



THE HONG KONG  
POLYTECHNIC UNIVERSITY

香港理工大學

Pao Yue-kong Library

包玉剛圖書館

---

## Copyright Undertaking

This thesis is protected by copyright, with all rights reserved.

**By reading and using the thesis, the reader understands and agrees to the following terms:**

1. The reader will abide by the rules and legal ordinances governing copyright regarding the use of the thesis.
2. The reader will use the thesis for the purpose of research or private study only and not for distribution or further reproduction or any other purpose.
3. The reader agrees to indemnify and hold the University harmless from and against any loss, damage, cost, liability or expenses arising from copyright infringement or unauthorized usage.

### IMPORTANT

If you have reasons to believe that any materials in this thesis are deemed not suitable to be distributed in this form, or a copyright owner having difficulty with the material being included in our database, please contact [lbsys@polyu.edu.hk](mailto:lbsys@polyu.edu.hk) providing details. The Library will look into your claim and consider taking remedial action upon receipt of the written requests.

**REMOTE SENSING OF FOREST SUCCESSION IN HONG KONG'S  
COUNTRY PARKS**

**SAWAID ABBAS**

**Ph.D**

**The Hong Kong Polytechnic University**

**2017**



**The Hong Kong Polytechnic University**  
**Department of Land Surveying and Geo-Informatics**

**Remote Sensing of Forest Succession in Hong Kong's Country  
Parks**

**Sawaid ABBAS**

**A thesis submitted in partial fulfillment of the requirements  
for the degree of Doctor of Philosophy**

**August 2016**



## **Certification of Originality**

I hereby declare that this thesis is my own work and that, to the best of my knowledge and belief, it reproduces no material previously published or written, nor material which has been accepted for the award of any other degree or diploma, except where due acknowledgement has been made in the text.

\_\_\_\_\_ (Signed) \_\_\_\_\_

Sawaid ABBAS \_\_\_\_\_ (Name of Student)



## **Dedication**

To my father and brother with love



## Abstract

This study aimed to use remotely sensed images to investigate the dynamics of secondary forest succession after a complete clearance of forest in Hong Kong during WWII. The study area (~2800 ha), included Tai Mo Shan and ShingMunCountryParks in the NewTerritories of Hong Kong. A multi-scale object-based approach was applied to sequential aerial photographs and recent high-resolution satellite images to map structural changes in natural vegetation over the last 70 years, from 1945 to 2014. Temporal changes in the spatial extents of structural classes, and rates of change were determined for each of the periods; from 1945 to 1963, 1963 to 1989, 1989 to 2001, and 2001 to 2014. Also, spatial patterns of forest succession related to topography and morphology of the landscape were analyzed to determine the influence of changes in specific landscape structural parameters on forest succession. The mapping of structural changes associated with forest recovery over the past 70 years also enabled the recording and study of changes in species composition along the successional and environmental gradients for better understanding of the processes of ecosystem recovery in the degraded tropical landscape. Therefore, a forest inventory data consisting of 28 quadrats (20 x 20 m) was collected to analyze patterns of species composition associated with different stages of the succession, as well as explain the influence of topography, soil properties, and age of forest on the species assemblages.

Spatial analysis of forest succession showed that natural forest has established rapidly in areas where a shrub cover was able to colonize in fire protected grasslands. The fastest period of forest regeneration, at 10.9% annually between 1989 and 2001, occurred when the landscape achieved greatest habitat diversity and juxtapositioning of habitat patches. This rapid regeneration occurred by infilling from the remnant forest in adjacent valleys rather than by an advance along a broad forest front, and led to a simplification of the landscape and declining habitat diversity. After 2001, succession to forest was slower, at 7.8% annually, as forest patches consolidated and edge habitats reduced. Significantly, the birds of open habitats including bulbuls and hwamei, known to disperse seed in the study area, may become less effective as forest patches consolidate, and this is a concern, given the loss of most forest mammals. Consequently, progression to a mature, biodiverse and stable forest ecosystem may depend on dispersal agents other than those which have operated over recent decades.

Additionally, the practice of afforestation as a nursery stage on degraded hillsides, for the establishment of forest seedlings by natural invasion, is not supported by the evidence, as when the native *Pinus massoniana* plantations were eliminated by disease during the 1970s, no forest or woody species were seen in the areas affected. In fact, there was a reversion to grassland, which persisted there for almost three decades, until recent shrub invasion.

Secondary forest successions in Hong Kong starts with the transition of fire protected grassland into shrubland and colonization of early successional tree species that pave the way for intermediate or late successional tree species. Analysis of community data along the environmental gradients indicated that the topography and successional stages play an important role in the distributional patterns of species assemblages in the study area. At the landscape scale, elevation divided the species composition into two components, and these were further distinguished by successional stage at localized scale. Micro scale variations were further explained by convexity of terrain. Forest at higher elevation was found to be more diverse and had markedly higher concentration of soil carbon relative to nitrogen. Therefore, for restoration of the degraded ecosystem, it is recommended to recognize the distinctiveness of ecosystems at these two different elevations in the study area. Additionally, effective forest management policies could include sowing of native shrubs extending linearly from established forest, to maximize edge length between woody species and grasslands for better colonization, and planting of late successional species in areas where forest pioneers are dying out. Thus, for effective forest restoration, the roles of GIS and Remote Sensing are important in locating sites for assisting shrub encroachment, as well as for accelerating secondary succession where shrubland has already been established, and for managing natural succession by planting late successional tree species where the oldest forest pioneers are established.

**Key Words:** *Tropical Forest, Degraded Landscape, Succession, Secondary Forest, Remote Sensing, Hong Kong, Spatial Ecology, Change Detection, Biodiversity Conservation.*

## Publications Arising from the Thesis

### Journal

Abbas, S., Nichol, J.E., Gunter, A. F. (2016). A 70-year perspective on tropical forest regeneration, *Science of the Total Environment*, 544, 544-552.

Abbas, S., Nichol, J.E., Gunter, A. F. (2017). Mapping and assessment of impacts of cold and frost on secondary forest in the marginally tropical landscape of Hong Kong, *Agricultural and Forest Meteorology*, 232, 543-549

### Conference

Abbas, S., Nichol, J.E. (2015). Spatial patterns of vegetation succession in degraded tropical landscape of Hong Kong, *2<sup>nd</sup> International Conference on Remote Sensing Applications in Tropical and Subtropical Areas (RSATSA)*, Hong Kong, 8<sup>th</sup> – 10<sup>th</sup> December.

Abbas, S., Nichol, J.E. (2016). Monitoring secondary forest succession in Hong Kong using Remote Sensing and GIS, *AsiaFlux mini-workshop on Remote Sensing and Ecological/Environmental Monitoring*, Taipei, Taiwan, 1<sup>st</sup> – 5<sup>th</sup> March.

## Acknowledgments

All praises to Almighty Allah, the creator of the universe, who blessed me with the knowledge and enabled me to complete this thesis. All respects to the Holy Prophet Muhammad (May Allah grant peace and honor to him and his family), who is the last messenger, whose life is a perfect model for the whole humanity.

I would like to express my highest respect and profound thanks to my supervisor, Janet E. Nichol, for her kind supervision, patience, correction of drafts, and encouragement throughout my study period. Apart from my research, she also encouraged and trained me to play squash. I enjoyed every bit of the discussions we made in squash courts. She also helped me in some field surveys.

I also extend my gratitude to Dr. Man Sing Wong Charles, for being my supervisor after the retirement of Prof. Janet E. Nichol. He was always helpful, especially I am grateful for his efforts to obtain various spatial data sets and aerial photographs from the Lands Department of Hong Kong.

I am very grateful to the head of LSGI, chair of departmental research committee and all the other faculty members of LSGI for their support. I am sincerely thankful to the General Office (GO), the Research Office (RO), the Finance Office (FO) and the Student Affair Office (SAO) for their continuous support during the academic period.

Field survey was the most demanding part of my research project that would not be possible without the substantial supports from my friends, colleagues and student helpers. For this, I am greatly indebted to Mr. Syed Muhammad Irteza, Dr. Majid Nazeer, Mr. Muhammad Usman, Mr. Waleed Umer, Dr. Pankaj Kumar (KFBG), Mr. Joseph, Ricky, Eric, Nick, Keith, Bobo, Stephy, and Christine for their help during field surveys. I am extremely grateful to Ms. Rashmi Supriya (Department of Health Technology and Informatics, PolyU) for her motivation and cooperation during field surveys, especially for storing and managing soil samples.

I would also like to acknowledge the support drawn from Kadoorie Farm and Botanic Garden (KFBG), Agriculture, Fisheries and Conservation Department (AFCD), and Lands Department of Hong Kong. I also benefitted from discussions and comments from Dr.

Gunter A. Fischer (KFBG) and Dr. Jinlong Zhang (KFBG). Dr. Jinlong Zhang also guided me to set up field survey plots for vegetation census and helped in species identification.

Special thanks to my friends, Mr. Faisal M. Qamer, Dr. Muhammad Bilal, Dr. Imran Shahzad, Dr. Ghaffar Ali, and Muhammad Bilal Sadique.

I am also grateful to Mr. Waseem Mir, Mr. Syed Raza Shamsi and Mr. Hafeez-ur-Rahman for being like brothers and local guardians in Hong Kong.

I express my indebtedness and my deepest sense of gratitude to all of my family members, especially my parents, for their endless love, moral support, encouragement, and prayers for successful completion of this study.

Lastly, I am very thankful to Research Grants Council (RGC), Hong Kong, for awarding me Hong Kong Ph.D. Fellowship, which supported me during my studies and gave me such wonderful opportunities for cultural and personal engagement.

Sawaid ABBAS

# Table of Content

Abstract	i
Publications Arising from the Thesis	iii
Acknowledgments	iv
Table of Content	vi
List of Tables	viii
List of Figures	ix
List of Abbreviations	xi
<b>Chapter 01</b>	<b>14</b>
<b>1. Introduction</b>	<b>14</b>
1.1. Introduction	14
1.2. Research objectives	18
1.3. Dissertation Overview	19
<b>Chapter 02</b>	<b>20</b>
<b>2. Study Area</b>	<b>20</b>
<b>Chapter 03</b>	<b>23</b>
<b>3. Literature Review</b>	<b>23</b>
3.1. History of Hong Kong's forest	23
3.1.1. Forest restoration efforts	24
3.1.2. Natural secondary forest	26
3.2. Drivers and barriers to forest succession in Hong Kong	27
3.2.1. Hill Fires in Hong Kong	27
3.2.2. Seed availability and dispersal agents	28
3.2.3. Climate change and succession in Hong Kong	31
3.2.4. Plantationecology	31
<b>Chapter 04</b>	<b>33</b>
<b>4. Object Based Classification to Detect Structural Changes in Vegetation Succession</b>	<b>33</b>
4.1. Introduction	33
4.2. Materials and Methods	37
4.2.1. Data acquisition	38
4.2.2. Pre-processing	38
4.2.3. Habitat classification scheme	39
4.2.4. Object based habitat classification	39
4.2.5. Accuracy assessment	40
4.2.6. Extent, rate and transitions of structural stages	40
4.2.7. Annual rate of change	41
4.3. Results and Discussion	42
4.3.1. Habitat mapping	42
4.3.2. Changes in structural stages: gains, losses, net change and total change	43
4.3.3. Succession in vegetation communities	43
4.3.4. Rate of change in structural stages	46
4.4. Conclusion	47
<b>Chapter 05</b>	<b>58</b>
<b>5. Changes in Spatial Morphology of the Landscape along the Successional Gradient</b>	<b>58</b>
5.1. Introduction	58

5.2. Materials and Methods	61
5.2.1. Landscape metrics	61
5.2.2. Topographic analysis	62
5.3. Results	64
5.3.1. Change in spatial structure of the landscape	64
5.3.2. Change in spatial patterns of structural classes	65
5.3.3. Topographic patterns of vegetation successional stages over time	66
5.4. Discussion	68
5.5. Conclusion	69
<b>Chapter 06</b>	76
<b>6. Diversity and Compositional Traits of Forest Succession</b>	76
6.1. Introduction	76
6.2. Materials and Methods	80
6.2.1. Vegetation survey	80
6.2.2. Soil sampling	82
6.2.3. Topographic variables	83
6.2.4. Vegetation data analysis	86
6.3. Results	90
6.3.1. Regression analysis	90
6.3.2. Canonical Correspondence Analysis (CCA)	91
6.3.3. Variation partitioning	92
6.3.4. Multivariate Regression Tree	92
6.4. Discussion	94
6.5. Conclusion	99
<b>Chapter 07</b>	120
<b>7. Conclusions and Recommendations</b>	120
<b>References</b>	124
<b>Appendices</b>	143

## List of Tables

<b>Table 4.1</b>	Description of remotely sensed data used	38
<b>Table 4.2</b>	Description of habitat classes	39
<b>Table 4.3</b>	Distribution of habitat classes over the years	54
<b>Table 4.4</b>	Error matrix generated for accuracy assessment of habitat map of 2001	54
<b>Table 4.5</b>	Contingency matrix showing transitions between habitat classes and/or structural stages of vegetation (1945-1963, 1963-1989)	55
<b>Table 4.6</b>	Contingency matrix showing transitions between habitat classes and/or structural stages of vegetation (1989 -2001, 2001-2014)	56
<b>Table 4.7</b>	Annual rate of change in structural stages of the landscape	57
<b>Table 5.1</b>	Description of landscape metrics used for the spatial analysis	63
<b>Table 5.2</b>	Spatiotemporal patterns of landscape indices in the landscape, at landscape level	71
<b>Table 5.3</b>	Spatiotemporal patterns of landscape indices in the landscape, at class level	72
<b>Table 6.1</b>	Topographic characteristics of the sample sites	112
<b>Table 6.2</b>	Soil characteristics of the sample sites	113
<b>Table 6.3</b>	Community traits of the sample site.	114
<b>Table 6.4</b>	Descriptive statistics of community traits	115
<b>Table 6.5</b>	Pearson correlation of among the community variables and the environmental variables	116
<b>Table 6.6</b>	Results of linear regression model of community traits with three different categories of explanatory variables and their combinations	117
<b>Table 6.7</b>	Statistics of CCA analysis and variation explained by the first six CCA-axis	118
<b>Table 6.8</b>	Results of MRT analysis	119

## List of Figures

<b>Figure 2.1</b>	Location map of the study area	22
<b>Figure 2.2</b>	Climatology of Temperature and Rainfall in Hong Kong, 30-year monthly means, 1981-2010	22
<b>Figure 4.1</b>	Flow diagram for habitat classification and assessment of structural changes	37
<b>Figure 4.2</b>	Processed aerial photographs of 1945, 1963, and 1989, and panchromatic bands of satellite images of 2001 and 2014	49
<b>Figure 4.3</b>	Penta-temporal habitat classification maps of the landscape for the years 1945, 1963, 1989, 2001 and 2014	50
<b>Figure 4.4</b>	Plantation patches at their earlier growth stage, recognizable from their spatial pattern and arrangement in 1963.	51
<b>Figure 4.5</b>	Monocultural plantation stands recognizable from their texture, appeared in 1989.	52
<b>Figure 4.6</b>	Image sequence showing loss of plantations during 1970s	53
<b>Figure 5.1</b>	Process of spatial analysis of the landscape	61
<b>Figure 5.2</b>	Change in Path Density (PD) and Mean Patch Size (MPS) over the years	73
<b>Figure 5.3</b>	Mean topographic characteristics of structural classes over the years	73
<b>Figure 5.4</b>	Structural changes in vegetation communities along aspects	73
<b>Figure 5.5</b>	Annual rate of change (%) of forest along the topographic variable	74
<b>Figure 5.6</b>	Histogram distribution of increase in forest along elevation	74
<b>Figure 5.7</b>	Increase or decrease in area of structural stages during the each period of time	75
<b>Figure 6.1</b>	Flow chart of methodology to analyse diversity and compositional traits of forest succession	79
<b>Figure 6.2</b>	Locations of sample sites	101
<b>Figure 6.3</b>	Layout design of each sample site (20m × 20m) with 16 subplots (5m × 5m)	102
<b>Figure 6.4</b>	Pair-wise correlation matrix plot of topographic variables	103
<b>Figure 6.5</b>	Pair-wise correlation matrix plot of soil variables	103
<b>Figure 6.6</b>	Chronosequence of species richness, abundance, Basal Area and No of dead stems	104
<b>Figure 6.7</b>	Matrix plot between community traits and the environmental variables	105

