersal into plantations seems to be a limiting factor for forest succession in the understorey, as in degraded grassland in Hong Kong (Hau, 2000) and elsewhere in the tropics (Parrotta et al., 1997; Holl, 1999; Holl et al., 2000). In areas that are far away from seed sources and have poor soil conditions, the plantation understorey is dominated by a few early successional shrub species even 40 years after plantation establishment. Martínez-Garza and Howe (2003) point out that this ‘pioneer desert’ could retard the influx of deep-forest trees and slow down the natural succession process. Plantations may be needed to control soil erosion on severely degraded sites, but encouraging natural succession is preferable where the principal aim of reforestation is the restoration of natural habitats. In Hong Kong, the control of anthropogenic fires is the main step needed to promote forest succession. In view of the large areas of already established exotic plantations in Hong Kong, management measures such as thinning of the exotic trees, planting shade-tolerant native tree species (such as many of the Fagaceae) and planting native tree species with fleshy fruits for attracting seed dispersers, are needed to rehabilitate the understorey community and speed up natural succession.

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## References

- Ashworth, J.M., Corlett, R.T., Dudgeon, D., Melville, D.S., Tang, W.S.M., 1993. Hong Kong Flora and Fauna: Computing Conservation. Worldwide Fund for Nature Hong Kong, Hong Kong.
- Carnevale, N.J., Montagnini, F., 2002. Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. *For. Ecol. Manage.* 163, 217–227.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretations*, 2nd ed. Primer-E Ltd., Plymouth, UK.

- Corlett, R.T., 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *J. Trop. Ecol.* 12, 819–833.
- Corlett, R.T., 1999. Environmental forestry in Hong Kong: 1871–1997. *For. Ecol. Manage.* 116, 93–105.
- Corlett, R.T., 2005. Vegetation. In: Gupta, A. (Ed.), *The Physical Geography of Southeast Asia*. Oxford University Press, Oxford, pp. 105–119.
- Corlett, R.T., Xing, F.W., Ng, S.-C., Chau, K.C., Wong, L.M.-Y., 2000. Hong Kong vascular plants. *Memoirs Hong Kong Nat. History Soc.* 23, 1–157.
- Cusack, D., Montagnini, F., 2004. The role of native species plantations in recovery of understorey woody diversity in degraded pasturelands of Costa Rica. *For. Ecol. Manage.* 188, 1–15.
- Dudgeon, D., Corlett, R.T., 2004. *The Ecology and Biodiversity of Hong Kong*. Joint Publishing and Friends of the Country Parks, Hong Kong.
- Duncan, R.S., Chapman, C.A., 2003. Consequences of plantation harvest during tropical forest restoration in Uganda. *For. Ecol. Manage.* 173, 235–250.
- FAO, 2001. *State of the World’s Forests*. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Fimbel, R., Fimbel, C.C., 1996. The role of exotic conifer plantations in rehabilitating degraded tropical forest lands: a case study from the Kibale Forest in Uganda. *For. Ecol. Manage.* 81, 215–226.
- Haggard, J.P., Wightman, K., Fisher, R., 1997. The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. *For. Ecol. Manage.* 99, 55–64.
- Hau, B.C.H., 2000. Promoting native tree species in land rehabilitation in Hong Kong, China. In: Elliott, S., Kerby, J., Blakesley, D., Hardwick, D., Woods, K., Anusarnsunthorn, V. (Eds.) *Forest Restoration for Wildlife Conservation*. International Tropical Timber Organization and The Forest Restoration Research Unit, Chiang Mai University, Thailand, pp. 109–120.
- Hau, B.C.H., 2001. Is the paper bark tree becoming invasive in Hong Kong? *Porcupine* 24, 19–20.
- Hau, B.C.H., Corlett, R.T., 2002. A survey of trees and shrubs on degraded hillsides in Hong Kong. *Memoirs Hong Kong Nat. History Soc.* 25, 83–94.
- Healey, S.P., Robert, I.G., 2003. The effect of a teak (*Tectona grandis*) plantation on the establishment of native species in an abandoned pasture in Costa Rica. *For. Ecol. Manage.* 176, 497–507.
- HK Lands Department, 2004. Hong Kong Geographic Data (online). <http://www.info.gov.hk/landsd/geodata/landandarea> (accessed 30 June 2004).
- Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* 31, 229–242.
- Holl, K.D., Loik, M.E., Lin, E.H.V., Samuels, I.A., 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor. Ecol.* 8, 339–349.
- Kuusipalo, J., Ådjers, G., Jafarsidik, Y., Otsamo, A., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. *J. Veg. Sci.* 6, 205–210.



