



Original Research Article

Spatial patterns of degraded tropical forest and biodiversity restoration over 70-years of succession

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ABSTRACT

Landscape metrics have often been used to analyse the spatial dynamics of habitat fragmentation accompanying forest loss. However, there are few studies of the spatial dynamics of natural forest succession, especially over periods longer than the operational period of imaging satellites. This study applies spatial metrics to understand the spatial processes of a 70-year tropical secondary forest succession in Hong Kong, since World War 2. The highest rate of forest regeneration at 11% a year from 1989 to 2001 occurred when the landscape achieved greatest habitat diversity and juxtapositioning of habitat patches. This rapid regeneration occurred by infilling from remnant forest in adjacent valleys rather than by an advance along a broad forest front, and led to simplification of the landscape and declining habitat diversity. It was also accompanied by declines in species richness and abundance in regenerated forest patches. Thus both habitat and woody plant species diversity show a humped trend over the successional period as disconnected forest patches amalgamate, and shade-intolerant pioneers are shaded out by taller pioneers. From this point onwards, the birds of mixed habitats including bulbuls and hwamei known to disperse seed in the study area, may become less effective as forest patches consolidate, and only a few forest mammals remain. The observed improved connectivity within forest patches and reduced edge disturbances accompanying landscape simplification provide better conditions for dispersion within forest of light-intolerant climax species from the oldest, species-rich valley sites to the newly regenerated areas. However, in addition to the loss of forest dispersal agents, other natural dispersal agents such as gravity, flash floods and slope wash involving downward processes may be ineffective, as forest has regenerated upwards to higher elevations. Progression to a mature, biodiverse and stable forest ecosystem may depend on introduction of dispersal agents other than those which have operated over recent decades. Forest patches with high internal connectivity, indicated by high Mean radius of Gyration (MRG) and low Mean Perimeter-to-Area Ratio (MPAR) would appear to offer the best movement opportunities and least disturbance to such introductions.

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1. Introduction

Recent evidence from detailed time series of satellite images indicates a 62% increase in deforestation in the humid tropics from the 1990s to the 2000s (Kim et al., 2015). This contradicts previous estimates of a 25% reduction in deforestation over this period (FAO, 2010). But, whether the rate of loss is increasing or decreasing, humid tropical forests show a continuous and long-term decline in area globally, along with increased fragmentation of habitats and areal-related impacts on flora and fauna. It is generally known that reduction in size of habitat patches is associated with loss of species due to a changed microclimate, edge disturbances, small population size and reduced range of movement. Many studies have demonstrated the impacts of such spatial trends on shrinking forests. For example, Rocha-Santos et al. (2016) observed that an increasing perimeter-to-area ratio as Brazil's forests became more fragmented, was associated with reduced seed dispersal and establishment due to loss of forest fauna and forest microclimate. However, Araujo et al.'s (2015) study of forest beetle populations in Brazil showed that reduced area was less influential than loss of connectivity in maintaining beetle species diversity, due to greater availability of host fungi in well-connected areas.

However, how spatial factors may affect forest and biodiversity recovery in naturally regenerating forests is less understood, as there are fewer suitable, long-term study sites and most spatial studies involve afforestation programmes (e.g. Geri et al., 2010; Qi et al., 2013). Those dealing with natural forest regeneration are mainly descriptive and do not establish any relationship between spatial landscape attributes and ecological processes accompanying the succession (Faber-Langendoen, 1992; Grainger, 1988; Guevara and Laborde, 1993; Hartshorn, 1980; Helmer, 2000; Perz and Skole, 2003; Saldarriaga et al., 1988; Sann et al., 2016; Turner et al., 1997). Thus there are few spatial analyses of forest regeneration, especially over time periods longer than the operational period of earth resource satellites i.e. the last four decades. One study of functional diversity during succession in New Guinea (Whitfield et al., 2014) used landowner recollection to establish plot age, rather than archival images which permit boundary delineation at previous periods; thus spatial parameters were not addressed. It remains to be addressed how the changing spatial morphology of the landscape affects processes and biodiversity trends in natural forest succession. For example, it is not known if recovery of species and habitat diversity in regenerating forested landscapes are related to patch size and connectivity in the same way, or at similar rates, as in forest fragmentation. Models of species diversity trends such as the hump-backed curve in species richness and abundance from early to late forest succession (Pausas and Austin, 2001), have not been examined in the context of changing landscape and patch morphology in regenerating forested landscapes. The hump-backed curve results from initially increasing species richness and abundance as open ground is colonized by heliophytic and easily dispersed woody pioneers, followed by decline with their progressive shading out as the canopy closes. Since spatial landscape parameters such as patch size, edge length, compactness and canopy openness affect access to forest and its susceptibility to disturbance, these spatial parameters would affect species trends.

This paper describes a 70-year period of forest dynamics in Hong Kong which has seen accelerating natural regeneration of forest since the Second World War (WW2), from small protected remnant sites to a significant proportion of the landscape today. The landscape meanwhile has undergone stages of increasing and decreasing fragmentation and consolidation of habitats, each stage offering different opportunities for natural forest succession and species establishment. These observations of landscape morphology at different successional stages, can be used to guide forest management policies in controlled successions.

2. Background

Following the destruction of Hong Kong's forests before and during WW2, natural regeneration along a successional gradient from open ground to forest, presents a rare opportunity to observe these structural changes related to biodiversity recovery, as the landscape has changed over the 70-year period. The increasing structural complexity from open grass and shrubland, to open, then closed canopy forest is accompanied by changing landscape structure, and at each structural stage, landscape parameters such as patch size, shape, contiguity and distance vary. Because future change is a result of cumulative augmentation following the Compound Interest Law (Teferi et al., 2013), once a mid successional stage has been reached over a significant proportion of the landscape, subsequent increase in forested area would be expected to occur more rapidly up to a certain point. At the same time, increase in patch size reduces external disturbances, and brings the edges of adjacent patches closer together, permitting better seed dispersal between patches, again implying faster regeneration in the later succession. The Patch Matrix Model (PMM) of landscape structure (Lausch et al., 2015) permits quantification of temporal changes in spatial structure (Turner et al., 2001), which accompany restoration of biodiversity in naturally regenerating forest. The model is applied to a 70-year period of forest regeneration in Hong Kong, which is enabled by the protected status of 40% of Hong Kong's land area and a substantial archive of aerial photography.