<b>Figure 6.8</b>	CCA ordination diagram-1 showing the relationship of species with the environmental variables	106
<b>Figure 6.9</b>	CCA ordination diagram-2 showing the relationship of species with the environmental variables, with sites names	107
<b>Figure 6.10</b>	CCA ordination diagram-3 showing the relationship of species with the environmental variables, with sites names ellipsoids of age categories	108
<b>Figure 6.11</b>	Portioning of the variation of species explained by topography, soil and Age	109
<b>Figure.6.12</b>	Multivariate regression tree analysis	110
<b>Figure.6.13</b>	Selection of the tree was made by 1-SE rule.	111

## List of Abbreviations

Abbr	Abbreviation
ACH	Altitude above Channel
AFCD	Agriculture, Fisheries and Conservation Department
AIC	Akaike Information Criterion
ANc	Absolute Net Change
AP	Aerial Photograph
APG	Angiosperm Phylogeny Group
AspE	Eastness - (sine [Aspect])
AspN	Northness - (cosine [Aspect])
BA	Bare Area
BU	Built up Area
C	Carbon
C:N	Carbon – Nitrogen ratio
CCA	Canonical Correspondence Analysis
CI	Convergence Index
CL	Class level
Cl	Clay
cm	Centimeter
CoV	Coefficient of Variation
Curv	Curvature
CVRE	Cross Validation Relative Error
dbh	Diameter at breast height
DEM	Digital Elevation Model
dpi	Dots per inch
ED	Edge Density
Elv	Elevation
F	Forest
FAO	Food and Agriculture Organization
G	Gain
g	Gram
GCP	Ground Control Point
GIS	Geographic Information System
GL	Grassland
GPS	Global Positioning System
GT70	Greater than 70 year old forest (forest since 1945)
ha	Hectare
HC	Horizontal Curvature
HK	Hong Kong
HRS	High Resolution Satellite Images
IJI	Juxtaposition Index

KFBG	Kadoorie Farm and Botanic Garden (KFBG)
km	Kilometer
L	Loss
LCCS	Land Cover Classification System
LL	Landscape Level
LPI	Largest Patch Index
LS	Length of Slope Factor
LT14	Less than 14 year old forest (forest since 2014)
LT26	Less than 26 year old forest (forest since 2001)
LT52	Less than 52 year old forest (forest since 1989)
LT70	Less than 70 year old forest (forest since 1963)
m	Meter
M	Moisture Content
MAUP	Modifiable Aerial Unit Problem
Max	Maximum
MED	Mean Euclidean Distance
MED	Mean Euclidean Nearest Neighbor Distance
Med	Median
Min	Minimum
MPAR	Mean Perimeter to Area Ratio
MPI	Mean Proximity Index
MPS	Mean Patch Size
MRG	mean radius of gyration
MRT	Multivariate Regression Tree
MSE	Mean Standard Error
MSI	Mean Shape Index
N	Nitrogen
n	No. of Sample
NP	Number of Patches
OBIA	Object Based Image Analysis
OF	Open Forest
OM	Organic Matter
PCC	Post-Classification Comparison
PD	Patch density
PF	Plantation Forest
PMM	Patch Matrix Model
RMSE	Root Mean Square Error
IVI	Important Value Index
RPC	Rational Polynomial Coefficients
RS	Remote Sensing
S	Sand
SAGA	System for Automated Geoscientific Analyses
SD	Standard Deviation

SE	Standard Error
SG	Open Shrubland or Shrubby Grassland
SH	Shrubland
SHDI	Shannon's Diversity Index
Si	Silt
slp	Slope
SR	Solar Radiation
SS-MRT	Sum of Squares – Multivariate Regression Tree
Tc	Total Change
TWI	Topographic Wetness Index
UNEP	United Nation' Environment Program
VC	Vertical Curvature
VIF	Variance Inflation Factor
W	Water
WV2	World View 2
WWII	World War II

# Chapter 01

## Introduction

### 1.1. Introduction

The loss and degradation of the world's forests are major contributors to global environmental and climate change (Nobre et al., 1991). Forested areas of the world decreased by 129 million ha (3.13 %), from 4,128 million ha to 3,999 million ha, during the past quarter-century, and today forest occupies only 30.6 % of the global land area, of which only 35 % is primary forest. Because most of the world's forests are now secondary forests, they are therefore more important for biodiversity conservation, catchment protection, climate control, and the ecological services they provide (FAO, 2015).

Natural habitats, particularly tropical forest ecosystems, are being degraded at an alarming pace and have suffered immense destruction (FAO, 2010; Halle and Fattorini, 2004). Tropical forests are acknowledged for providing important ecosystem services, including carbon sequestration. 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).

A broad outline prediction of the future of tropical forest indicates extensive agricultural encroachment into old-growth forest due to an expected 2 billion increase in population of tropical countries over the next few decades (Geist and Lambin, 2002). On the other hand, secondary succession has regained 15 % of the area deforested during the 1990s (Wright, 2005) and this regenerated secondary forest is becoming more abundant (Aide and Grau, 2004; Wright and Muller-Landau, 2006; Wright, 2005). This is the result of millions of hectares of tropical landscape being abandoned following massive deforestation and large-scale agricultural activities (Grainger, 1988; Perz and Skole, 2003), such as, in Brazil (Perz and Skole, 2003), Puerto Rico (Grainger, 1988), Costa Rica (Hartshorn, 1980; Helmer, 2000), Mexico (Guevara and Laborde, 1993), Colombia (Faber-Langendoen, 1992), Venezuela (Saldarriaga et al., 1988),

Myanmar (Sann et al., 2016), and Singapore (Turner et al., 1997). Most recently, remote sensing based estimates by Kim et al., (2015) also indicated an accelerated forest gain in some parts of tropical Asia and decrease in deforestation in Brazil.

A significant body of scientific literature has focused on patterns and processes of land cover changes. However, ecologists have not given much attention to the nature of recovering secondary forest and its ecological implications for degraded landscapes (Lugo and Helmer, 2004). Therefore, refinement and advancement in knowledge is required to understand the ecological processes involved in secondary succession for adequate management of fast-growing secondary forest (Guariguata and Ostertag, 2001).

Secondary forest succession refers to regrowth of woody vegetation following complete destruction of forest, and the succession process is influenced by stochasticity, a species' biology and its interaction with other flora and faunal species, as well as environmental conditions (Walker and Chapin, 1987). A particular floristic composition exists along a successional gradient that is determined by factors influencing the earlier and later successional stages. In earlier successional stages landscape is colonized by forest pioneers which depends on seed germination conditions, seed dispersal mechanisms, and presence of soil-stored seeds. The late succession is controlled by the competitive ability and tolerance of environmental conditions which in turn determine the species specific growth rates, endurance, maximum size at maturity, and the proportion of species that are shade-tolerant (Guariguata and Ostertag, 2001; Walker and Chapin, 1987).

A recovering secondary forest ecosystem can be referred to as a functional forest ecosystem, although it may or may not contain pre-disturbance species composition. For example, species compositions of recovering secondary forests on degraded or post-agricultural abandoned lands are observed to be significantly different from primary forests in Puerto Rico and New England (Bellemare et al., 2002; Lugo and Helmer, 2004). This is because the ecological processes associated with disturbance, species range expansion, and competition may result in temporary or permanent change in forest composition either independently or due to human activities (Catterall et al., 2008). For example, the fast growing pioneers of secondary-forest species are lower in wood density (King et al., 2006), which could alter the long-term carbon sequestration

capacity of the secondary forests(Körner, 2004). Therefore, understanding the shifts in species structure, composition, diversity and ecosystem functioning is critical to ascertain the long-term conservation values of these forests and their role in climate change mitigation(Rhemtulla et al., 2009).

There is now a general consensus among ecologists that ecosystems do not exhibit a single defined equilibrium to which they return via succession after disturbance. The system may exhibit multiple successional pathways and equilibria that depend on the environmental and historical context (Wu and Loucks, 1995). This view point implies that the state of an ecosystem at any particular point in space or time will be difficult to ascertain(Frelich and Reich, 1999), and this is an issue ecologists must address if they are going to forecast the future of the biosphere (Clark, 2001). Knowledge of recovery rates, variation in regrowth rates across time and space, and the responses of post-disturbance regeneration of tropical forest to environmental gradients may facilitate our understanding of these recovering ecosystems for better management of their recovery,and biodiversity conservation(Cole et al., 2014; Holl et al., 2000).

Information on environmental determinants of ecological structure and composition along the environmental gradient has been a persistent topic of ecological studies for informed ecosystem management practices (Anderson et al., 2011). Research has shown that spatial patterns of landscape have an influence on species composition of recovering forest. There are very few studies on spatial interactions of species composition at different successional stages of forest recovery. Generally, studies have focused on either the spatial patterns of forest recovery or on species composition, but few studies have investigated how the spatial patterns of recovering forest structure influence species composition and diversity along successional gradient(China and Helmer, 2003).

Hong Kong's vegetation is extremely diverse, with more species of vascular plants in its 1,100 km<sup>2</sup> of land area than the whole of Great Britain (Dudgeon and Corlett, 2011). However, Hong Kong is one of the earliest examples of tropical degradation, as it is estimated that complete clearance of the broad-leaved evergreen forest occurred around 400-600 years ago (Meachem, 1994). Nonetheless, Hong Kong is also one of the rare examples where natural tropical secondary tropical is regenerating on land abandoned after agricultural use and/or deforestation. Although plantation forestry for

environmental purposes commenced in mid-19th century (Evan, 1992), complete destruction of forest including plantations took place during the blockade years of World War II, accompanied by soil erosion on the steep slopes. Hong Kong's present day flora and fauna represent recovery since 1945 due to both natural regeneration from tiny remnants in inaccessible sites and possibly from post-war plantation of a limited range of native and exotic species.

Remotely sensed data are an indispensable source of information for observing spatial patterns of the rapidly changing forest environment (Gao and Liu, 2012). Aerial photographs and satellite images have been widely used by ecologists for fine scale mapping of tropical forest to assist conservation planning and management (Etter et al., 2005; Galo, 2016; Turner et al., 1996). A combination of well-documented flora, a complex mixture of environmental gradients, easy access to field sites, recovering secondary forest since 1945, and availability of historical archived aerial photographs, make the degraded tropical landscape of Hong Kong an ideal study area to ascertain spatial patterns of vegetation structural changes.

Black and white aerial photographs provide the earliest temporal record of Remote Sensing (RS) data and therefore are an invaluable source of information for studies of changes in ecosystem dynamics over time (Allard, 2003; Dissanska et al., 2009; Pellerin and Lavoie, 2003; Pringle et al., 2009; Rabia and Terribile, 2013). However, the delineation of habitat patches from high resolution remotely sensed data, including black and white aerial photographs, especially when combined with other image types, is difficult due to the tonal and structural complexity of habitat patches. Thus, analysis based on different types and scales of earth observation data may not explicitly represent landscape entities independent of the units used. In this study, an objective methodology will be devised to use a long term black and white remote sensing data to map the structural changes in natural vegetation in Hong Kong over the last 70 years, 1945 to 2014. During a structural succession of vegetation, the structural complexity of landscape increases. And, at each structural stage, landscape parameters such as patch size, shape, contiguity and distance vary. The 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 second objective of the study is to determine the changes in the spatial

structure of the landscape over the period and identify the influence of spatial landscape parameters on the forest. The structural changes associated with forest recovery influences the species assemblages process along the successional and environmental gradients. The third part of the study is to analyze spatial and temporal patterns of species composition in secondary forest succession and to explain the influence of topography, soil properties, and age of forest on the species assemblages using forest inventory data collected from the study area. In a nutshell, mapping the structural changes, changing the morphology of spatial structure of the landscape, and species composition and diversity along the environmental and successional gradient will help to understand the process of ecosystem recovery in the degraded tropical landscape of Hong Kong. And the framework of the study, especially delineating habitat boundaries from black and white photographs, is adaptable from similar studies elsewhere in the world and the results of the study will facilitate conservationist and ecologist to support the natural succession of the tropical secondary forest

## **1.2. Research objectives**

The aim of this study is to use remotely sensed images to investigate patterns and processes of vegetation succession in the degraded tropical landscape of Hong Kong since the complete clearance during WWII, to understand structural and compositional traits of secondary forest, as well as their implications for regeneration of similar forests elsewhere.

The specific objectives of the study are to:

1. Develop a methodology for objective change detection to investigate vegetation successional patterns by sequential analysis of aerial photographs and satellite images, from 1945 to 2014.
2. Examine the changes in spatial morphology of the landscape along the successional gradient by quantifying changes in spatial structure, composition, and diversity of the landscape over time.
3. Determine the influence of topography, soil properties, and age of forest on the patterns of plant species composition and diversity along the successional gradient using forest inventory data.

### **1.3. Dissertation Overview**

The dissertation consists of seven chapters.

Chapter 1 is an introductory chapter, which outlines the dynamics of tropical secondary forest succession and objectives of the study.

Chapter 2 describes the geography of Hong Kong and the specific study area.

Chapter 3 provides a brief history, dynamics and ecology of secondary forest succession in Hong Kong.

Chapter 4 deals with mapping structural changes in vegetation over a 70-year period of vegetation succession.

Chapter 5 examines the morphological changes over time using the Path Matrix Model (PMM) of landscape structure.

Chapter 6 describes the floristic composition, diversity and richness of vegetation, and the impacts of local environment on species composition along the successional gradient.

## Chapter 02

### Study Area

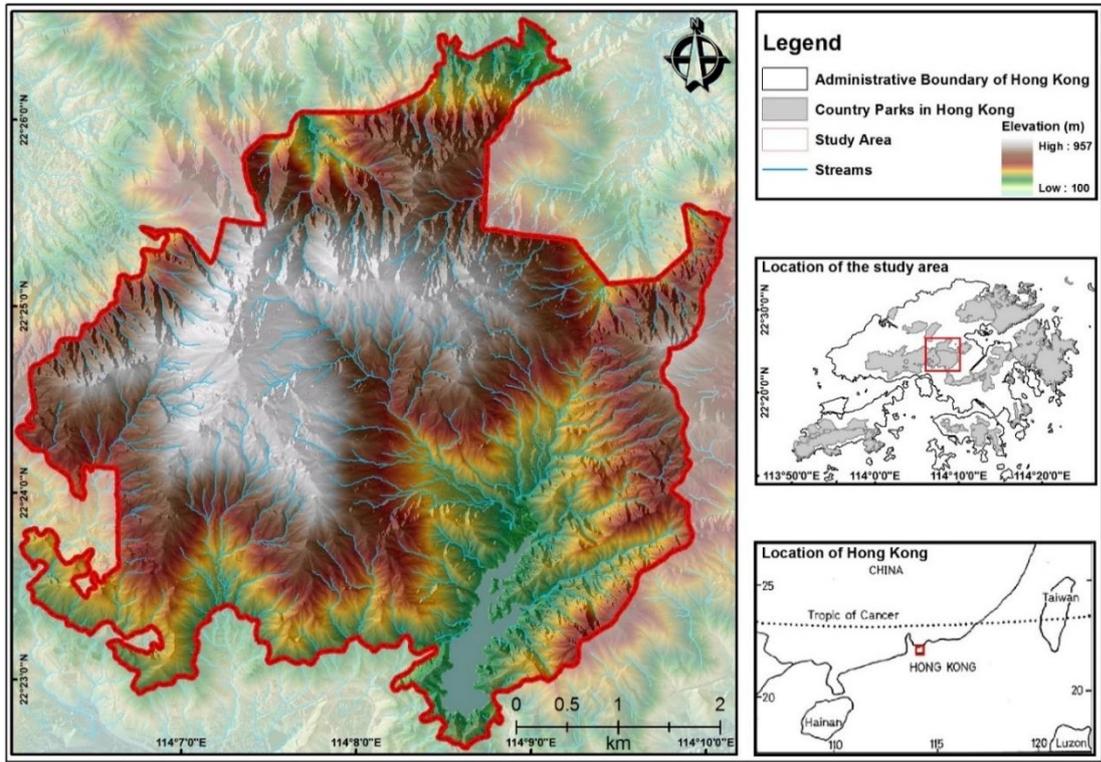
Hong Kong is a special administrative region of Mainland China, located on the eastern shore of the Pearl River Estuary, having an area of ~ 1100 km<sup>2</sup>. It shares a border to the north with Guangdong province of China and is surrounded by the South China Sea on east, west and south. Hong Kong is situated between 22°09' to 23°37' latitudes and 113°52' to 114°30' longitudes on the northern margins of Asian tropics (figure 2.1). The topography of the area is rugged with the highest point of 957m at Tai Mo Shan in the New Territories. Due to rugged terrain, more than 75 % of the area is undeveloped and the population is squeezed into less than 25% area(Corlett, 1999).