- 456 Lamb, D., 1998. Large-scale ecological restoration of degraded  
457 tropical forest lands: the potential role of timber plantations.  
458 Restor. Ecol. 6, 271–279.
- 459 Lugo, A.E., 1992. Comparison of tropical tree plantations with  
460 secondary forests of similar age. Ecol. Monogr. 62, 1–41.
- 461 Lugo, A.E., 1997. The apparent paradox of reestablishing species  
462 richness on degraded lands with tree monocultures. For. Ecol.  
463 Manage. 99, 9–19.
- 464 Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell  
465 Science, Malden, USA.
- 466 Martínez-Garza, C., Howe, H.F., 2003. Restoring tropical diversity:  
467 beating the time tax on species loss. J. Appl. Ecol. 40, 423–429.
- 468 Otsamo, R., 2000. Secondary forest regeneration under fast-growing  
469 forest plantation on degraded *Imperata cylindrica* grasslands.  
470 New For. 19, 69–93.
- 471 Parrotta, J.A., 1992. The role of plantation forests in rehabilitating  
472 degraded tropical ecosystems. Agric. Ecosyst. Environ. 41, 115–  
473 133.
- 474 Parrotta, J.A., 1995. Influence of overstorey composition on under-  
475 storey colonization by native species in plantations on a  
476 degraded tropical site. J. Veg. Sci. 6, 627–636.
- 477 Parrotta, J.A., Knowles, O.H., 1999. Restoration of tropical moist  
478 forests on bauxite-mined lands in the Brazilian Amazon. Restor.  
479 Ecol. 7, 103–116.
- Parrotta, J.A., Turnbull, J.W., Jones, N., 1997. Catalyzing native  
480 forest regeneration on degraded tropical lands. For. Ecol. Man-  
481 age. 99, 1–7.
- Powers, J.S., Haggard, J.P., Fisher, R.F., 1997. The effect of over-  
483 storey composition on understorey woody regeneration and  
484 species richness in 7-year-old plantation in Costa Rica. For.  
485 Ecol. Manage. 99, 43–54.
- Senbeta, F., Teketay, D., Näslund, B.-A., 2002. Native woody  
487 species regeneration in exotic tree plantations at Munessa-  
488 Shashemene Forest, southern Ethiopia. New For. 24, 131–145.
- 489 Turner, C.E., Center, T.D., Burrows, D.W., Buckingham, G.R., 1998.  
490 Ecology and management of *Melaleuca quinquenervia*, an  
491 invader of wetlands in Florida U.S.A.. Wetlands Ecol. Manage.  
492 5, 165–178.
- 493 Wagner, W.L., Herbst, D.R., Sohmer, S.H., 1990. Manual of the  
494 Flowering Plants of Hawaii. University of Hawaii Press, Bishop  
495 Museum, Honolulu, HI.
- 496 Yirdaw, E., Luukkanen, O., 2003. Indigenous woody species diver-  
497 sity in *Eucalyptus globulus* Labill. ssp. *globulus* plantations in  
498 the Ethiopian highlands. Biodiv. Conserv. 12, 567–582.
- 499 Zhuang, X.Y., 1997. Rehabilitation and development of forest on  
500 degraded hills of Hong Kong. For. Ecol. Manage. 99, 197–201.
- 501 Zhuang, X.Y., Corlett, R.T., 1997. Forest and forest succession in  
502 Hong Kong, China. J. Trop. Ecol. 14, 857–866.
- 503  
504