The specific objectives of this paper are: 1) to analyse the changing morphology and spatial structure of the landscape over a 70-year natural forest succession, 2) to identify the relationship between landscape spatial metrics and known seed dispersal agents in the study area, and 3) to determine the influence of spatial landscape parameters on forest succession and biodiversity recovery.

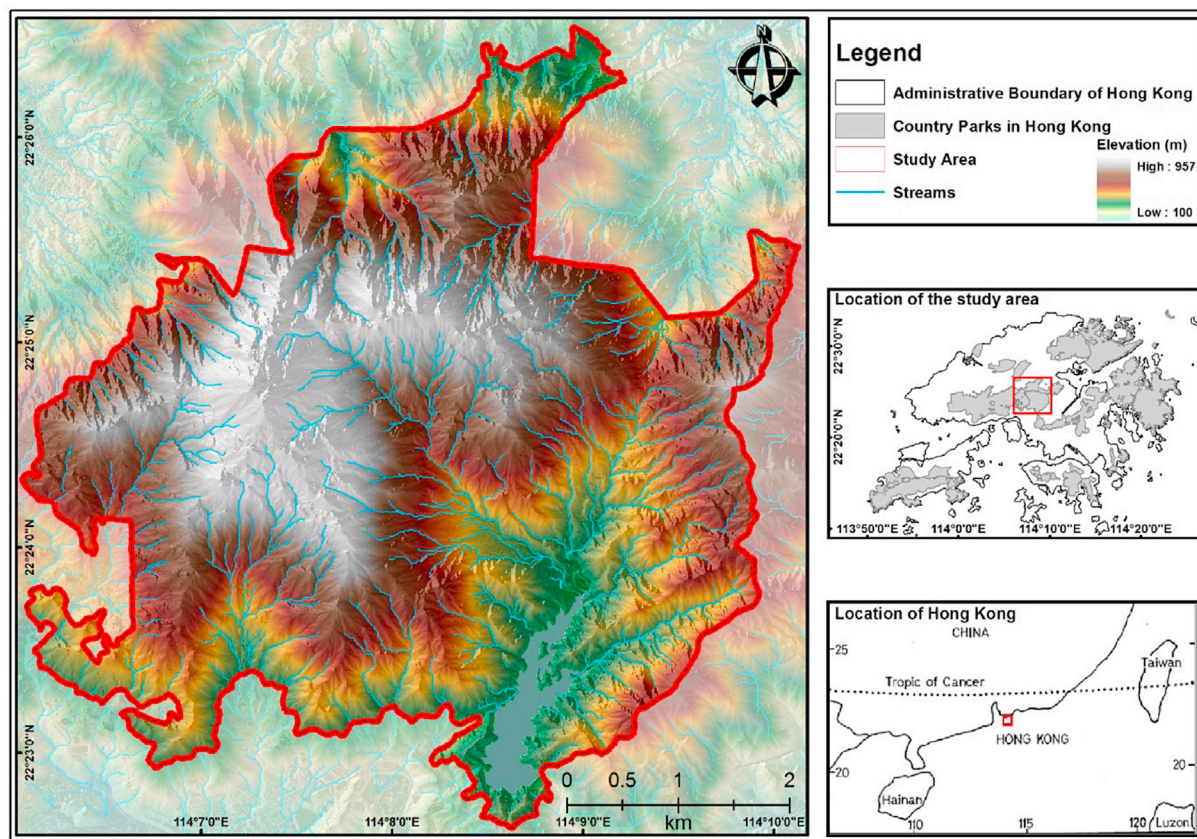


Fig. 1. Location map of the study area.

3. The study area

Hong Kong is situated on the edge of the Asian tropics (Fig. 1) between 22 and 23° N. The climate is seasonal, with summer rainfall, and mean annual temperature of 23° C over recent decades. Hong Kong's primary vegetation was a diverse evergreen rain forest, with up to 120–180 woody species per hectare, as observed in nearby protected areas in south China (Cao et al., 2013; Fang et al., 2004). Freezing temperatures above 400 m several times a decade favour sub-tropical over tropical species at higher elevations (Abbas et al., 2017; Dudgeon and Corlett, 2011; Weir and Corlett, 2006), and the mixture of tropical and sub-tropical species results in very high floral and faunal diversity (Dudgeon and Corlett, 2011). More than 75% of Hong Kong's land is steeply sloping and approximately 40% of Hong Kong's land is protected in Country Parks and nature reserves. The current flora and fauna have undergone forest recovery over the 70 years since 1945, mainly by natural regeneration from remnant patches in steep valleys and ravines. Some post-war plantation of a few native and exotic species, aimed at controlling soil erosion in the degraded hills and water catchments (Corlett, 1999) may have assisted the recovery by providing perches for seed-dispersing birds (Holl, 1999). Currently, secondary vegetation is succeeding in vertical structure as well as horizontal expansion (Wang et al., 2006), and field and image observations suggest that forest is regenerating naturally, and independently from afforestation programmes. However preliminary observations from field plots indicates much greater woody species diversity, higher density and larger size (DBH) of trees in the pre-WW2 forest remnants, than in the regenerated areas.