The study area spans over an area of ~2800 ha comprising the Tai Mo Shan and Shing Mun country parks in New Territories of Hong Kong (figure 2.1). The study area lies on the northern borders of the tropics climate with cool dry winters and hot wet summers. The topography of the area is rugged characterized by convex slopes rising to the tallest peak (957 m) Tai Mo Shan and steep-sided slopes around Shing Mun reservoir. Upper valleys are covered with mostly fire-maintained grasses and lower elevations are covered with patches of secondary forest and plantations (Delang and Hang, 2009). Temperature falls below zero above 400 m elevation, several times in a decade, and rainfall increases with elevation (Dudgeon and Corlett, 2011; Weir and Corlett, 2006).

The climate of Hong Kong includes features of both the tropics and subtropics with highly seasonal rainfall and temperature. Despite being located 100 km south of the Tropic of Cancer, the climate is best described as subtropical due to temperature and rainfall seasonality with a hot humid summer from May to September and a cool dry winter from November to February (figure 2.2). Mean annual rainfall is 2398 mm but 80% of this amount is confined to May to September, and mean annual temperature is 23.3° C with minimum and maximum temperature in January and July, respectively (Leung et al., 2008).

Volcanic rhyolite and granite are the most common rock types in Hong Kong. Rhyolite is distributed over the eastern New Territories, Tai Mo Shan, southern Hong Kong Island,

and along western Lantau Island. The western New Territories, eastern Lantau Island, and northern Hong Kong Island are dominated by granite (Chiu et al., 1986). Generally, hills soil in Hong Kong are characterized by strong acidity, sandy texture, low contents of nitrogen, potassium, phosphorus, and soil organic matter, and are well drained. Red-yellow podzol and kranozem soil types comprise 80% of all the soil of Hong Kong. The red-yellow podzol is derived from weathering of granite and can support only a sparse vegetation cover whereas kranozem is developed on volcanic parent material and its fine texture supports denser vegetation (Dudgeon and Corlett, 2011).



Figure

2.1 Location map of the study area

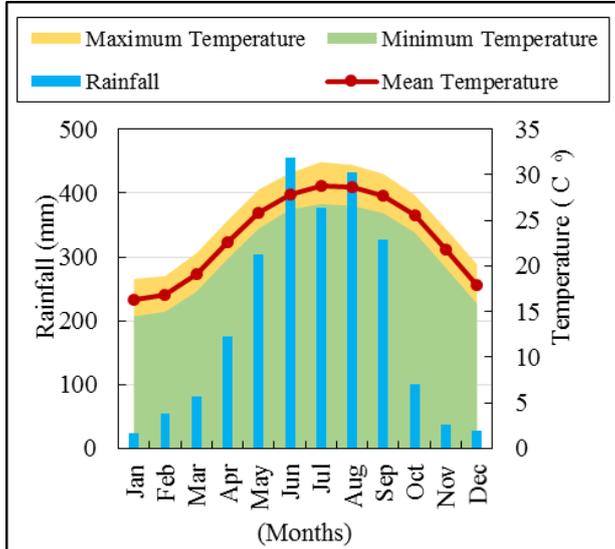


Figure 2.2 Climatology of Temperature and Rainfall in Hong Kong, 30-years' monthly means, 1981-2010

## Chapter 03

### Literature Review

Current forest cover in Hong Kong comprises Feng Shui Woods<sup>1</sup>, natural secondary forest, and plantations. Since 1841, 390 native tree species (Corlett, 1999), belonging to 61 families have been recorded in Hong Kong (Zhuang and Corlett, 1996). The majority of the secondary forest has developed through structural succession on lands protected from fire since 1945. Hong Kong's primeval vegetation was a diverse seasonal rain forest with at least 150-180 woody species per hectare as found in nearby protected areas in South China (Cao et al., 2013; Jingyun et al., 2004). Natural forest succession from grassland is said to be very slow, and dominated by hardy native pioneers and often invasive exotic species (Dudgeon and Corlett, 2011).

#### 3.1. History of Hong Kong's forest

It is estimated that complete deforestation in Hong Kong was completed around 400-600 years ago. As a result, primary forest occurs only in a few patches as feng shui wood (Chinese system of geomancy) and in topographic ravines (Dudgeon and Corlett, 2011; Hau, 1997). In last few hundred years, the uplands of Hong Kong are assumed to have been cultivated as evident from the presence of remnant agricultural terraces on steep terrains, on historic aerial photographs of 1945 and 1963. Despite the forest climate, there is no substantial primary forest present in the landscape (Dudgeon and Corlett, 2011). In the currently forested landscape of Hong Kong, most vegetation consists of semi-natural plant communities, secondary forest, successional shrublands, fire-maintained grasslands, and monoculture plantations of exotic species and mixed plantations (Leung et al., 2008). Despite total deforestation and defaunation which took place over 300 years ago, Hong Kong has a large number of tropical rainforest plant species (Turner and Corlett, 1996).

---

<sup>1</sup>Feng shui woods are those near to villages, and preserved over centuries by villagers, often having multi-layered canopy, large trees, and large woody lianas. They are considered the closest present-day representation of primary forest in Hong Kong (Zhuang and Corlett, 1997).

### 3.1.1. Forest restoration efforts

European travelers of 18<sup>th</sup> and 19<sup>th</sup> century described Hong Kong's landscape as barren, grassy without woods (Osbeck, 1771), and remarkably barren with a few shrubs and herbs in ravines and along streams (Abel, 1818). After colonization in 1841, European visitors invariably used words like 'barren', 'bleak', and 'bare', to describe the landscape of the new colony and these comments became the main reasons to start afforestation efforts in Hong Kong. However, these expressions were misleading because Hong Kong Island did have some substantial fragments of primary forest and supported a rich vascular plant flora for such a small area. Also, in the New Territories fragments of primary forest were found in fung shui woods behind villages, and in some small scattered patches in high altitude ravines (Zhuang and Corlett, 1996).

The British administration started large-scale forest restoration activities on Hong Kong Island in the 1870s and the efforts were also extended to New Territories after its inclusion in the administration in 1898. Dominantly, seeds of the native pine species, *Pinus massoniana*, were collected, nursed for 1 year, and planted on a large scale due to its successful growth on sites where nothing else would grow. Anthropogenic hill fires were the major hurdles faced by foresters in the 19<sup>th</sup> century, apart from unreliable rainfall and poor soil. In 1928, *Acacia Confusa* was introduced in Hong Kong and plantation of the species was increased over the years due to its success in the barren hills and its local seed production ability. By 1938, plantations covered an area of 57 km<sup>2</sup> (47 km<sup>2</sup> on Hong Kong Island and 10 km<sup>2</sup> on the New Territories) in Hong Kong (Corlett, 1999).

During WWII, extensive cutting of the forest occurred due to acute shortages in firewood supply from the Mainland, which resulted in complete destruction of Hong Kong's plantations by 1946 (Corlett, 1999). Large scale forestry activities restarted immediately after the war but the choice of species plantation was limited due to shallow and infertile soil on steep slopes. However, *Pinus massoniana* remained the major plantation tree with the other broad-leaved species of *Lophostemon confertus*, *Eucalyptus robusta* and *Melaleuca quinquenervia*. The prime aim of afforestation was to control the soil erosion and improve water supply, conservation of natural vegetation and wildlife, and encouragement of the recreational use of the countryside (Corlett, 1999).

In early 1977, the Country Park system was developed in Hong Kong and 40% of the land area of Hong Kong came under the Country Park protection. As a result, urban areas are now concentrated in confined areas and a balance has been achieved between conservation and development (Zhang and Jim, 2013). Over time, exotic species plantations become dominant due to their lower sensitivity to fire as compared to the native *P. massoniana*. However, in the late 1970s, *P. massoniana* was struck by two new deadly pests and within 10 years most of the species was eradicated. It is assumed that the dead plantation was replaced by natural secondary forest as many of the older pine plantations developed understory native shrubs and trees (Corlett, 1999).

Over the years, exotic species remained a dominant part of the plantations in Hong Kong for successful and fast vegetation recovery, primarily due to the nitrogen fixation ability of *Acacia Confusa* and *Casuarina Equisetifolia*, and fire resistance capability of *L. Confertus* and *Eucalyptus spp.* (Zhang and Jim, 2013). By 1997, one-third of total forest (i.e. 5000 ha out of 15000 ha) in Hong Kong was recognizably plantation forest and the natural secondary forest had also replaced many of the dead and dying trees. During the last 30 years (1982 – 2011), a total of 16.5 million seedlings of 209 species were planted in the Country Parks. The relative abundance of exotic species was 32.1 % (57.4 % of seedlings), and 67.9 % (42.6 % of seedlings) were native species. Over the period, seedlings of *Acacia Spp.* were dominant, with more than one quarter (25.37 %) of total planted seedlings (16.83 % of *Acacia Confusa* and 8.44 % of *Acacia Aruriculiformis*). The second highest planted seedlings also belonged to the exotic *Lophostemon Confertus*, with 10.95 %, whereas the common native species was *Castanopsis Fissa*, with 4.76 % of seedlings (Zhang and Jim, 2013). The use of native species and mixed plantations increased in the 1990s due to reservations of ecologists about the ecological values of exotic monocultures (Corlett, 1999; Dudgeon and Corlett, 1994; Zhuang and Corlett, 1996). The trend of planting native species has increased since 1999, as native seedlings have contributed more than 50% of the total plantings each year (1999-2013), except the years 2000 (45.68 %) and 2007 (49.51 %; AFCD, 2012, 2013; Zhang and Jim, 2013). In 2013 and 2012 native seedlings comprised of 80% and 70 % of the total seedlings planted. In 2009, AFCD (Agriculture Fisheries and Conservation Department) of Hong Kong launched a Country Park Enrichment Scheme to enhance the ecological value of plantations by removing exotic trees in poor condition and planting suitable native species (AFCD, 2013, 2012).

### **3.1.2. Natural secondary forest**

Since 1841, 390 native tree species (Corlett, 1999), belonging to 61 families and 162 genera, have been recorded in Hong Kong (Zhuang and Corlett, 1996). Primarily, Hong Kong's forest cover is composed of feng shui woods, natural secondary forest, and plantations.

The natural secondary forest in Hong Kong has grown on fire protected slopes. The young secondary forest invades into fire protected grassland, starting with light-demanding shrubs which disappear when a closed canopy is formed (Zhuang and Corlett, 1997). Furthermore, very large trees of different species, that must be older than the surrounding forest, are observed on aerial photographs of 1945 and 1963 within shrubland or shrubby grassland and around abandoned agricultural terraces.

Secondary forest plays a significant role in the ecology of a landscape by maintaining genetic sources, preventing soil erosion, and providing habitats to wildlife (Wang et al., 2006). The majority of Hong Kong's secondary forest has developed through succession on lands protected from fire, and by plantation efforts after 1945. The natural secondary forest consists of many native species that are invading into grassland in the company of 'light-demanding shrubs' as a nurse crop (Zhuang and Corlett, 1996). The natural secondary forest has also invaded into many exotic broad-leaved plantations. It is evident that plantations in a tropical environment act as a catalyzer or nurse crop to provide a forest environment for species-rich native forest succession (Parrotta et al., 1997). However, in the absence of plantations, long-term protection from fire could lead to rapid development of grassland into shrubs and then secondary forest. Therefore, on sites suitable for forest, it is difficult to distinguish the effects of plantations and absence of hill fires on secondary forest succession (Zhuang and Corlett, 1996; Zhuang, 1997). Most of the plantations in Hong Kong consisting of exotic species are not favorable to ecological restoration of native species due to their low tree diversity and relatively simple structure (Zhuang and Corlett, 1996). Secondary forest growth in the understory of the exotic monocultures is very slow, and they also do not attract wildlife that serve as seed dispersal agents (Kwok and Corlett, 2000)

Feng shui woods are located behind villages (abandoned or current) and are characterized by multi-layered canopy, big trees, and large woody lianas (Zhuang and Corlett, 1997). Patches of feng shui woodland are also present throughout south and

southeast Asia and seem to have a wide range of origin. A few surviving 'sacred groves' are also found in south China (Gadgil and Vartak, 1976) and India (Chandrakanth and Romm, 1991). A mature secondary forest area in neighboring south China, similar to feng shui woods in Hong Kong, is in Ding Hu Shan Biosphere Reserve. The 266 ha forest is located near to a temple, 190 km northwest of Hong Kong, and believed to be at least 400 years old. Besides this, there are no significant remnants of primary lowland forest in south China because of the history of severe human impact similar to that of Hong Kong (Gadgil and Vartak, 1976). The presence of these fragments of forest significantly enhances the diversity of landscape and increases the likelihood of the indigenous biota or at least a portion of it. The small remnants and regrowth patches can provide valuable habitat for some forest birds and forest mammal and insect species. However, near-complete deforestation as occurred in Hong Kong could be expected to eradicate virtually all the native species as has happened with the forest vertebrates. These fragments can also act as a source of recolonization of nearby areas undergoing succession. Many rainforest species possess limited powers of dispersal, and reestablishment of primary species in secondary forest is limited if there is no primary forest patch nearby (Turner and Corlett, 1996).

### **3.2. Drivers and barriers to forest succession in Hong Kong**

#### **3.2.1. Hill Fires in Hong Kong**

Fire is an integral component of landscape ecology and culture in southeast Asia (Stott, 1991). Hill fires in Hong Kong are undoubtedly the greatest threat to plant biodiversity. They are mostly caused by anthropogenic activities, especially during the traditional Chinese grave-sweeping festivals, the Ching Ming and Chung Yeung festivals. The general pattern of fire frequency in Hong Kong is bi-modal, and starts from late-September and ends in early-April with the first peak in mid-October and the second highest peak in late-December. Most of the hill fires in Hong Kong last for less than 90 minutes, and few last for up to 3 hours (Chau, 1994). The succession of woody plants in grasslands is limited by fire in the degraded upland landscape of Hong Kong. Grasslands can be colonized by successive shrubs and trees provided that the grasses are protected from fire for at least 10-15 years (Au et al., 2006). However, seasonal droughts, low soil nutrients and competition with grasses may also be limiting factors reducing the subsequent growth rate of established tree seedlings (Hau and Corlett, 2003). Most fire

affected areas are located on the drier and warmer south-facing slopes which receive more solar radiation than flat areas and colder, wetter north-facing slopes. More than half of the total area covered by the Country Parks burnt at least once and one-quarter of the area was burnt at least twice from 1981 to 1993. Susceptibility to fire decreases along the successional stages (from grasslands to open shrublands, shrublands, open forest and forest) and ease of fire ignition decreases after a few years of succession. In normal conditions, it is very rare for woodlands and shrublands to catch fire. Interestingly, the native pine species, *Pinus massoniana*, is fire intolerant even at mature growth stages (Chau, 1994).

Hill fire occurrence is common in Tai Mo Shan and most of its southern slopes have burnt three to six times during the 1980s, but fire frequency in the south of the country park is lower due to shrublands and plantations. In contrast to Tai Mo Shan, fire occurrence is very rare in Shing Mun as lowland areas in the park are covered with plantation and secondary forest which reduce the chances of fire. In Shing Mun, mostly fires occurred in uplands areas above 500 m, which are contiguous with Tai Mo Shan on the northern and western sides (Chau, 1994).

### **3.2.2. Seed availability and dispersal agents**

Secondary forest succession highly depends on seed source and seed dispersal agents. Generally, seed dispersal is very slow in the human-dominated tropical landscapes (Corlett, 1995). Although succession is taking place on the degraded land of Hong Kong, natural forest succession is very slow to incorporate many forest specialists. Even when the secondary forest is contiguous with primary forest segments, lack of dispersal agent is probably preventing the arrival of new species (Turner and Corlett, 1996).

The current fauna of Hong Kong's forest is few and lacks forest specialists, and even squirrels, *Callosciurus flavimanus*, were absent a few decades ago. These were re-introduced in the 1970s and have now spread widely across the forest (Corlett and Turner, 1997). The absence of wildlife in the landscape implies that the deforestation was near-complete, with the unexpected survival of rich tree flora in the form of feng shui woods and small fragments in topographically protected spots. Therefore, reforestation in Hong Kong may contribute few conservation benefits without reintroducing the forest wildlife (Zhuang and Corlett, 1997). Apart from these reservations, it was reported that the increased forest area has given birth to the

existence, probably re-existence, of various butterflies and forest birds (Kwok and Corlett, 1999; Zhuang et al., 1995).

### ***Availability of seeds under natural vegetation***

Availability of seeds in degraded landscapes is one of the major limiting factors in vegetation recovery. However, although it is found that seed rain in the degraded uplands of Hong Kong is sufficient for woody vegetation succession, it is thought that human mediation will be required to reinstate tree flora diversity in succeeding the secondary forest (Au et al., 2006). In the landscape, seed rain frequency is recorded to be highest in isolated female shrubs in grassland matrices followed by isolated trees, male isolated shrubs, shrubland, forest, and open grasslands. In terms of total numbers of seed taxa, shrublands received the highest number of seed taxa, followed by isolated trees and forest, female isolated shrubs, male isolated shrubs, and grasslands. Seed rain in grasslands was dominated by many-seeded fruits whereas shrubland and forest were dominated by few-seeded fruits. Overall, it is found that seed availability in the degraded landscape is not a limiting factor in natural secondary forest succession (Au et al., 2006).

### ***Seed rain under *Lophostemon confertus* plantation***

Monocultures of exotic species plantations stands do not support forest succession. The diversity of woody plant species in the natural secondary forest is much higher than in the understory of the exotic plantations (Lee et al., 2005). Similar to seed rain in spontaneous secondary forest (Au et al., 2006), the majority of seeds in exotic plantations are also dispersed by birds (Lee et al., 2007). However, the density of the bulbuls in exotic plantations is observed to be three times less than in neighboring secondary forest (Kwok and Corlett, 2000).

### ***Seed dispersal agents***

In protected landscapes, seed dispersal distances are of great importance for the rate of vegetation recovery from existing forest fragments (Howe and Miritti, 2004) as well as, for persistence of species (Johst et al., 2002). Floral species with fleshy fruits in Hong Kong are dispersed by birds, bats, mammals, and civets, whereas non-fleshy fruit species are dispersed by wind, water, and mechanical methods (Corlett and Turner, 1997; Corlett, 1999, 1996, 1995). However, the majority of the original mammalian

fauna was lost when most of the forest was cleared around 400 to 600 years ago (Meachem, 1994).

Only two bulbuls (*Pycnonotus sinensis* and *P. jocosus*) and Japanese white-eye (*Zosteror japonica*) are responsible for dispersion of majority of the seeds in the degraded landscape of Hong Kong. Bulbuls are the most important seed dispersal agents in the degraded tropics and subtropics of Asia and Africa, and they are the main high-quality seed dispersal agent in the uplands of Hong Kong. Bulbuls were the most sighted species crossing the open areas, providing a connection between habitat patches. Both species spread the majority of seeds far away from the parent source patch, and a few seeds are spread to distances of over 1 km, which would allow plant movement between well-separated habitat fragments (Weir and Corlett, 2006). Bulbuls move within forest and shrubland, from forest patches to adjacent shrubland, and can also fly across grassland matrices from one forest fragment to another distant forest segment, isolated trees, shrubs, rocks, tall grasses, and perches within the grassland (Weir, 2004). These movements act as nexuses between fragmented habitats and also assist woody succession in grassland and shrubland. The bulbuls in the uplands of Hong Kong have potential to spread seeds of almost 84 % of tree flora species, and 274 out of 355 wild fruit species, present in the area (Corlett, 1996). However, the seeds of larger fruit are dispersed in greater quantity but over shorter in distances and smaller seeds are dispersed fewer in quantity but over longer distances (Fukui, 2003).

Another considerable seed dispersal fauna is 'huwamei'. However, it adds very little to dispersal services provided by bulbuls because it is found to be less abundant, less frugivorous, and unlikely to move between habitat fragments. Additionally, two civet species (*Paguma larvata* and *Viverricula indica*) serve as seed dispersal agents. Civets can regularly move seeds to a distance of more than 1 km, and they carry selective seeds of species that have fruits too large for bulbuls to carry, such as *Diospyros morrisiana* and *Gnetum luofuense* (Dudgeon and Corlett, 2011; Weir and Corlett, 2006). Other mammals such as the Indian muntjac, rodents, and macaques (*Macaca mulatta*, *M. fascicularis* and their hybrids) also disperse larger seeds (Weir and Corlett, 2006). The macaques which were accidentally and deliberately introduced play an important role in dispersing large seeded climax species such as *Garcinia*, *Machilus*, and *Canarium* (Lucas and Corlett 1998; Corlett, 2011).

### ***Seed predation as barrier to regrowth***

Along with other limiting factors of forest regrowth in degraded landscapes, seed predation is also a critical barrier to the regeneration of natural forest in abandoned landscapes (Nepstad et al., 1991). Rats are found to be primary seed predators in Hong Kong's landscape, and the density of seed removal in shrubland is higher than in grassland. Thus seed predation is a biotic barrier, influencing regeneration and species composition of Hong Kong's secondary forest (Hau, 1997).

### **3.2.3. Climate change and succession in Hong Kong**

Species migration through seed dispersal agent in degraded landscapes is relatively faster than floristic impact due to climate change (Pearson and Dawson, 2005). Weir and Corlett, (2006) hypothesized certain plant species in Hong Kong would require a 100 m vertical movement per decade in order to compensate a predicted temperature increase of 0.6 C° per decade due to global warming. And, this expected vertical movement of 100 m is equivalent to 150 – 450 m horizontal displacement taking into account the rugged terrain of Tai Mo Shan (Weir and Corlett, 2006). These migration distances are well within the range of seed dispersal distance by bulbuls. However, vertical movement in Hong Kong will be restricted by the altitudinal limits in the area as the highest point is 957 m above sea level. Therefore according to Weir and Corlett, (2006), "Temperature compensation by plant migration that depends on internal seed dispersal by birds is unlikely to be effective for more than a few decades in this landscape".

### **3.2.4. Plantation ecology**

Plantation in degraded lands is supposed to stimulate regeneration of native plant species and increase biodiversity by shading out grasses, decreasing soil erosion, reducing fire hazard and improving soil nutrients and micro-climatic conditions (Cusack and Montagnini, 2004).

Field investigations by Zhuang, (1997) and Lee et al., (2005) in Hong Kong's plantations, indicate that species diversity in understory is significantly higher in natural secondary forest patches than in plantation sites. Among the plantation sites, *A. Confusa* and *L. Confertus* have very poor natural invasion, however, *M. Quinquenervia* and mixed plantation sites shown a rich diversity of woody plant species. The abundance of natural

regeneration in the understory of *M. Quinquenervia* is similar to in natural secondary forest. But these results, at least partially, can also be consequences of site quality and location (Lee et al., 2005). Furthermore, the understory in plantations with poor soil conditions and far away from seed sources is dominated by only a few early successional shrubs species after 40 years of plantation. Experience from exotic tree planting in Hong Kong suggests that planting exotic monocultures is not sufficient to restore the ecological functioning of degraded hills without considering the other limiting factors such as, seed availability (Au et al., 2006), seed dispersal abilities from plant communities (Holl, 1999; Holl et al., 2000; Weir and Corlett, 2006), soil conditions, and anthropogenic impacts such as fire. Although the primary aim of plantation was to control soil erosion in the degraded hills of Hong Kong, the natural succession should also promote restoration of the natural habitat (Lee et al., 2005).

## Chapter 04

# Object Based Classification to Detect Structural Changes in Vegetation Succession

### 4.1. Introduction

Deforestation is occurring at an alarming rate in tropical forests and therefore is one of the primary threats to biodiversity (Sodhi and Brook, 2008; Turner and Corlett, 1996). Despite the large scale exploitation of these tropical resources, a few areas including Hong Kong have been given chance to regrow. Although many governments expend large resources on afforestation projects, natural succession may be equally effective if objective data on rates and pathways of secondary forest succession can be provided.

Forestry plantations in Hong Kong started in mid of the 19th century (Evan, 1992), is an early example of large scale tropical afforestation. Initially, the objective of afforestation was to make the barren hills green, attractive, and to make nearby urban areas healthy; but in mid of the 20<sup>th</sup> century objectives changed to ecological restoration in the degraded hills (Corlett, 1999). However, complete destruction of forest including plantations took place during the blockade years of World War II (WWII). Hong Kong's present day flora and fauna represent recovery since 1945 due to both natural regeneration from tiny remnants in inaccessible sites and possibly from post-war plantation of a limited range of native and exotic species. Currently, secondary vegetation is succeeding in vertical structure as well as horizontal expansion, and observations suggest that forest may be regenerating naturally, and independently of assistance from afforestation programs (Corlett, 1999; Wang et al., 2006)

As in many developed countries, Hong Kong's natural vegetation is confined to steeply sloping mountainous areas unsuitable for building, and 40% of Hong Kong's land area is reserved in Country Parks, where natural regeneration is evident. These changing patterns of landscape, with vegetation succession from open ground to forest, are indicative of changing ecological processes operating along the successional gradient, and can be informative for devising realistic conservation policies. Each structural stage exhibits different canopy structure and stand height that produce distinctive tone and

texture in aerial photographs and satellite images (Geri et al., 2010; Munsi et al., 2010; Song and Woodcock, 2002; Teferi et al., 2013). Therefore, succession in structural stages can visually be mapped using high resolution historic aerial photographs and recent satellite images (Lucas et al., 2002; Qi et al., 2013).

Mapping and analysis of habitat changes in a landscape is important in ecology and conservation planning (Braumoh, 2006). The estimation of change in composition and characteristics of landscape elements can reveal vital ecological information for science-oriented management of a landscape (Cihlar, 2000). The situation of recovering secondary forest in Hong Kong, coupled with post war aerial photographs since 1945, and recent high resolution satellite imagery, provides an opportunity to monitor and assess natural vegetation succession. Black and white aerial photographs provide the earliest temporal record of Remote Sensing (RS) data and therefore are an invaluable source of information for studies of change in ecosystem dynamics over time (Allard, 2003; Dissanska et al., 2009; Pellerin and Lavoie, 2003; Pringle et al., 2009; Rabia and Terribile, 2013). However, the delineation of habitat patches from high resolution remotely sensed data, including black and white aerial photographs, especially when combined with other image types, is difficult due to spectral and structural complexity of habitat patches. Therefore, a rule-based approach to the methodologies utilized is required to link habitat components at their respective hierarchical levels (Hay et al., 2005).

Landscapes exhibit characteristics of multi-scale hierarchical interaction, unexpected behaviour and self-organization. All of these give spatial patterns which may change depending upon their scale of observation. Arbitrarily defined and variable spatial units of multi-source data acquired over a geographic area are susceptible to modifiable areal unit problem (MAUP) (Marceau et al., 1994). Thus, analysis based on different types and scales of earth observation data may not explicitly represent landscape entities independent of the units used. Furthermore, as the role of observer and choice of scale are of fundamental importance in the process of habitat delineation, it is necessary to understand the processes that generate such patterns (Hay et al., 2005). Considering, the subjectivity of determining the boundary between the habitat classes, and the different types and scales of imagery used, a semi-automated multi-scale object-based

paradigm of habitat delineation was devised to segment the image into multi-pixel image object primitives according to both spatial and tonal characteristics.

The first step of object based image analysis (OBIA) is segmentation of the image into multi-pixel image object primitives. During this process a new image object level is created, or the morphology of already existing objects are altered. The result of segmentation is controlled by user-defined parameters (scale, shape, compactness) which must be assigned accurately according to the feature being extracted (Mathieu et al., 2007). The scale parameter is constituted by weighted heterogeneity of shape and colour and defines the homogeneity of required image objects, the higher the scale parameter higher the allowed heterogeneity and vice versa. Although, Möller et al., (2007) proposed a comparison index to support the selection of an optimal segmentation scale, it is suggested that beyond quantitative evaluation of segmentation procedures, no segmentation result is fully convincing if it does not satisfy the human eye (Mathieu et al., 2007). For the current image analysis, these parameters were defined by a trial and error approach in order to acquire image objects of interest (Mathieu et al., 2007; Flanders et al., 2003). The defined objects maximize inter-object and minimize intra-object variability according to the specified spatial scale of the objects (Flanders et al., 2003). An important aspect is that the segmentation process can be seen as an automated digitizing of target boundaries. In particular, it is a good alternative to manual digitizing of habitat patches from high resolution satellite images and airborne photographs (Mathieu et al., 2007). The semi-automated object based approach, which combines texture and tonal characteristics of image object primitives results in a precise classification of high resolution panchromatic (single channel) aerial photographs (Middleton et al., 2008).