The study area comprises Tai Mo Shan and Shing Mun Country Parks in the New Territories of Hong Kong (Fig. 1), an area of ~2800 ha. Topography is rugged, with convex slopes rising to Hong Kong's tallest peak (957 m) Tai Mo Shan. Currently the upper valleys are covered with fire-maintained grasses, and lower elevations support patches of shrubland, secondary forest and plantations. It is generally known that animals disperse most woody plants in the tropics, and birds, namely bulbuls (*Pycnonotus sinensis* and *P. jocosus*), Japanese whiteeye (*Zosterops japonicus*) and hwamei (*Garrulax canorus*) have been observed to be responsible for seed dispersal of small seeded species in the study area (Weir and Corlett, 2006) whereas mammals such as Indian muntjac (*Muntiacus muntjac*), rodents, civets (*Paguma larvata*, *Viverricula indica*) and macaques (*Macaca mulatta*, *M. fascicularis* and their hybrids) disperse larger seeds (Weir and Corlett, 2006). The important role of accidentally and deliberately reintroduced macaques in dispersing large seeded climax tree species such as *Garcinia* and *Canarium* spp. should be emphasized (Fischer pers. observ, Lucas and Corlett, 1998; Corlett, 2011). The majority of the original

mammalian fauna has now disappeared, although tigers, leopards and the large Indian civet (*Viverra zibetha*) persisted until the 1940s or 50s (Dudgeon and Corlett, 2011; Corlett, 2011).

4. Methods

Mapping and classification of habitats over the study area was undertaken using high resolution aerial photographs and satellite images for five time periods, 1945, 1963, 1989, 2001 and 2014 (Abbas et al., 2016). An 'a priori' habitat classification scheme was derived from previous habitat mapping in Hong Kong (Ashworth et al., 1993) as it was based on vegetation structural characteristics interpretable from remotely sensed images. The classes are unambiguous, mutually exclusive and commonly identifiable from satellite images and aerial photographs. Overall, mapping accuracy, based on over 500 field and air photo check points, was above 92%, with 98% for forest and 100% for plantation.

4.1. Annual rate of change

Annual rates of change were calculated using equation (1), which is based on the Compound Interest Law and calculates percentage change per year by considering nonlinear change across the timeline. This provides ecologically meaningful estimation of habitat change (Puyravaud, 2003), as it is insensitive to different time periods between observation dates (Teferi et al., 2013).

$$r = \left(\frac{1}{t_2 - t_1} \right) \times \left(\ln \frac{A_2}{A_1} \right) \times 100 \quad (1)$$

where r is the rate of change (% per year), A_1 and A_2 represent area corresponding to earlier time, t_1 , and late time, t_2 .

4.2. Landscape metrics

Spatial metrics were applied to describe and quantify changes in composition, structure, and diversity of landscape over time. At the landscape level (LL), structural composition was quantified using metrics related to patch density and size, shape, and isolation or proximity (LL on Table 1). These include patch density (PD), mean patch size (MPS), mean radius of gyration (MRG, a measure of connectivity within a patch), largest patch index (LPI), mean shape index (MSI), mean perimeter to area ratio (MPAR), and mean Euclidean nearest neighbor distance (MED). Diversity of the landscape was assessed using the interspersions and juxtaposition index (IJI), and Shannon's diversity index (SHDI) (Table 1). At class level (CL), metrics used to

Table 1
Landscape level (LL) and class level (CL) metrics used in this study.

Category	Metric Name	Acronym	Units	Level Used	Ecological Description
Patch size and Density	Number of Patches	NP		CL	Measure of extent of subdivision of a habitat class (Mcgarigal et al., 2012)
	Patch Density	PD	Number of patches per 100 ha	LL	PD is a fundamental aspect of landscape pattern. It explains degree of subdivision of landscape.
	Mean Patch Size	MPS	ha	LL, CL	Sum of area of all the patches divided by the number of patches of the class.
	Mean Radius of Gyration	MRG	m	LL, CL	Mean distance for each cell in one patch to the patch centroid. It measures connectivity inside habitat patches. Higher MRG means better connectivity within patches.
Shape and Edge	Largest Patch Index	LPI	%	LL, CL	Ratio of area of largest patch to total landscape area
	Mean Shape Index	MSI	—	LL, CL	Measures complexity of patch shape compared to a standard shape of the same size. Its value increases with complexity of shape.
	Edge Density	ED	m/ha	CL	Measures total length of edge per unit area. It explains complexity of patch shape.
	Mean Perimeter To Area Ratio	MPAR	—	LL, CL	Patch shape complexity, based on perimeter length to patch area. It explains shape complexity without standardization to a standard Euclidean shape (square)
Proximity/ Isolation	Mean Euclidean Nearest Neighbor Distance	MED	m	LL, CL	Measures minimum edge to edge distance to the nearest neighboring patch of the same type. It explains connectedness or isolation in landscape or habitat class
	Mean Proximity Index	MPI	—	CL	Measure of connectedness of a habitat class. Considers size and proximity of all patches with the same habitat type inside a specified search radius
	Interspersions And Juxtaposition Index	IJI	%	LL	Measures evenness of patch adjacencies, and represents intermixing of different patch types.
Diversity and Texture					At landscape level, decrease in IJI suggests reduced degree of mixture of vegetation communities
	Shannon's Diversity Index	SHDI	—	LL	Measure of diversity in landscape from the abundance of habitat categories. It increases as the number of categories increases or the distribution of land amongst the various classes equalises.

quantify structural changes in habitat classes (CL on Table 1) included the number of patches (NP), largest patch index (LPI), mean patch size (MPS), edge density (ED), mean shape index (MSI), mean proximity index (MPI), and mean Euclidean distance (MED). The metrics concerning patch density and size, shape and edge (MPS, MRG, MSI and MPAR) are applicable at both landscape and class level, and represent the extent to which patches are exposed to external influences or disturbances. For example, MRG at landscape level, represents connectivity within all habitat patches in the landscape, and at class level for forest, the degree to which forest patches are internally well connected or traversable by organisms. These metrics provide unique information contributing to better understanding of landscape and habitat structure at different stages of the natural succession.

4.3. Field data collection

A forest inventory consisting of 28 quadrats of 20 m by 20 m was undertaken. Quadrats were selected by stratified random sampling to include the five different age classes defined by the image interpretation, namely greater than 70 years, less than 70 years, less than 52 years, less than 26 years, and less than 14 years. Within each quadrat, all woody plants above breast height (1.3 m) were counted and their species identified.

5. Results

Immediately post WW2, forest (defined as broadleaf evergreen forest with closed canopy) comprised only 0.17% of the study area (4.82 ha), primarily confined to protected forest around villages, confirming Zhuang and Corlett's (1997) account. The 1945 landscape was dominated by a matrix of grassland covering 78.6% of the landscape, with many very small patches of shrubland, in steep gulleys or along landslide trails, and small patches of bare ground. Forest cover has increased over time (Fig. 2, Table 2), initiated by shrub colonization along valley bottoms and landslide areas, which is observed on all image datasets since 1945. Established shrubland communities appear to expand spatially up valley sides, as well as grow in vertical structure, giving way to forest, which by 2014, was the dominant class in the landscape. Forest cover in the landscape has increased at an annual rate of 7.76% since 1945, with the highest annual rate of 10.92% during 1989–2001 (Table 3).

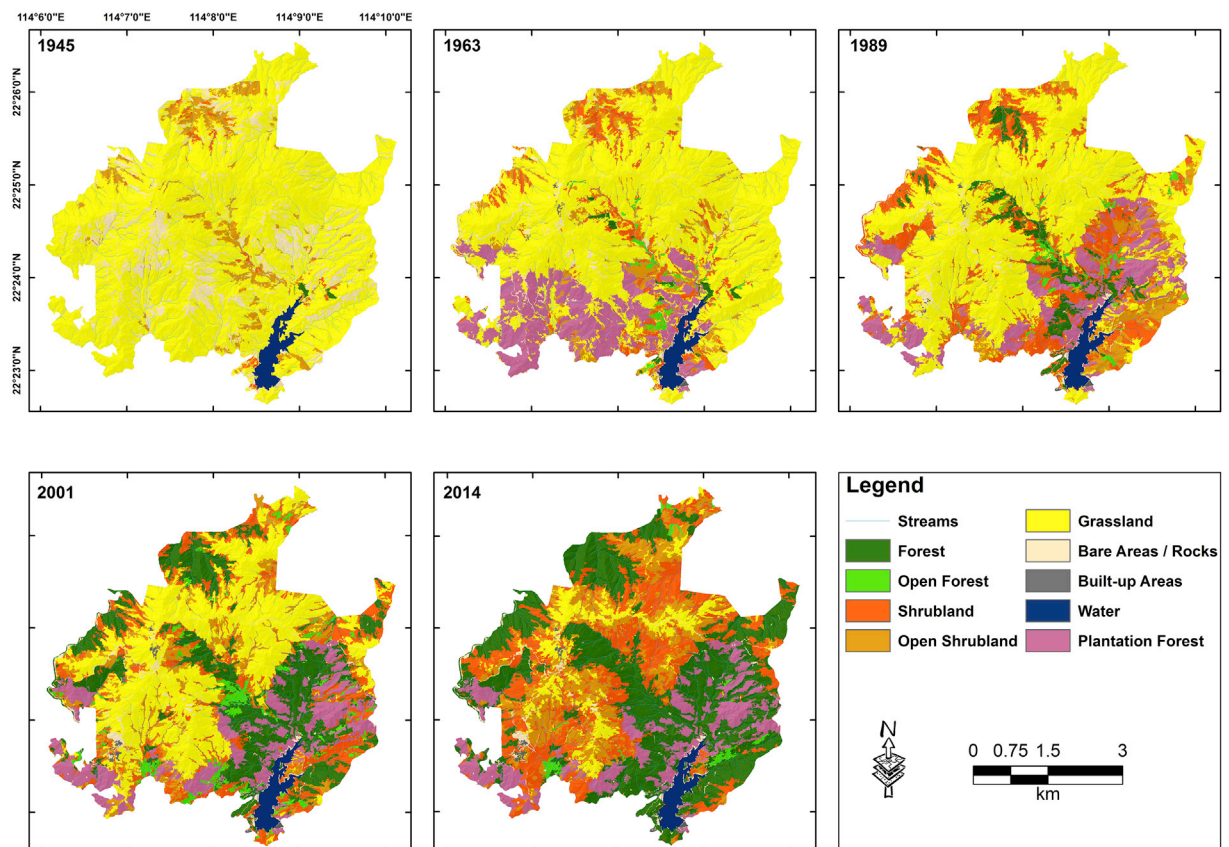


Fig. 2. Habitat classification maps of the landscape at five time periods.

Table 2

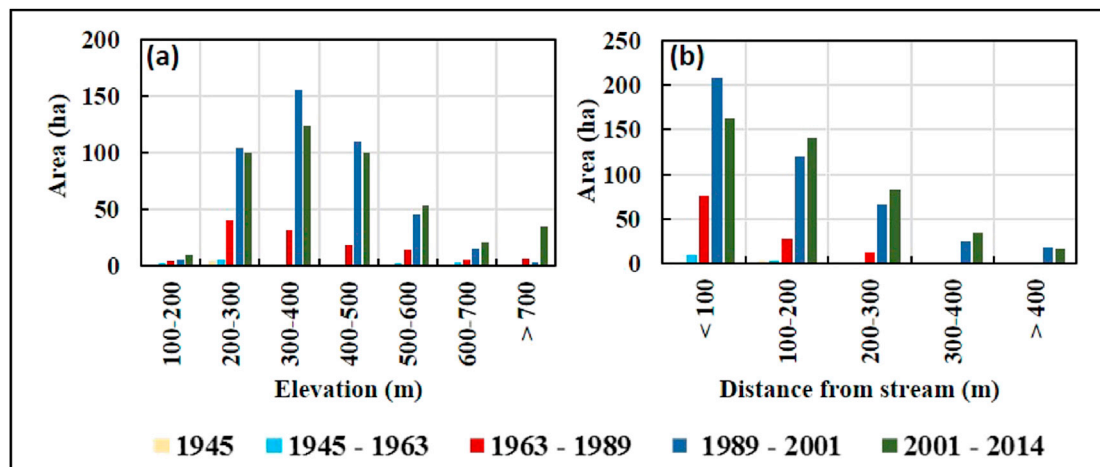
Area statistics of habitat classes for five time periods.