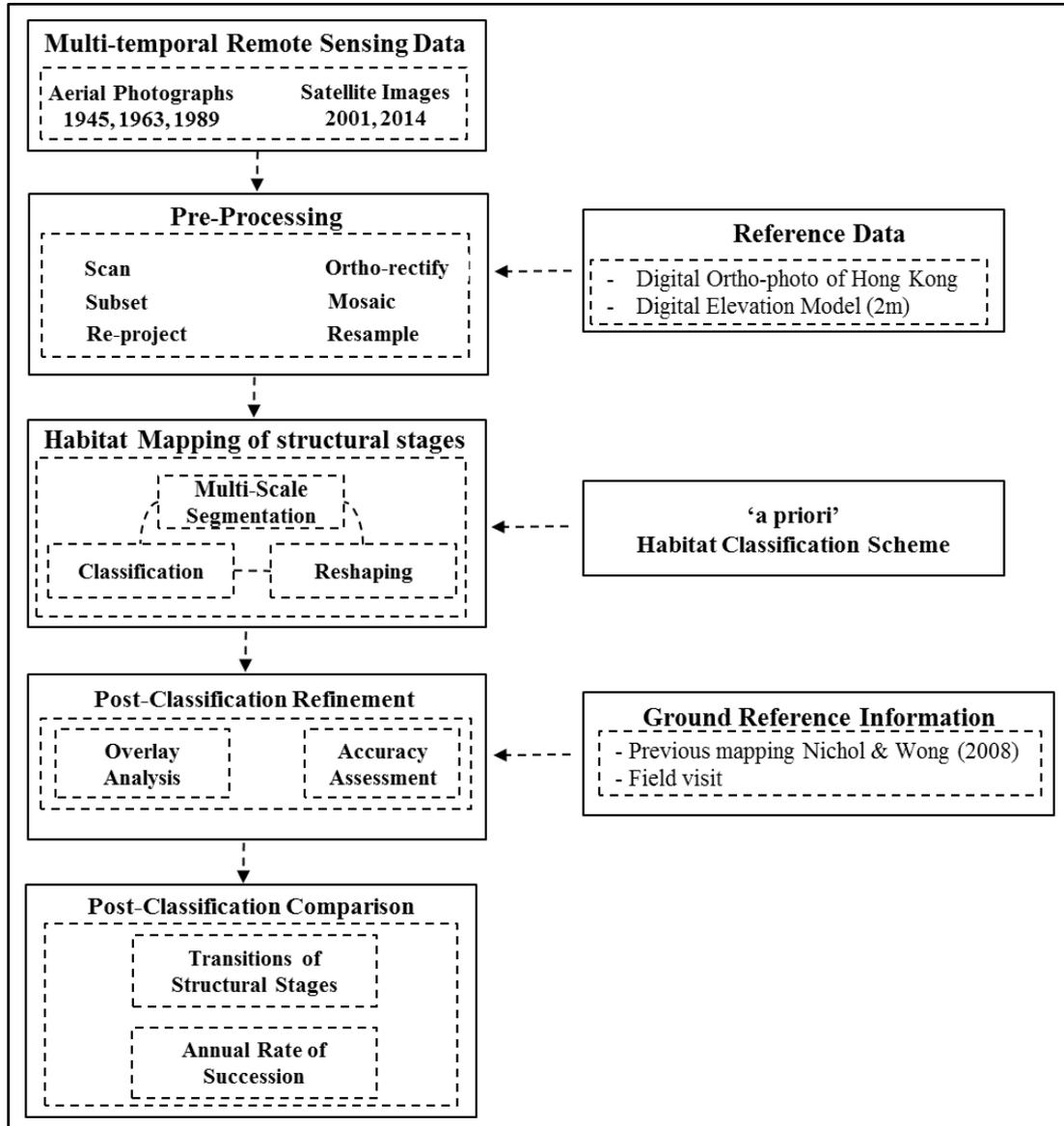
In this chapter, a semi-automated object based habitat classification methodology is used for objective change detection using sequential black and white aerial photographs and high resolution satellite images of different quality and resolution, to investigate vegetation successional patterns and their implications for the ecology of the landscape. The specific objectives are to:

- ascertain spatiotemporal patterns of natural vegetation recovery over 70 years by comparative analysis of five habitat maps based on historic aerial photographs and recent high resolution satellite images.

- determine the spatial extent and rate of recovery of natural secondary forest.
- quantify transitions among the structural stages of the vegetation along the successional gradient.

## 4.2. Materials and Methods

A brief illustration of the methodology is given in figure 4.1, which is explained in the following text.



**Figure 4.1** Flow diagram for habitat classification and assessment of structural changes

#### 4.2.1. Data acquisition

Remotely sensed data used for this study consisted of three subsets of archived aerial photographs since 1945 and two satellite images (table 4.1). The first set of aerial photographs of Hong Kong was captured in 1924, but it did not cover the whole territory. Complete coverage of Hong Kong is available since 1945, following WWII. Aerial photographs of 1945 (1:40,000), 1963 (1:14,000) and 1989 (1:20,000) of the study area were obtained from Lands Department of Hong Kong (HK-Landsd, 2014) and High Resolution Satellite (HRS) images for years 2001 (IKONOS – spatial resolution of 1 m) and 2014 (World View 2 - spatial resolution of 0.5 m) were procured from Digital Globe. The imagery utilized for this study was cloud-free.

**Table 4.1** Description of remotely sensed data used

<b>Data</b>	<b>Year of Acquisition</b>	<b>No. of Photographs</b>	<b>Scale</b>	<b>Resolution (m)</b>
Aerial Photographs	1945	18	1:40,000	
	1963	12	1:14,000	--
	1989	13	1: 20,000	
Satellite Images	2001			1
	2014	--		0.5
DEM	--	--		2

#### 4.2.2. Pre-processing

In total 43 photos (18 for 1945, 12 for 1963 and 13 for 1989) were scanned at resolution of 1200 dpi and ortho-rectification was done using 15 to 20 well distributed GCPs (Ground Control Points) for each photo. X and Y coordinates of the GCPs were collected from a 0.5 m digital orthophoto of Hong Kong and Z values were taken from a 2 m Digital Elevation Model (DEM) - provided by the Lands Department of Hong Kong. After geometric correction, the individual orthophotos were clipped and mosaicked to form unified images (figure 4.2). The satellite images were also ortho-rectified using the RPC (Rational Polynomial Coefficients) with the ortho-photo and the DEM. Later, all data sets were re-projected into Hong Kong's local projection system – Hong Kong 1980 Grid system. For consistency, all the data sets were co-registered with the digital orthophoto with an RMSE (Root Mean Square Error) ranging from less than 1, to 5 m, depending on the scale and resolution of the data sets. For subsequent analysis, all data sets were resampled to a common pixel size (0.5 m) and radiometric level (8 bit grey scale).

### 4.2.3. Habitat classification scheme

Prior knowledge and description of habitat classes is critical for precise and reliable mapping. 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 observable on remotely sensed images. The general structural stages of vegetation succession in the degraded hills are grassland, open shrubland (shrubby grassland), shrubland, open forest and forest. Descriptive information of the classification scheme was based on a standardized classification scheme of Land Cover Classification System (LCCS) (Congalton et al., 2014). The LCCS has been designed by FAO (Food and Agriculture Organization) and UNEP (United Nations’ Environment Program) to cope with growing needs of accessing reliable and standardized information on land cover/land use systems. At present, it is the standalone universally applicable classification system that is in use (Gregorio and Janson, 2005). A list containing names and descriptions of the mapped habitat classes is given in table 4.2. The classes were unambiguous, mutually exclusive and commonly identifiable from satellite images and aerial photos.

**Table 4.2** Description of habitat classes

<b>Class Name</b>	<b>Description of class</b>
Forest (F)	Tree Cover, broadleaved, evergreen, close to open (canopy > 60-70%)
Open Forest (OF)	Mosaic: Tree Cover, broadleaved, evergreen, open canopy (15 - 60 %) and Shrubland and / or Grassland
Shrubland (SH)	Shrubland, broadleaved, evergreen, close, canopy > 60 - 70 %
Open Shrubland (SG)	Mosaic: Shrubland, broadleaved, evergreen, open canopy > 15 - 60 % and Grassland
Grassland (GL)	Ground story grasses as dominant vegetation form
Bare Areas (BA)	Areas without significant vegetation forms; consists of exposed soil / rocks / tracks
Built up Area (BU)	Manmade features
Water (W)	Natural / Manmade water bodies
Plantation Forest (PF)	Primarily monoculture stands plantation forest - <i>Melaleuca quinquenervia</i> , <i>Lophostemon confertus</i> , <i>Acacia confusa</i> , and few mixed plantation patches

### 4.2.4. Object based habitat classification

Habitat patches occur at a variety of spatial and temporal scales and are dynamic in nature. A patch at any scale includes patchiness at finer scale which represents the internal structure of the patch and we may say that a mosaic is defined by patchiness at broader scale. Therefore, in this study, a three level of hierarchical image object

primitives was created, with minimum object sizes of 50 m<sup>2</sup>, 500 m<sup>2</sup>, and 1000 m<sup>2</sup>, through multi-resolution segmentation. Primarily, upper level segments were used for big patches of grassland, forest and monoculture plantation stands; while medium level objects mainly corresponded to open shrubland and shrubland. Finer scale objects were used for isolated forest and shrubland patches. Contiguous regions of similar class were merged together to form continuous patches.

Classifying / interpreting the segments is the next steps that was done subjectively, based on tone and texture of image object primitives. A gradient of black to grey tone, rough to smooth texture, large to small crown size, and long to short shadow, was used to recognize forest, open forest, shrubland, open shrubland and grassland. Plantation stands were recognised through homogenous tonal pattern and multi-temporal analysis – as it was easier to recognize plantations from their regular pattern at their early stages. After classification, all the habitat maps were converted to raster grids of 1 m.

#### **4.2.5. Accuracy assessment**

An error matrix was generated to determine the degree of error in the maps by calculating the producer's accuracy, user's accuracy and Kappa coefficient (Lillesand et al., 2008). The matrix compares the classified points on the map with ground reference points and the Kappa coefficient indicates proportionate decrease in error produced by a classification process compared with the error of completely random classification (Reddy et al., 2013). Accuracy assessment of the mapping was performed for the habitat map of 2001 (table 4.3 ) using the comprehensive ground truthing available from a previous habitat mapping study in the study area, in the form of 352 field surveyed GPS points and 215 additional check points on very high resolution color aerial photographs (Nichol and Wong, 2008).

#### **4.2.6. Extent, rate and transitions of structural stages**

Temporal changes in the spatial extent of structural classes of the landscape were determined through post-classification comparison (PCC) of habitat maps, also known as 'delta classification' (Coppin et al., 2004). Maps were sequentially paired (1945-1963, 1963-1989, 1989-2001, and 2001-2014) and change matrices were produced from the five habitat maps, by overlapping and cross tabulation of two habitat maps of the successive time periods (equation 4.1). Habitat changes occur in random process of

change, where a habitat category is replaced by another category in an equal proportion, or a systematic transition, where changes in a habitat class is driven by a gradual or constant process of development (Guida Johnson and Zuleta, 2013; Zewdie and Csaplovics, 2016). To summarize the transition, further analysis were carried out to determine gain, loss, persistence, swap, net change and total change in each structural class for each of the periods (Pontius et al., 2004).

$$Change_{Matrix} = Cross\ tabulation(t_1, t_2) \quad \text{Equation 4.1}$$

Gain ( $G$ ) refers to the percentage of a habitat category in the later landscape after subtracting its proportion in the earlier landscape (equation 4.2), and the Loss ( $L$ ) was the difference between percentage of a category in the earlier landscape and its proportion that persisted in the landscape over a transition period (equation 4.3).

$$G_j = P_{+j} - P_{jj} \quad \text{Equation 4.2}$$

$$L_j = P_{j+} - P_{jj} \quad \text{Equation 4.3}$$

Absolute Net Change ( $ANc$ ) was the absolute difference of proportion of a category in the earlier and the later landscape (equation 4.4).

$$(ANc)_j = |P_{+j} - P_{j+}| \quad \text{Equation 4.4}$$

Swap represents the amount of a habitat category lost at one location while the same amount is added at a different site in the landscape (equation 4.5).

$$S_j = 2 \min(P_{j+} - P_{jj}; P_{+j} - P_{jj}) \quad \text{Equation 4.5}$$

The total change ( $Tc$ ) was calculated to conclude the overall change in a category by summing up the Gain and Loss (equation 4.6).

$$(Tc)_j = (P_{j+} - P_{jj}) + (P_{+j} - P_{jj}) \quad \text{Equation 4.6}$$

#### 4.2.7. Annual rate of change

The annual rates of change in structural classes were computed using equation 4.7. The formula is based on the Compound Interest Law and calculates percentage change per year by considering nonlinear change across the time period. It estimates ecologically meaningful habitat change (Puyravaud, 2003) and is a standard method of comparing change rates, due to its insensitivity to different time periods between observation dates (Teferi et al., 2013).

$$r = \left( \frac{1}{t_2 - t_1} \right) \times \left( \ln \frac{a_2}{a_1} \right) \times 100 \quad \text{Equation 4.7}$$

where  $r$  is the rate of change (% per year),  $a_1$  and  $a_2$  represent area corresponding to earlier time,  $t_1$ , and later time,  $t_2$ .

### 4.3. Results and Discussion

#### 4.3.1. Habitat mapping

Five habitat maps with five structural stages of vegetation were produced (figure 4.3). Initially, 'plantation forest' was classified into four sub-categories of monoculture stands of *Melaleuca quinquenervia*, *Lophostemon confertus*, *Acacia confusa*, and mixed plantation that were merged into a single class of plantation forest for simplicity in subsequent change analysis.

Remote sensing observation at multiple time steps gave a better visualization of structural classes that substantially improved the mapping. The element of subjectivity in allocating image objects delineated by segmentation to structural classes, was assisted by observation at multiple time steps, as the successional stages tend to proceed logically, and this substantially improved the mapping. For example, the greatest difficulty was in distinguishing mature plantation stands from lowland forest on a particular image date (figures 4.4, 4.5). Mature plantation stands appeared to be merged with lowland forest and were difficult to distinguish due to structural similarity. However, temporal mapping provided an additive advantage of delineating plantation patches by providing a reference to earlier growth stage (either young plantation preceding mature plantation, or open shrubland preceding forest), as young plantations were recognizable from their regular spatial pattern and arrangement (figure 4.5). The high quality of aerial photographs, orthorectification with the high resolution DEM (2m), previous field knowledge, mapping expertise, and the long period of approximately 200 days taken for the interpretation contributed to high accuracy of mapping. Overall, mapping accuracy was above 92 % (table 4.4).

Forest cover has increased over time (figure 4.3, table 4.3) but immediately post WWII, forest comprised only 0.17% of the landscape (4.82 ha), primarily confined to *Feng Shui Woods* around Shing Mun Reservoir, confirming Zhuang & Corlett's (1997) account. The 1945 landscape was dominated by a matrix of grassland covering 78.6% of the

landscape, with only scattered patches of shrubs mainly in valley bottom, and steep gulleys with landslide trails. Shrub colonization along valley bottoms and landslide trails appears on all image datasets from 1945 to 2014, probably due deeper soil and more nutrients at the foot-slopes as well as open ground seed establishment on landslide trails. Established shrubland communities tend to expand spatially up the valley sides, as well as grow in vertical structure, and give way to forest, which is now the dominant class in the landscape. Forest cover has now increased to 36.44% (~1020 ha) as a result of natural regeneration of secondary forest in the study area. The proportion of shrubland and open shrubland has increased gradually over the course of 70 years. Shrubland increased from less than 1% of the landscape to 23.25 % while grassland decreased to only one-tenth of its area in the earliest landscape. About 12 % of the current landscape comprises plantation forest of mainly exotic monoculture stands of *Lophostemon confertus*, *Melaleuca quinquenervia*, and *Acacia confusa*.

#### **4.3.2. Changes in structural stages: gains, losses, net change and total change**

Better understanding of the process of vegetation succession from grassland to forest is enabled by observing the change dynamics over the five time periods, related to management practices applied within those times. Inter-category transitions of each habitat class was calculated using contingency matrices to show the proportion of each structural stage transitioning from one stage to another along the successional gradient. The diagonal elements of the contingency matrix (tables 4.5) represent the proportion of landscape that persisted in the same structural category over time period. Off-diagonal elements represent the proportion of landscape that has transitioned from one category earlier to another category in the later landscape. Losses from a class are represented along the rows of that class, and gains into a class are shown in the column of that class and represent the proportion of the later landscape covered by each category in that column.