Habitat Classes	1945		1963		1989		2001		2014	
	Area (ha)	Area (%)	Area (ha)	Area (%)	Area (ha)	Area (%)	Area (ha)	Area (%)	Area (ha)	Area (%)
Forest	4.82	0.17	19.85	0.71	140.03	5.01	579.04	20.70	1019.23	36.44
Open Forest	0.22	0.01	27.69	0.99	38.09	1.36	108.32	3.87	27.54	0.98
Shrubland	24.03	0.86	175.05	6.26	464.18	16.59	418.70	14.97	650.43	23.25
Open Shrubland	170.99	6.11	203.57	7.28	245.27	8.77	261.49	9.35	421.29	15.06
Grassland	2203.17	78.75	1805.62	64.54	1479.82	52.90	969.92	34.67	219.92	7.86
Bare Area/Rocks	336.95	12.04	71.76	2.56	52.57	1.88	52.16	1.86	51.23	1.83
Built-up Area	0.41	0.01	5.21	0.19	8.80	0.31	12.51	0.45	12.51	0.45
Water	57.21	2.04	57.21	2.04	57.21	2.05	57.21	2.05	57.21	2.05
Plantation Forest	0.00	0.00	431.85	15.44	311.20	11.13	337.81	12.08	337.81	12.08

Table 3

Annual rate of change in habitat classes of the landscape.

Structural Stages	1945–1963	1963–1989	1989–2001	2001–2014	1945–2014
	(% change per year)				
Forest	7.86	7.51	10.92	4.71	7.76
Open Forest	26.91	1.23	8.04	–11.41	7.01
Shrubland	11.03	3.75	–0.79	3.67	4.78
Open Shrubland	0.97	0.72	0.49	3.97	1.31
Grassland	–1.11	–0.77	–3.25	–12.37	–3.34
Bare Area/Rocks	–8.59	–1.20	–0.06	–0.15	–2.73
Built-up Area	14.17	2.02	2.70	0.00	4.97
Water	0.00	0.00	0.00	0.00	0.00
Plantation Forest	0.00	–1.26	0.63	0.00	0.00

**Fig. 3.** Total gain in forest area between the five time periods, with (a) altitude and (b) distance from streams.

Forest is seen advancing towards elevated areas in the landscape and away from watercourses (Fig. 3). During 1963–1989 and 1989–2001, annual rates of percentage increase in forest were significantly higher at mid-elevations, but this shifted to higher elevations from 2001 to 2014. Also, forest gain has increased away from streams, as the forest conversion rate was higher near streams in earlier years of succession than in later years.

5.1. Change in spatial structure of the landscape (landscape level metrics)

In the earliest landscape in 1945, many tiny patches of bare ground and open shrubland around the minimum ground mapping unit of 50 m² existed within a matrix of grassland. At this earliest stage the Largest Patch Index (LPI) was highest, due to the grassland matrix comprising one large patch of grassland (Table 4). However, the shrubland patches within the matrix, having lowest mean patch size (MPS), as well as connectivity within patches (denoted by the Mean Radius of Gyration (MRG)

Table 4
Landscape level metrics of vegetation succession.

Year	Patch Density and Size					Shape and Edge			Proximity/Isolation	Diversity and Texture	
	NP	PD no. per ha	LPI (%)	MPS (ha)	MRG (m)	MSI	MPAR	ED (m/ha)	MED (m)	IJI	SHDI
1945	6224	222.46	76.56	0.45	7.95	1.75	16193.46	89.3	9.82	30.48	0.75
1963	4012	143.40	58.75	0.70	13.76	2.01	13460.64	101.1	18.11	65.17	1.20
1989	4585	163.88	46.80	0.61	15.40	2.03	10894.13	123.0	20.59	71.22	1.47
2001	3459	123.66	27.96	0.81	22.07	2.22	6273.16	128.9	24.90	74.13	1.76
2014	2266	80.99	19.84	1.23	26.58	2.35	8359.23	118.7	28.26	65.97	1.67

which describes the mean distance for each cell on one path to the patch centroid) probably had low viability as habitats for organisms.

Over 70 years, the LPI which is an effective indicator of habitat uniformity at landscape level, has steadily decreased from 78% to 20%, and in 2014 the largest patch was no longer grassland, but forest. The decreased LPI indicates greater heterogeneity of habitats in the present landscape. Considered along with two other parameters, Number of Patches (NP) and Patch Density (PD), which by 2014 had decreased drastically to approximately one third of the 1945 levels (Table 4), a gradual consolidation of the landscape is understood, as fewer patches and reduced patch density would suggest the landscape has become less subdivided. This is supported by the observed increase in the Mean Radius of Gyration (MRG), which was lowest in 1945, and increased steadily over the 70-year period, indicating that the resulting patches had better internal connectivity i.e., easier traversability for organisms such as civets, macaques, wild boar and deer which prefer to move within forest. Since the forest climax trees are mostly restricted to the oldest forest remnants of 1945 in steep valleys and protected places near villages (Fig. 2), the improved connectivity within patches today offers better opportunities for dispersal agents of the remaining mother trees. This would be further enhanced by the observed steady decline in the Perimeter-to-Area Ratio (MPAR) over the study period. The decreasing MPAR indicates a lowering of the amount of habitat edge, meaning fewer disturbances to organisms moving within patches, as patches become larger and the landscape simplifies. For example, between 1989 and 2001 MPAR was greatly reduced because the main increase in forest was by infilling across interfluvies, between adjacent linear valleys (Fig. 2), rather than by advance along a broad front, as front advance would not affect MPAR significantly. This infilling may be attributed to the shorter dispersal distances across interfluvies for forest seeds, as the main patches of forest in 1989 may have been too far apart for effective seed dispersal by birds. However, distances across interfluvies between adjacent parallel valleys are generally below 150 m, which is within the normal movement range for bulbuls and hwamei. Their median gut passage time of 10 min puts the displacement over 40–130 m (Weir and Corlett, 2006). Accordingly, in the recent stage from 2001 to 2014, when net gain in forest was greatest, MPAR did not change significantly, and the main areal gains were made along a broad advancing front, where interfluvies merged into upper slopes. The decline in MPAR, meaning lower forest edge lengths relative to area, would decrease susceptibility to external factors such as fire, desiccation and wind chill.

Diversity and texture in the landscape was measured through Shannon's Diversity Index (SHDI) and the Interspersion and Juxtaposition Index (IJI). Both parameters show a humped trend, increasing steadily after 1945, peaking in 2001, then decreasing up to 2014 (Fig. 4). The time 2001 was the tipping point, after which the majority of the landscape converted into later successional stages, forest became dominant, with 38% of the landscape, and landscape diversity decreased as indicated by declining SHDI. Thus although the earliest landscape lacked spatial interface between different classes, the overall spatial distribution of classes became more proportional up to 2001, giving better access by species to other types of neighbouring habitats, and would favour those species whose activities, life cycle or propagation require both open and closed habitats. In this context it is significant that the period following 2001 saw the greatest increase in forest area. The observed decline in both SHDI and IJI after 2001 indicates a return towards homogeneity and disproportionality, perhaps implying reduced opportunities for species which move between patches.

5.2. Change in spatial structure of successional classes (class level metrics)

The gradual consolidation and simplification of the landscape indicated by reductions in the landscape metrics NP, PD, MPAR and increase in Mean Edge Distance (MED) over the study period are not replicated by the class level metrics (Table 5). For example, the MED, that is minimum distance to the nearest similar patch, increased at landscape level, as patches became larger and the landscape less fragmented. However, for forest the MED decreased drastically from 319 m in 1945 to 19 m in 2014, while that of shrubland did not change significantly. As early as 1963, and certainly by 1989, when the MED of forest was approximately 80 m and 40 m respectively, this had become within the dispersal distance for the main dispersal agents, bulbuls and hwamei, which can travel distances of 40–130 m during the median gut passage time (Weir and Corlett, 2006). In this context it is significant that the greatest increase in forest area from 1989 to 2001 followed 1989, when forest edge distances became optimal for seed dispersal across the intervening gaps, and when MED fell further (to 17 m in 2001) the rate of increase in forest area was reduced.

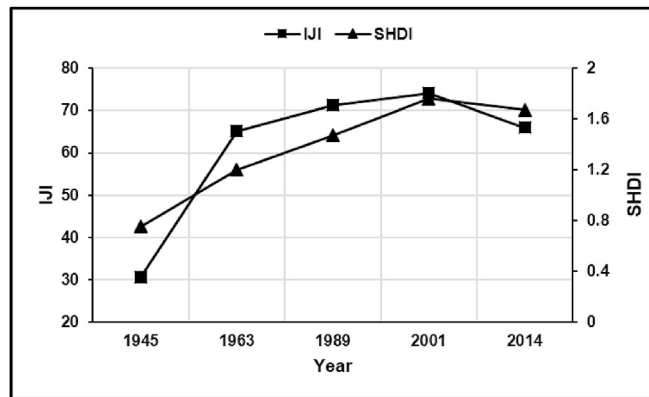


Fig. 4. Changes in Shannon's Diversity Index (SGDI) and Interspersion and Juxtaposition Index (IJI) at landscape level.

Table 5

Class level metrics of vegetation succession.

Structural Stage		Patch Density and Size				Shape and Edge			Proximity/Isolation	
		NP	LPI (%)	MPS (ha)	MRG (m)	ED (m/ha)	MSI	MPAR $\times 10^3$	MPI	MED (m)
Forest	1945	2	0.1	2.41	75.61	1.51	3.38	0.88	0.24	319.51
	1963	49	0.18	0.41	17.61	8.16	1.89	16.73	972	79.45
	1989	217	0.83	0.65	19.97	58.16	2.15	13.96	2765	38.81
	2001	414	8.15	1.4	23.44	135.24	2.18	7.84	16810	17.77
	2014	316	19.84	3.23	26.74	152.21	2.02	15.32	62246	9.33
Open Forest	1945	6	0.01	0.04	6.3	0.23	1.52	22.88	189.55	5.87
	1963	65	0.18	0.43	24.68	15.53	2.53	7.86	221.87	86.48
	1989	87	0.14	0.44	26.1	23.1	2.76	6.89	554	85.57
	2001	285	0.66	0.38	21.06	53.36	2.28	5.45	515	31.26
	2014	35	0.31	0.79	28.6	10.94	2.44	8.72	1307	86.22
Shrubland	1945	187	0.09	0.13	11.67	19.43	1.98	18.10	195	12.67
	1963	710	0.61	0.25	14.62	98.85	2.02	14.37	1017	20.5
	1989	1369	1.76	0.34	14.77	200.27	2.01	11.79	2496	12.21
	2001	837	1.3	0.5	24.46	185.12	2.41	4.13	1201	17.78
	2014	584	3.3	1.11	26.38	197.15	2.33	9.51	5637	16.27
Open Shrubland	1945	810	0.82	0.21	10.36	95.56	1.91	15.94	3117	13.41
	1963	895	0.62	0.23	16.53	135.03	2.31	10.20	440	18.78
	1989	1338	1.16	0.18	13.41	146.26	2.1	8.28	729	18.92
	2001	1087	0.44	0.24	15.89	134.35	2.02	7.87	373	18.34
	2014	469	2	0.9	27.69	157.05	2.55	5.70	2442	25.9
Grassland	1945	1879	76.56	1.17	4.73	329.67	1.49	22.32	927161	4.36
	1963	1300	58.75	1.39	9.39	236.95	1.76	16.88	366313	8.56
	1989	908	46.8	1.63	11.7	187.61	1.74	14.55	252950	11.61
	2001	261	27.96	3.72	29.56	136.01	2.21	4.81	129908	29.03
	2014	269	1.62	0.82	26.49	76.58	2.5	5.02	3371	33.77
Plantations	1945	—	—	—	—	—	—	—	—	—
	1963	53	9.34	8.14	73.76	80.59	3.41	2.07	24322	30.71
	1989	83	1.6	3.97	72.92	70.82	3.21	1.67	2313	19.68
	2001	85	1.6	3.97	73.7	72.77	3.22	1.60	2225	20.17
	2014	85	1.6	3.97	73.7	72.77	3.22	1.60	2225	20.17

It is notable that the hump-backed curve shown by the landscape parameters SHDI and IJI, representing diversity and texture in the landscape (Fig. 4), is mirrored by some shape and size metrics at class level (ie. show an opposite trend). Thus for forest, the parameters Mean Patch Size (MPS) and Mean Radius of Gyration (MRG), indicate an initial decrease in size (MPS) and internal connectivity (MRG) of forest patches, followed by an increase over the 70-year period (Table 5). This means that as the landscape has become more, then less heterogeneous, disproportional and diverse, forest patches have declined then increased in compactness and internal connectivity. This indicates that the greatest rate of forest advance was in the mid-successional stage, when landscape diversity was highest, and forest patches were smallest, with lowest internal connectivity.