#### **4.3.3. Succession in vegetation communities**

##### **1945 - 1963**

In 1945, grassland was the dominant habitat accounting for 78.62 % of the landscape, whereas the later successional stages of vegetation structure in the study area (forest, open forest, shrubland and open shrubland) were limited to 7.28 %. Forest was

primarily confined to feng shui woods and other small patches, accounting for a total area of 4.82 ha (0.17%). During this 18-year period of (1945 – 1963) following complete forest clearance during WWII, succession was very slow, with the only natural changes being the 10.59 % of the landscape which transformed from grassland to shrubland (5.52 %) and open shrubland (5.09 %). Forest increased minimally as a small portion of shrubland evolved to forest, but still occupied less than 1 % (0.71%) of the landscape by 1963. Grassland with 64.54 %, remained the dominant vegetation community in the landscape (table 4.5). However, by 1963, 15.44 % of the area, mainly in the southwest, became covered with plantation patches (figure 4.3) as a result of large scale afforestation activities started immediately after the WWII, and the native *Pinus massoniana* was the major plantation tree during this period (Corlett, 1999; Zhang and Jim, 2013). Overall, 61.91 % of the landscape remained unchanged, whereas 22.94 % was swapped and the net change was 15.97 % (table 4.5).

### **1963-1989**

During this 26-year period, shrubland increased rapidly, doubling its area to 25 % the landscape and a significant portion (3.68%) of the shrub area (120.18 ha) transitioned to forest. Thus forest reached 5.01 % of the landscape in 1989 from 0.71 % in 1963. Also, a total of 13.04 % of the landscape converted from grassland to open shrubland and shrubland (table 4.5). The year 1965 was the turning point of forestry policies in Hong Kong. The Forestry Division was renamed 'Conservation and Forestry' and the Country Park system was developed in the early 1970s aimed at enhancing the recreational and conservation value of countryside. In 1977, 40% of Hong Kong's area came under Country Park protection (Zhang and Jim, 2013). By 1989, extensive plantations, mainly of *Pinus massoniana* in the southwest of the study area, had disappeared, to be replaced by grassland (figure 4.3), and this was due to the native *Pinus massonina* suffering from two deadly new pests in the late 1970s which eradicated most of this species (Corlett, 1999). The aerial photographs of 1989 indicate almost total disappearance of the woody vegetation planted between 1945 and 1963, from these areas southwest of the study area. Moreover, it is clear that by 2001 the landscape was almost exactly the same as it had been in 1945, over 50 years earlier, with shrubland confined to ravines and topographic depressions, and the shrub-grassland boundaries in almost exactly the same positions (figure 4.6). This appears contrary to Corlett's (1999) observation that many of the older pine plantations had

developed understory native shrubs and trees, and had been under planted with broad-leaved species, because these should have survived the disease, whereas the images indicate loss of all woody cover by 1989. During this period, the exotic species plantations mainly in the south east of the study area around Shing Mun Reservoir (figure 4.5) became dominant due to their lower sensitivity to fire than the native *Pinus massoniana* (Zhang and Jim, 2013). Thus overall, plantation areas reduced from ~15 % to ~11 % of the landscape between 1963 and 1989, with more area lost (9.25 %) than gained (4.94 %). Only 6.18 % of the area persisted as plantation cover, and most of the plantations established during 1945 – 1963 had changed back to grassland (6.90 %) by 1989.

### **1989-2001**

During this 12-year period the trend of increasing forest cover continued but the rate of increase was dramatic (table 4.6). By 2001, 15.69 % of the landscape had converted to forest, quadrupling the previous area in the short span of 12 years. Thus, forest reached 20.70 % of the landscape in 2001 from 5.01 % in 1989. This took place almost exclusively around the edges of forest established during the previous period in steep-sided stream valleys and on lower slopes. Thus forest extended upwards to higher mid-slope levels, replacing shrubland and filling the interfluves between ribbon-shaped forest patches in valleys. Grassland cover reduced to 34.67 % from 52.90 % during this period by succession to shrub and open shrubland, with less than 1% changing directly to forest.

The rate of conversion of shrub to forest (10.16 %) was twice faster than the rate of conversion of grassland to shrub (4.39 %), and the north and western portion of the study area remained in the early successional stage of grassland especially on all middle and upper slopes and interfluves. This is thought to be due to frequent hill fires in Tai Mo Shan country park, as according to fire records held by AFCD and Landsat images, most of its southern slopes were burnt three to six times in the 1980s, whereas 10-15 years of fire protection is needed for colonization with woody vegetation (Au et al., 2006). In the south of the country park and in the Shing Mun catchment, frequency of fire is lower due to faster colonization by shrublands, secondary forest and plantations which are less fire prone (Chau, 1994). Plantation activities continued during this period and the plantation area increased slightly from 11.12 % to 12.08 %.

### **2001 - 2014**

The progression to later successional stages continued accelerating during the 13-year period 2001 to 2014 and the greatest overall change in the landscape of 50.18 % was observed during this period (table 4.6). The area of forest reached 36.44 % of the landscape in 2014, from 20.70 % in 2001: an increase of 440 ha, which is almost double the area in 2001. Also accelerating in this period is the conversion of 27% of the area from grassland to shrubland and open shrubland, which is the largest loss of grassland over the whole study period. Notably during this period, forest became the dominant cover type in the landscape, reaching 36.44 %, and grassland was reduced to 8 % from its original 79 % in 1945. The proportion of shrubland (23.25 %) and open shrubland (15.06 %) also increased to a maximum in 2014 compared with the whole study period. Grasslands experienced a net loss of 26.81 % that is also highest transformation of grassland to later successional stages over the whole study period. During this period, forest was the most persistent cover (22.77 %) in the landscape, while in previous periods grassland was the most persistent (54.23 %, 45.28 %, 34.67 % and 7.86 % over the period 1945-1963, 1963-1989, 2001-2014 (table 4.6). Overall, by 2014 natural woody vegetation, i.e. forest, open forest, shrubland, and open shrubland, had increased to about three quarters of the landscape with an additional 12.08 % in plantation forest (figure 4.3).

#### **4.3.4. Rate of change in structural stages**

Annual rates of change were calculated according to equation 4.7, which is insensitive to different time periods between observations. Change rates helped in understanding the magnitude and direction of change in structural stages. Increase and decrease in area is represented with positive and negative sign, respectively (table 4.7). Forest cover in the landscape has increased at a high annual rate of change of 7.76 % since 1945. The highest annual rate of change in forest was 10.92 % between 1989 and 2001, although the highest annual gain in forest was from 2001 to 2014, with a near-doubling of the area to 1019 ha (table 4.3). During the former period 1989 to 2001, the rate of transformation of intermediate structural stages (shrubland and/or open shrub) to forest, was significantly higher than the rate of conversion of grass to shrub. This

suggests that there is a lag, or bottleneck, in grassland invasion by woody vegetation, but that once woody cover is established, the succession can proceed rapidly. The evidence from satellite images points to frequent fire during the 1980s, as the main impediment to shrub colonization in grasslands, but an apparent decrease of hill fires is also noted during the 1990s as the succession proceeds.

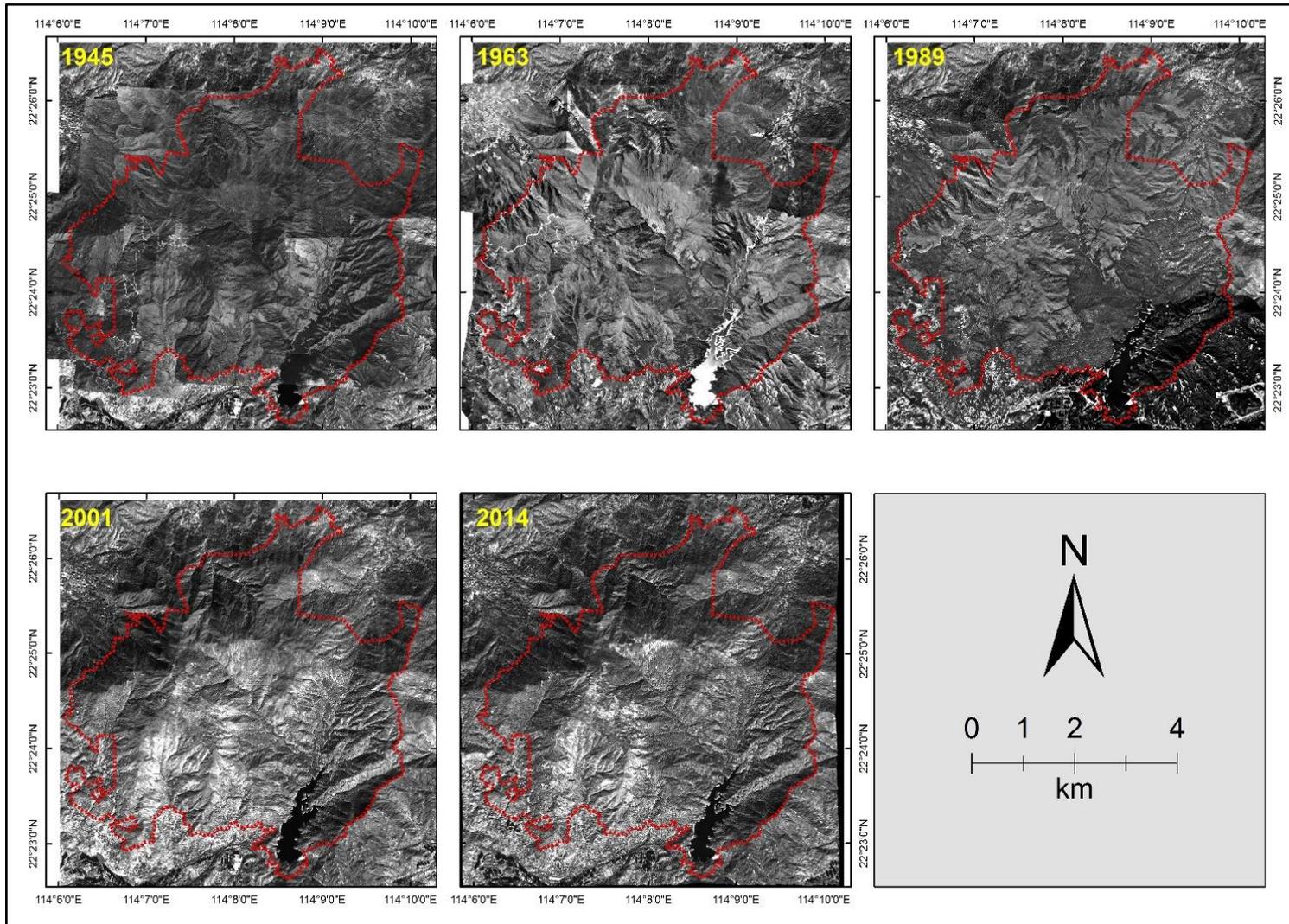
From 1989 to 2001, the very high 10.92 % annual gain of forest was mainly by infilling of interfluves between existing gallery forest in steep-sided valleys, as well as forest boundary advance to higher elevations where shrubs had already colonized. The major barrier to forest advance at this time 1989 to 2001 appears to be the plantations established in earlier decades which occupied many interfluves, thus preventing shrub colonization and subsequent succession to forest. Even in the later period 2001 to 2014 the plantations established in the earlier decades remain unchanged, occupying valley and interfluve sites which elsewhere have succeeded naturally to forest. This, along with Lee et al's (2005) observation of poor colonization of exotic plantation sites by native species speaks poorly for plantation policies in Hong Kong.

#### **4.4. Conclusion**

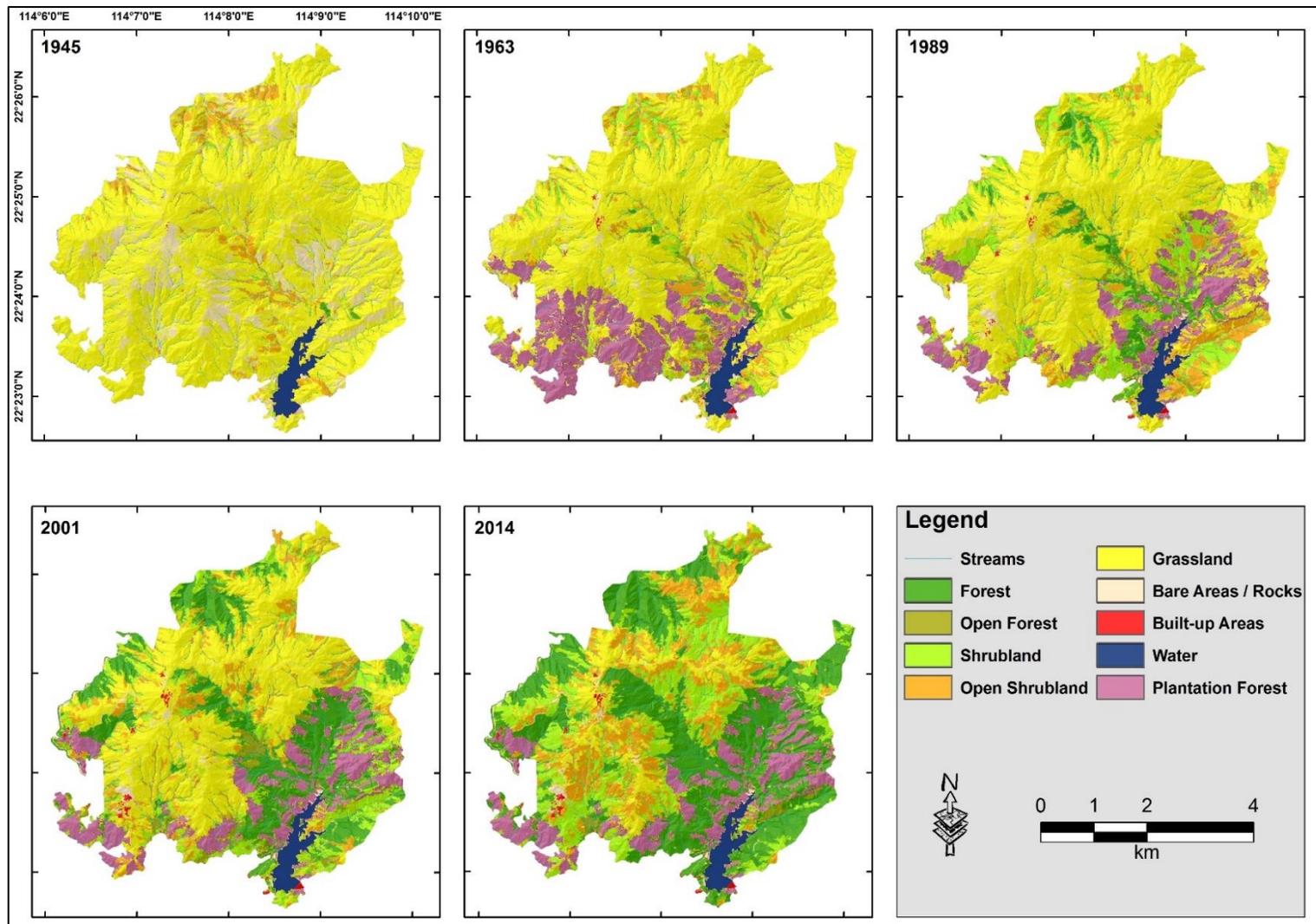
It is evident that if the landscape is protected from fire, natural succession to forest is very fast (e.g., 10.8% a year between 1989 and 2001), and much faster than by artificial afforestation by monocultural stands of exotic broadleaved species. No evidence of plantations acting as a nurse crop and facilitating natural species establishment was observed, as removal of plantations by disease in 1963-89 showed reversion to grassland, in 1989 with no trees or shrubs in the former plantation areas. This does not support Corlett's (1999) suggestion that for forest to colonize on the degraded hillsides a nurse crop of plantation species may be required. In fact this research observed plantations acting as barriers to the natural shrub to forest succession. Lee et al. (2005) also observe that poor regeneration of native species occurs in exotic plantations, and that the major factor is the control of fire. Thus AFCD's policy and great expense of planting 300-350,000 trees a year (Corlett, 1999) could perhaps be simply substituted by better fire control in grasslands. The 'lag' in conversion of grassland to shrubland as observed from the late 1970s to present in the southwest of the study area, may not pose an impediment if the succession can be managed, as grassland is not part of Hong Kong's native flora, except in specialized habitats. Direct colonization by shrubs can be

seen along landslide trails where bare ground is exposed near to an existing shrub source, suggesting that an initial grassland stage may not be necessary. Furthermore, since grasslands harbor fewer species than forest, the decline in habitat diversity as forest advances and consolidates, would be compensated by shrub planting, in terms of overall species numbers.