Changes in spatial structure of grassland were opposite to changes in structure of forest, as most of the landscape has converted from an earlier, to later successional stage with dominance of forest. Overall, grassland patches have become

fragmented (reduced LPI), geometrically complex (increased MSI), isolated (increased MED) and patch size has decreased (reduced MPS).

For plantations, the large reductions in LPI and MPS after 1963 are attributable to the large plantations of *Pinus massoniana* established in southwest of the study area between 1945 and 1963, being wiped out by a nematode during the 1980s. Since this event, the position, length and density of the remaining plantation edges have changed little over time, with virtually no change in ED and MPAR since 1989 (Table 5), in this otherwise dynamic landscape.

5.3. Species richness and abundance

Trends in woody species richness and abundance within the forest plots (Fig. 5) show a hump-backed curve, with a rapid increase from 1945 to 1989, followed by a gradual, then sharp decline up to 2014. The peak results from the temporary coexistence of shade-intolerant, low-growing pioneers, which are later shaded out, and equally shade-intolerant tall long-lived pioneers, which later dominate the canopy. The humped curve is replicated by landscape level metrics SHDI and IJI (compare Figs. 4 and 5), which show an increase followed by decline as forest advance changed from infilling across valleys and from adjacent patches, to advance along a broad front. Due to this, external influences would have been reduced, and replaced by a more stable environment within the patch promoting internal movement and competition. At class level, the spatial metrics for forest show a decrease in patch size (MPS) and internal connectivity (MRG) in mid-succession mirroring the humped curve in species richness and abundance (ie. showing opposite trends) (Fig. 5). The smaller and disconnected forest patches in mid-succession are likely to be more exposed to external influences and thus unsuitable for any late successional and light-intolerant species arriving.

6. Discussion

6.1. Forest regeneration rates

The highest rate of increase in forest, of 11% a year between 1989 and 2001, appears to be due to a process of infilling across interfluvies between linear valley patches, rather than across a broad forest front. This infilling resulted in the observed lowest Mean Perimeter to Area Ratio (MPAR) for forest in mid-successional stage in 2001, as well as the lowest landscape complexity, or the simplest landscape. But this simpler landscape was able to generate the highest increase in forest area, which occurred from 2001 to 2014. Thus, although the rate of increase slowed to 4.7% a year from 2001 to 2014, the net gain in forest was greatest at this period. The succession appears to have passed a 'tipping point' in 2001 when the landscape was more heterogeneous, but conversely, forest patches were larger, more compact, internally-connected and environmentally stable. These larger forest patches are able to support more disperser organisms, which are observed to increase in both density and diversity with forest succession (Kwok, 2007). Thus seed rain into open areas is increased with forest succession, mostly from bulbuls (Leven, 2000), which have been abundant in Hong Kong at least since the 1930s (Herklots, 1934). It may be significant that the reduction of hill fires in the study area which occurred after 1999 contributed to the highest net gain in forest area after this time. However, hill fire records and satellite images from 1956 to 2015 (authors' unpublished data) indicate that forest and open forest almost never burn, and shrubland only one third the frequency of grassland. This once a woody cover is established, succession to forest is fast. The infilling and consolidation of forest habitats up to 2001 also resulted in decreased landscape diversity, as indicated by reductions in SHDI and IJI. However this may not be a major concern, as woody diversity is

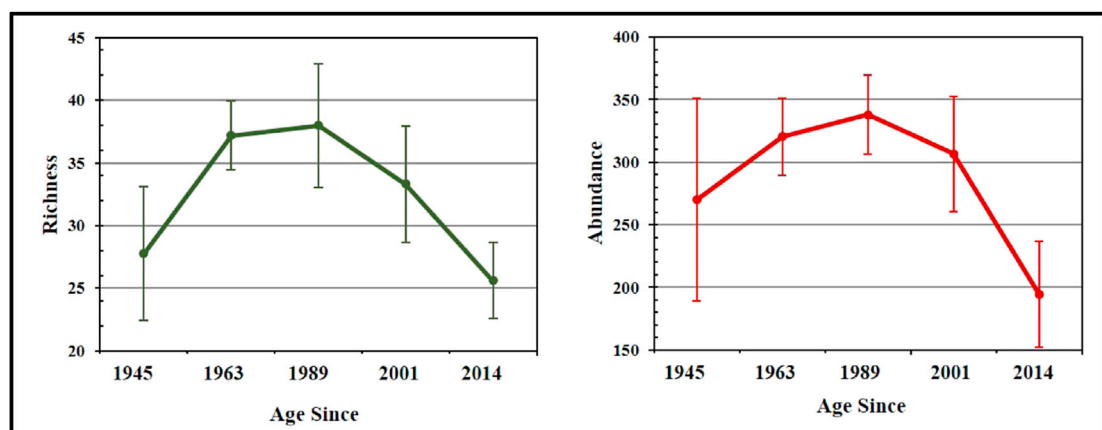


Fig. 5. Chronosequence of species richness and abundance of stems above 1.3 m, in forest plots, GT70 = greater than 70-years old (forest since 1945), LT70 = less than 70-years old (forest since 1963) LT52 = less than 52-years old (forest since 1989), LT26 = less than 26-years old (forest since 2001), and LT14 = less than 14-years old (forest since 2014).

still mostly in the small remnant patches that were never deforested, thus future forest species enrichment is more likely to originate from within forest. With the exception of these oldest forest remnants, natural succession to forest appears to be dominated by a restricted number of hardy native pioneers (Dudgeon and Corlett, 2011), and many of the climax trees are absent. As the forest consolidates however, and taller pioneers shade out shorter ones, the greater diversity of disperser organisms supported, including several species of frugivorous babblers, laughingthrushes, leaf barbets and leaf birds (Leven, 2000) may assist dispersal within the forest from the diversity-rich remnants.