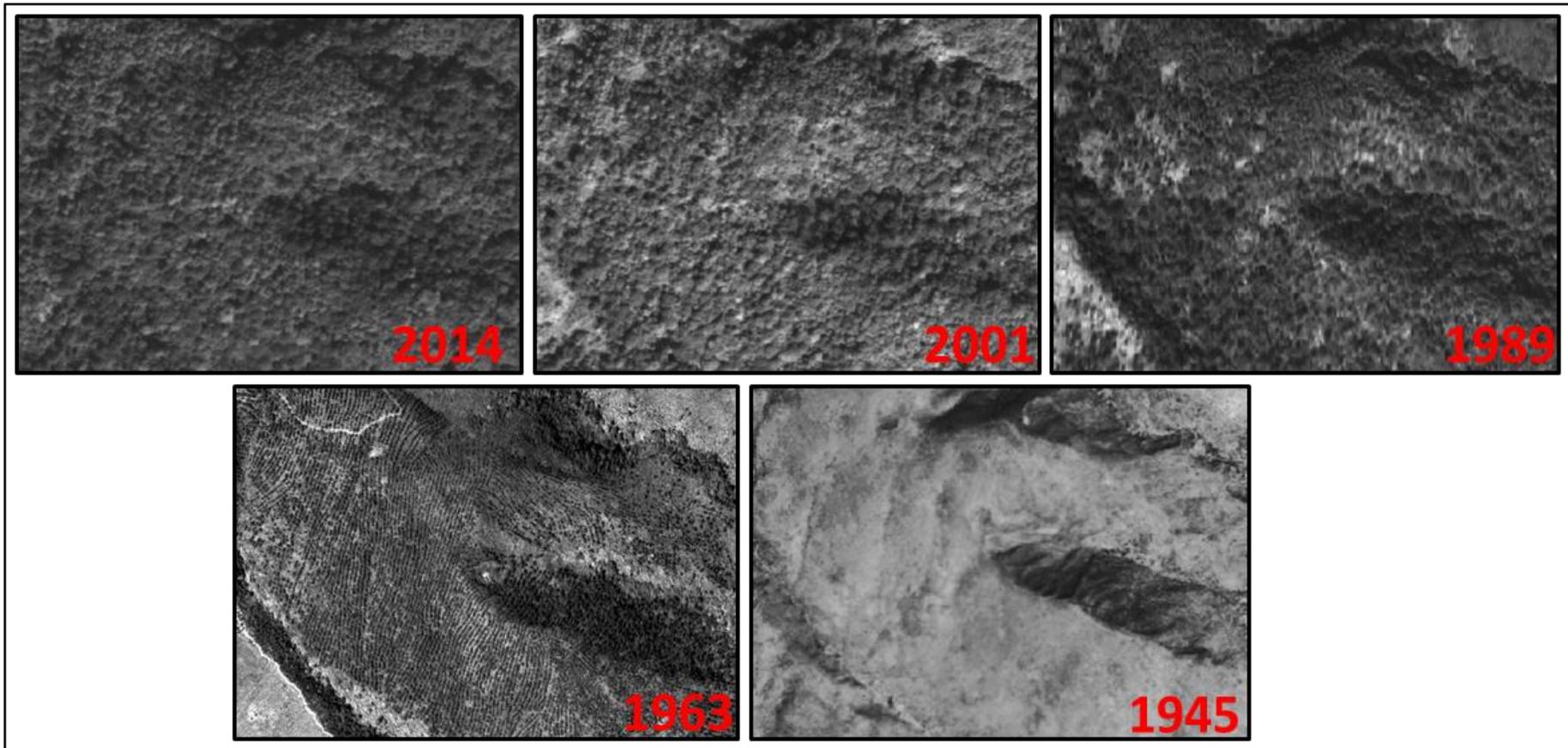
It is interesting that the rate of increase in forested area greatly decreased in the latest period 2001-2014, to 4.7% annually, and this is attributed to spatial factors of the landscape. When the shape of existing forest plots is linear there is more edge for forest to colonize along a broader front, but as linear forest patches along valleys are connected by forest across interfluves, the edge length is reduced over time. Thus, although the increase in forest area initially follows the law of compound interest with accelerating growth as the total area of forest increases, a stage is then reached where the advancing forest front becomes shorter due to consolidation and compaction, thus the rate of increase is reduced. Therefore, one method to facilitate structural succession to forest may be to replace broad scale plantation with linear-shaped patches of native shrubs, extending outwards from existing forest. Shape consolidation into large patch sizes also decreases the habitat diversity, and planting linear shrubs would also help to maintain the habitat diversity at this intermediate successional stage, as well as provide cover in grasslands for forest birds such as bulbuls which disperse seeds (Weir and Corlett, 2006). As forest is the climax vegetation in Hong Kong, the inevitable decline in habitat diversity as succession proceeds to closed forest, may be viewed as a natural and desirable first step in restoration of the ecosystem. However, the absence of specialist forest fauna may be an issue in the future structure of this regenerated landscape, especially since the shade-tolerant, later successional forest species have poor dispersal abilities. Therefore, to manage natural succession and to guarantee enough genetic diversity in Hong Kong's newly establishing forests, climax trees may be planted strategically in carefully selected plots, such as those mapped in 1989 (figure 4.3), where the oldest forest pioneers are established.



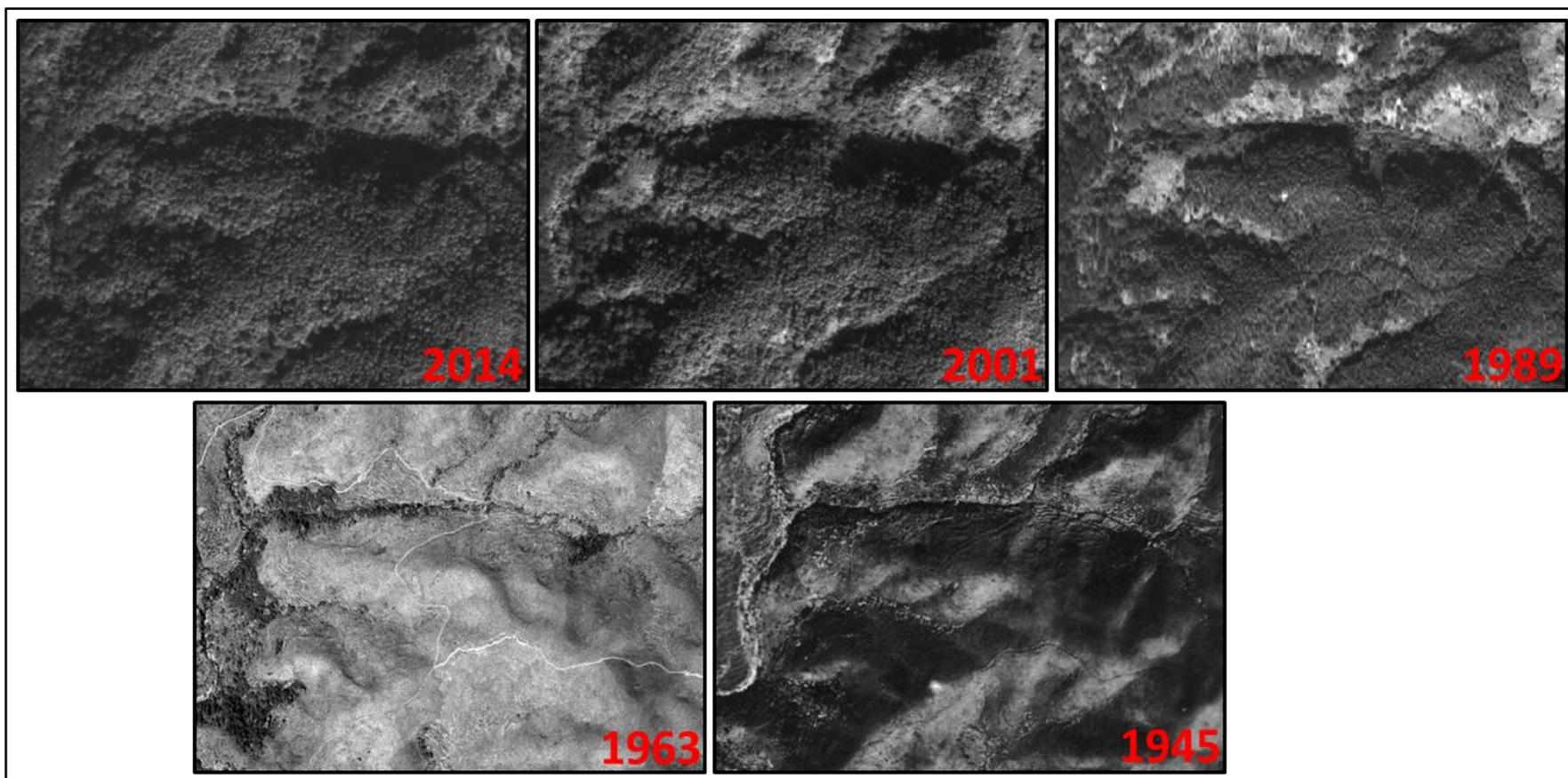
**Figure 4.2** Processed aerial photographs of 1945, 1963, and 1989, and panchromatic bands of satellite images of 2001 and 2014



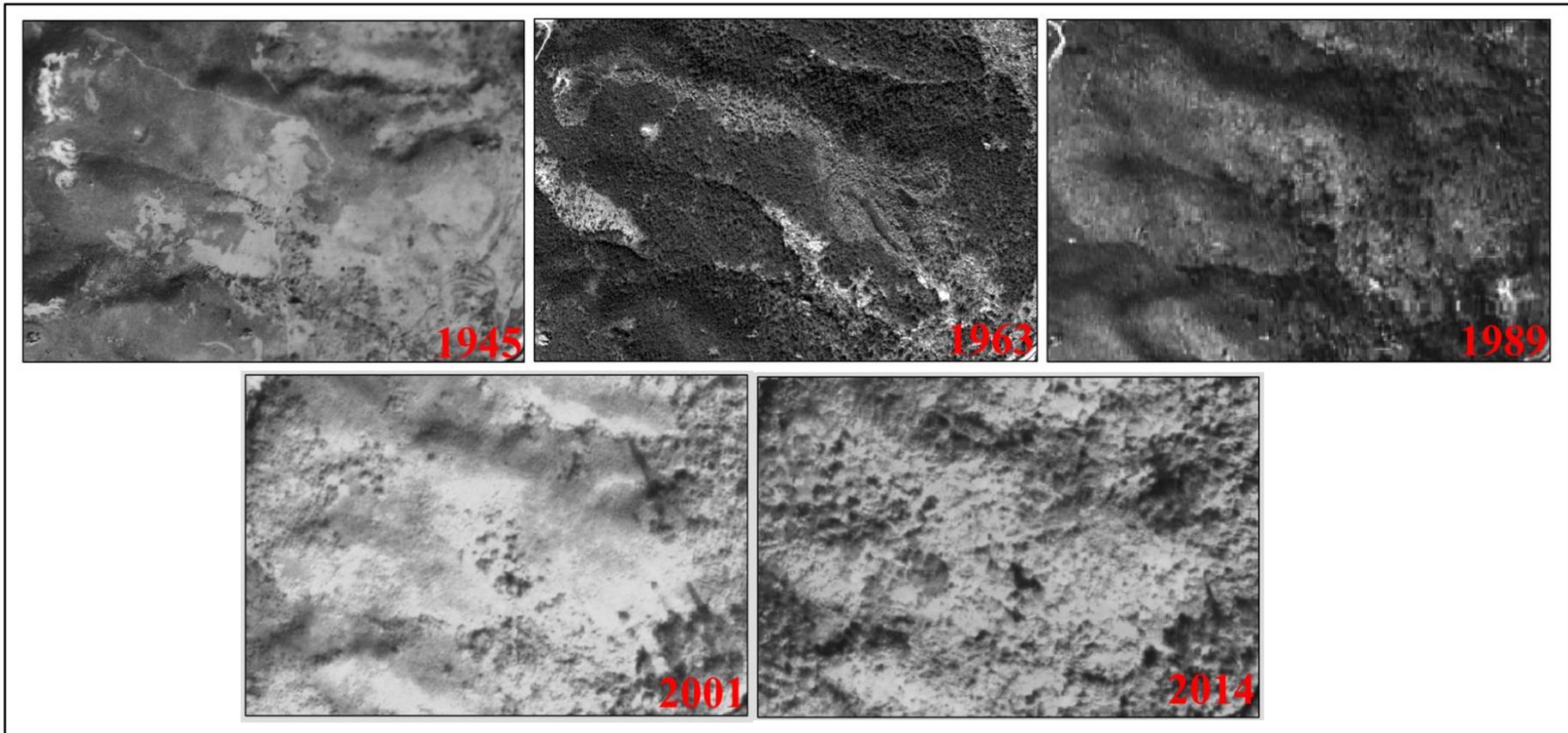
**Figure 4.3** Penta-temporal habitat classification maps of the landscape for the years 1945, 1963, 1989, 2001 and 2014



**Figure 4.4** Plantation patches at their earlier growth stage, recognizable from their spatial pattern and arrangement in 1963



**Figure 4.5** Monocultural plantation stands recognizable from their texture, appeared in 1989



**Figure 4.6** Image sequence showing loss of plantations during 1970s

**Table 4.3** Distribution of habitat classes over the years

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

**Table 4.4** Error matrix generated for accuracy assessment of habitat map of 2001

		Predicted Habitat Information										User's Accuracy (%)	
		F	OF	SH	SG	GL	BA	BU	W	PF	Sum		
Ground Reference Information	F	57	0	0	0	0	0	0	0	1	58	98.3	
	OF	0	9	0	0	0	0	0	0	0	9	100.0	
	SH	4	0	25	2	0	0	0	0	0	31	80.7	
	SG	1	0	1	25	2	0	0	0	0	29	86.2	
	GL	0	0	3	7	101	0	0	0	0	111	90.9	
	BA	0	0	0	0	2	18	0	0	0	20	90.0	
	BU	0	0	0	0	0	1	15	0	0	16	93.8	
	W	0	0	0	0	0	0	0	20	0	20	100.0	
	PF	2	0	0	0	0	0	0	0	47	49	95.9	
	Sum	64	9	29	34	105	19	15	20	48			
Producer's Accuracy (%)		89.1	100.0	86.2	73.5	96.2	94.7	100.0	100.0	97.9			
Total Samples = 343		Correct Samples = 317		Overall Accuracy = 92.42 %									Kappa Coefficient = 0.91

**Table 4.5** Contingency matrix showing transitions between habitat classes and/or structural stages of vegetation (1945-1963, 1963-1989)