6.2. Constraints from seed dispersal

Further constraints on biodiversity recovery arise from the main seed dispersers in the study area being birds which thrive in open and mixed habitats of the earlier period. Confinement of the climax trees to small remnant pockets of forest along streams and near former villages requires effective dispersal, and by 2014 these forest remnants had become connected to regenerated secondary forest. Thus the improved connectivity within forest patches (indicated by increased Mean Radius of Gyration (MRG)) provides opportunities for this dispersal within forest. Thus the reduced habitat diversity at landscape level in the later succession is now compensated by better internal connectivity within patches, enabling better seed dispersal by forest fauna in the future. However, as the current main seed-dispersers in the study area (bulbuls, the Japanese white eye and hwamei) are small birds with small gape-widths (Weir and Corlett, 2006) and most of the original forest mammals disappeared long ago (Corlett, 2011), dispersal of large-fruited forest trees from the original forest remnants, such as all Fagaceae and the larger-fruited Lauraceae, will be limited.

In the earlier successional stages before 2001, when forest reached 20% of the landscape, diversity and juxtapositioning of habitats at landscape level were high. Thus, up to 2001, SHDI and IJI achieved maximum values offering opportunities for species which move across open habitats. This was accompanied by the highest observed rate of forest regeneration mainly by a process of infilling between parallel valley patches, which occurred when the mean forest edge distance decreased to within the dispersal distance of birds known to disperse seeds in the study area. However, knowledge of dispersal distance for other species is not available and requires further research.

6.3. Grasslands

There are only a few grassland species of conservation interest, such as the Chinese grass bird (*Graminicola striatus*) and certain orchid species, and it is highly questionable whether aggressive human interventions such as burning or weeding trees can be justified to maintain the disappearing and increasingly fragmented grassland habitat since forests are naturally much richer in biodiversity (Thompson et al., 2009). Before human intervention such species would be restricted to areas unsuitable for the growth of trees such as rocky outcrops, swamps or large forest gaps caused by typhoon damage and landslides. It has previously been shown that massive human forest destruction leaves a few “winners” and many “losers” (Zhao et al., 2015). In the Hong Kong case it seems that a few species, such as the Chinese grass bird, were “winners” which benefitted from the large-scale destruction of forests by being able to extend their home ranges into secondary grasslands.

6.4. Plantations

Contrary to suggestions that plantations can act as a nurse crop for forest seedlings (Lamb, 1997; Lugo, 1997; Parrotta et al., 1997; Corlett, 1999), plantations appear detrimental to the succession. Fig. 2 indicates that the *P. massoniana* plantations in the southwest of the study area reverted to grassland following eradication by disease in the 1980s, and remained as grassland for the following three decades, long after other areas had succeeded to forest. Thus the natural progression through stages of greater habitat diversity followed by consolidation and simplification is not observed in *P. massoniana* plantation areas, as even in the later period 2001 to 2014, the plantations not eradicated by disease in earlier decades (Fig. 2) remain unchanged, occupying valley and interfluvial sites which elsewhere have succeeded naturally to forest. This, along with Lee et al.'s (2005) observation of poor colonisation of exotic plantation sites by native species speaks poorly for plantation policies in Hong Kong.

7. Conclusion

Hong Kong's forests are changing structurally, and in terms of microclimate and spatial dynamics into early successional stages of closed canopy forests, but their woody biodiversity remains low because of restricted distribution and dispersal limitations of climax trees. Significantly, as forest patches consolidate and mature, birds of mixed habitats including bulbuls and hwamei known to be the main dispersers of seeds into open and semi-open areas, will become less effective since the seeds of many of the mid-to late successional trees are larger than their gape-width. This is a concern, given the loss of many seed dispersing forest mammals and large forest birds. Such a situation could encourage invasive exotic species such as *Syzygium jambos* and *Acacia confusa*. The former is observed to be dispersed by fruit bats along stream lines in the study area (Leung et al., 2008), and the latter initially introduced as a plantation species, reported as an invasive from elsewhere (IUCN, 2017) and recently found by Fischer (personal observation) to be spreading in Hong Kong.

To restore biodiversity in the absence of late successional dispersal agents, climax trees should be planted in strategically selected plots over the territory, assisted by spatial metrics. This will increase the natural seed rain and stimulate further forest succession by providing new food sources to forest dwelling animals. Such artificially enriched forests would also allow the reintroduction of mobile seed dispersal agents such as forest birds, which is also necessary to avoid their niches being occupied by exotics. Secondary forest plots having high MRG and low MPAR would seem to offer the best movement opportunities and least disturbance to organisms such as forest birds and the remaining mammals. This is especially important, as forest regenerated from remnant forest patches in stream valleys has proceeded from lower to higher ground and upwards from stream sites to interfluvies, making it unlikely that seeds can be dispersed by natural forces such as gravity, flash floods and surface wash. Forest regeneration is seen to be particularly rapid following establishment of a woody cover, thus shrub colonization within grassland to reduce forest edge distances for seed dispersal agents may be facilitated, perhaps artificially. Our observations suggest that plantations do not fulfill this role.

It is significant that the highest rate of forest advance occurred when the landscape achieved maximum diversity (highest SHDI and IJI), as well as forest edge distances (ED) within the range of known seed dispersal agents of open and mixed habitats. But as the landscape shifts from complexity to simplicity and natural forest remnants containing climax trees become connected with more extensive forest habitats, full forest and woody biodiversity recovery may also depend on the reintroduction of specialised native forest dispersal organisms (McConkey et al., 2012) such as Edwards's long-tailed giant rat (*Leopoldamys edwardsi*) (Zhang et al., 2005). This has to be balanced by the recognition that long absence from an ecosystem may be disruptive to the new ecological equilibrium (Corlett, 2013).

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