	<b>F</b>	<b>OF</b>	<b>SH</b>	<b>OS</b>	<b>GL</b>	<b>BA</b>	<b>BU</b>	<b>W</b>	<b>PF</b>	<b>PLS<sub>E</sub></b>	<b>L</b>	<b>T<sub>c</sub></b>	<b>N<sub>c</sub></b>	<b>AN<sub>c</sub></b>	<b>S</b>
<b>1945 - 1963</b>															
<b>F</b>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.54	0.54	0.54	0.00
<b>OF</b>	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	1.00	0.98	0.98	0.02
<b>SH</b>	0.06	0.06	0.74	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.12	5.64	5.40	5.40	0.25
<b>OS</b>	0.47	0.93	2.53	2.19	0.00	0.00	0.00	0.00	0.00	6.11	3.93	9.02	1.16	1.16	7.85
<b>GL</b>	0.00	0.00	2.99	5.09	54.26	0.89	0.08	0.00	15.43	78.75	24.49	34.76	-14.21	14.21	20.55
<b>BA</b>	0.00	0.00	0.00	0.00	10.28	1.67	0.09	0.00	0.00	12.04	10.37	11.26	-9.48	9.48	1.78
<b>BU</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.17	0.17	0.17	0.00
<b>W</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	2.04	0.00	0.00	0.00	0.00	0.00
<b>PF</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.44	0.00	0.00	15.44
<b>PLS<sub>L</sub></b>	0.71	0.99	6.26	7.28	64.54	2.56	0.19	2.04	15.44	61.91					
<b>G</b>	0.54	0.99	5.52	5.09	10.28	0.89	0.17	0.00	15.44						
<b>A<sub>L</sub></b>	19.85	27.69	175.05	203.57	1805.62	71.76	5.21	57.21	431.85	19.85					
<i>At landscape level: Total change = 38.91 %; Persistence = 61.09 %, Absolute net change = 15.97 %, Swap = 22.94 %</i>															
<b>1963 - 1989</b>															
<b>F</b>	0.71	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.71	0.00	4.30	4.30	4.30	0.00
<b>OF</b>	0.75	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.75	1.87	0.37	0.37	1.50
<b>SH</b>	2.38	0.39	3.48	0.00	0.00	0.00	0.00	0.00	0.00	6.26	2.77	15.88	10.34	10.34	5.54
<b>OS</b>	0.85	0.13	3.59	2.71	0.00	0.00	0.00	0.00	0.00	7.28	4.57	10.63	1.49	1.49	9.14
<b>GL</b>	0.32	0.60	8.05	4.99	45.28	0.27	0.08	0.00	4.94	64.54	19.26	26.88	-11.63	11.63	15.25
<b>BA</b>	0.00	0.00	0.28	0.15	0.73	1.39	0.01	0.00	0.00	2.56	1.17	1.65	-0.68	0.68	0.97
<b>BU</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.19	0.00	0.13	0.13	0.13	0.00
<b>W</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.04	0.00	2.04	0.00	0.00	0.00	0.00	0.00
<b>PF</b>	0.00	0.00	1.19	0.91	6.90	0.22	0.04	0.00	6.18	15.44	9.25	14.19	-9.25	9.25	4.94
<b>PLS<sub>L</sub></b>	5.01	1.36	16.60	8.77	52.91	1.88	0.31	2.04	11.12	62.23					
<b>G</b>	4.30	1.12	13.11	6.06	7.63	0.48	0.13	0.00	4.94						
<b>A<sub>L</sub></b>	140.03	38.09	464.34	245.29	1480.22	52.59	8.81	57.21	311.21						
<i>At landscape level: Total change = 37.77 %; Persistence = 62.23 %, Absolute net change = 19.10 %, Swap = 18.67 %</i>															

*PLS<sub>E</sub>* = percentage of earlier landscape, *PLS<sub>L</sub>* = percentage of later landscape, *A<sub>L</sub>* = Area in ha in later landscape, *L* = amount of loss, *G* = amount of gain, *T<sub>c</sub>* = amount of total change, *N<sub>c</sub>* = amount of net change, *AN<sub>c</sub>* = absolute value of net change, *S* = amount of swap

**Table 4.6** Contingency matrix showing transitions between habitat classes and/or structural stages of vegetation (1989 -2001, 2001-2014)

	F	OF	SH	OS	GL	BA	BU	W	PF	PLS <sub>E</sub>	L	T <sub>C</sub>	N <sub>C</sub>	AN <sub>C</sub>	S
<b>1989 - 2001</b>															
F	5.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.01	0.00	15.69	15.69	15.69	0.00
OF	0.87	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.36	0.87	4.25	2.51	2.51	1.74
SH	11.94	1.85	2.81	0.00	0.00	0.00	0.00	0.00	0.00	16.59	13.79	25.95	-1.63	1.63	24.32
OS	2.81	0.74	3.88	1.34	0.00	0.00	0.00	0.00	0.00	8.77	7.42	15.43	0.58	0.58	14.85
GL	0.08	0.79	8.28	8.00	34.67	0.00	0.12	0.00	0.95	52.90	18.23	18.23	-18.23	18.23	0.00
BA	0.00	0.00	0.00	0.00	0.00	1.86	0.01	0.00	0.00	1.88	0.01	0.01	-0.01	0.01	0.00
BU	0.00	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.31	0.00	0.13	0.13	0.13	0.00
W	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05	0.00	2.05	0.00	0.00	0.00	0.00	0.00
PF	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.13	11.13	0.00	0.95	0.00	0.00	0.95
PLS <sub>I</sub>	20.70	3.87	14.97	9.35	34.67	1.86	0.45	2.05	12.08	59.68					
G	15.69	3.38	12.16	8.00	0.00	0.00	0.13	0.00	0.95						
A <sub>L</sub>	579.0	108.3	418.7	261.5	969.9	52.2	12.5	57.2	337.8						
<i>At landscape level: Total change = 40.32 %; Persistence = 59.68 %, Absolute net change = 19.39 %, Swap = 20.93 %</i>															
<b>2001 / 2014</b>															
F	20.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.70	0.00	15.74	15.74	15.74	0.00
OF	3.55	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.87	3.55	4.22	-2.89	2.89	1.33
SH	11.06	0.46	3.45	0.00	0.00	0.00	0.00	0.00	0.00	14.97	11.52	31.33	8.28	8.28	23.04
OS	1.08	0.20	6.97	1.09	0.00	0.00	0.00	0.00	0.00	9.35	8.25	22.22	5.71	5.71	16.51
GL	0.04	0.00	12.83	13.95	7.86	0.00	0.00	0.00	0.00	34.67	26.82	26.82	-26.81	26.81	0.01
BA	0.00	0.01	0.01	0.02	0.00	1.83	0.00	0.00	0.00	1.86	0.03	0.03	-0.03	0.03	0.00
BU	0.00	0.00	0.00	0.00	0.00	0.00	0.45	0.00	0.00	0.45	0.00	0.00	0.00	0.00	0.00
W	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.05	0.00	2.05	0.00	0.00	0.00	0.00	0.00
PF	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.08	12.08	0.00	0.00	0.00	0.00	0.00
PLS <sub>I</sub>	36.44	0.98	23.25	15.06	7.86	1.83	0.45	2.05	12.08	49.82					
G	15.74	0.66	19.81	13.97	0.00	0.00	0.00	0.00	0.00						
A <sub>L</sub>	1019.2	27.5	650.4	421.3	219.9	51.2	12.5	57.2	337.8						
<i>At landscape level: Total change = 50.18 %; Persistence = 49.82 %, Absolute net change = 29.73 %, Swap = 20.44 %</i>															

*PLS<sub>E</sub>* = percentage of earlier landscape, *PLS<sub>I</sub>* = percentage of later landscape, *A<sub>L</sub>* = Area in ha in later landscape, *L* = amount of loss, *G* = amount of gain, *T<sub>C</sub>* = amount of total change, *N<sub>C</sub>* = amount of net change, *AN<sub>C</sub>* = absolute value of net change, *S* = amount of swap

**Table 4.7** Annual rate of change in structural stages of the landscape

<b>Structural Stages</b>	<b>1945-1963</b>	<b>1963-1989</b>	<b>1989-2001</b>	<b>2001-2014</b>	<b>1945-2014</b>
	(% 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	-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

## Chapter 05

# Changes in Spatial Morphology of the Landscape along the Successional Gradient

### 5.1. Introduction

Landscape can be viewed as a heterogeneous area composed of a cluster of interacting eco-systems. It is a mosaic of habitat patches that are repeated in various shapes, sizes, and spatial relationships. Spatial patterns of landscape can change over time due to natural succession in ecosystem, and natural and/or human induced disturbances. The quantification of morphological structure of landscape is important to explain relationships between ecological processes and spatial patterns (Turner et al., 2001).

Forested areas of the world decreased by 129 million hectares during the past quarter-century, and 65 % of that remaining is secondary forest. Furthermore, recent evidence from long-term time series analysis of satellite images indicates a 62% increase in deforestation in the humid tropics from the 1990s to the 2000s (Kim et al., 2015). But, whether the rate of loss is increasing or decreasing, humid tropical forests are declining in area globally. Reduction in size of habitat patches is generally associated with loss of species of both flora and fauna due to a changed microclimate, edge disturbances, and reduced range of movement. However, even the presence of small remnant patches of primary forest can significantly enhance the recolonization of nearby areas undergoing succession (Turner and Corlett, 1996).

Quantification of the changing spatial structure of landscape is important to explain the dynamic ecological processes observed in successional communities, and to understand those processes conducive to restoring biodiversity. Landscape patterns in categorical data can be conceptualized and quantified using landscape metrics based on the Patch Matrix Model (PMM) of landscape structure (Lausch et al., 2015), and they permit objective description of temporal changes in spatial structure (Turner et al., 2001). For example, landscape metrics have been applied to quantify structural changes associated with forest fragmentation in Brazil (Rocha-Santos et al., 2016), to evaluate impacts of a 10% decrease in large core forest in Nepal's Kailash Sacred Landscape

(Uddin et al., 2015), to assess patterns of landscape dynamics associated with habitat loss in the Niger Delta (Onojeghuo and Blackburn, 2011), and to analyse the effects of fragmentation on beetle diversity in Brazil's Atlantic forests (Araujo et al., 2015).

On the other hand, there are few examples describing significant forest regeneration, especially over time periods longer than the operational period of earth resource satellites i.e. the last four decades since early 1970s. Furthermore, there have been few attempts to understand the processes and dynamics of forest regeneration in terms of spatial structure of the landscape. One such paper quantifies spatial patterns of vegetation succession as a result of ecological restoration projects in southwest China (Qi et al., 2013), and Geri et al. (2010) used spatial metrics to quantify habitat loss along with afforestation projects in the increasingly degraded Mediterranean landscape. However, neither of these projects addresses the spatial processes of natural vegetation succession.

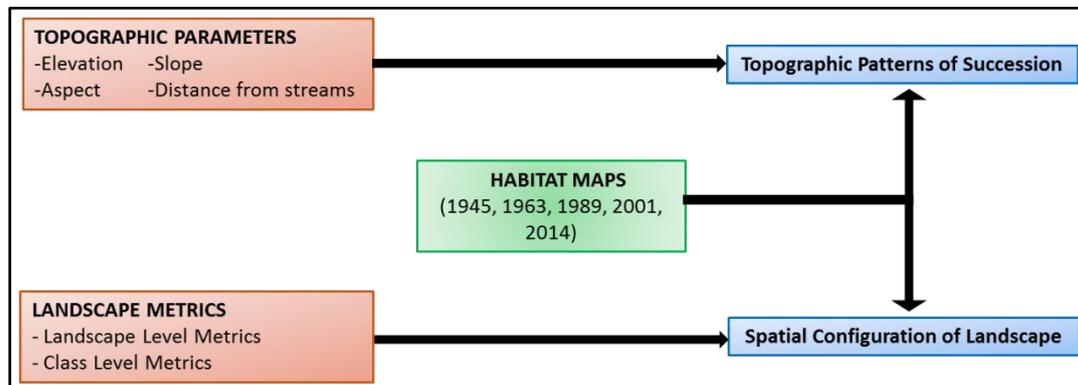
Following the destruction of Hong Kong's forest during WWII, natural regeneration along a successional gradient from open ground to forest, presents a rare opportunity to observe the changing ecological processes operating as the landscape has consolidated over the 70-year period. The increasing structural 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 late successional stage has been reached over a significant proportion of the landscape, subsequent change would be expected to occur more rapidly. At the same time, increase in patch size brings the edges of adjacent patches closer together, permitting better seed dispersal between patches, again implying faster regeneration in the later succession. Hong Kong's forest is accelerating by natural regeneration, and the landscape meanwhile has undergone stages of increasing and decreasing fragmentation and consolidation of habitats, each stage offering different opportunities for natural forest succession. These observations of landscape morphology at different successional stages, can be used to optimise forest management policies in controlled successions, assuming natural succession to forest is the desired outcome in the landscape.

In this chapter landscape metrics were applied to examine the changes in spatial morphology of the landscape along the successional gradient by quantifying changes in spatial composition, structure, and diversity of landscape over time. Results of this analysis will answer the following questions:

- How has the morphology of the landscape changed over a 70-year forest succession?
- What is influence of specific landscape structural parameters on forest succession?
- How are the patterns of forest succession related to topography?

## 5.2. Materials and Methods

This section describes the methodologies applied to the habitat maps presented in the previous chapter to determine spatial structure of the landscape and topographic patterns of forest succession (figure 5.1).



**Figure 5.1** Process of spatial analysis of the landscape

### 5.2.1. Landscape metrics

Landscape metrics were applied in the current landscape to determine changes in composition, structure, and diversity of landscape over time. Landscape composition was explained by the number of structural stages in a map, the area of each stage, and the percentage area of the landscape. 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 5.1). The metrics, including patch density (PD), mean patch size (MPS), mean radius of gyration (MRG), 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 juxtaposition index (IJI), and Shannon's diversity index (SHDI) (Table 1). At class level (CL on table 5.1), metrics used to 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). These metrics provide unique and ecologically meaningful information contributing to better understanding of landscape structure at different stages of the natural succession. Landscape metrics were applied using Fragstats software (Mcgarigal et al., 2012), to the five categorical habitat maps of the landscape (figure 4.3).

### **5.2.2. Topographic analysis**

Digital Elevation Model (DEM) and DEM-derived topographic variables are widely used to understand and explain ecosystem structure, biophysical processes, and community distribution in a variety of ecosystems. Habitat patterns in mountainous terrain are often influenced by regional climate coupled with micro-climatic conditions induced by topographic factors (Leempoel et al., 2015). In order to determine the influence of topography on changes in habitat classes, four topographic variables were derived from the DEM, namely elevation, slope, aspect and distance from stream network (proximity to channels). Proximity to channels was determined by first generating a stream network and then the Euclidean surface distance from the streams was calculated to form a 'distance to streams' layer. All these data sets were resampled to 1m resolution in order to match the spatial resolution of habitat maps. Topographic characteristics of the structural stages of each habitat map were extracted and analysed by generating zonal statistics and performing overlay analysis between the habitat maps and topographic variables. Annual rates of change were calculated using the formula give in equation 4.7. All the analysis was performed using the Hydrology and Spatial Analysis extensions of ArcGIS 10.

**Table 5.1** Description of landscape metrics used for the spatial analysis

Category	Metric Name	Acronym	Units	Level Used	Ecological Description
<b>Patch size and Density</b>					
	Number of Patches	NP		CL	Measure of extent of subdivision of a habitat class
	Patch Density	PD	Number of patches per 100 ha	LL	PD is fundamental aspect of landscape pattern, 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	Mean distance for each cell on one path to the patch centroid. It measures connectivity inside habitat patches. Higher gyrate represent better connectivity inside patches.
	largest patch index	LPI	%	LL, CL	Ratio of area of largest patch to total landscape area
<b>Shape and Edge</b>					
	Mean shape index	MSI	--	LL, CL	Measures complexity of patch shape to a standard shape of the same size. Its value increases with complexity of shape.
	Edge density	ED	m / ha	LL, CL	Measures total length of edge per unit area, explains complexity of patch shape.
	mean perimeter to area ration	MPAR	--	LL, CL	Patch shape complexity, that measure perimeter per area, explains shape complexity without standardization to a standard Euclidean shape (square)
<b>Proximity / Isolation</b>					
	mean Euclidean nearest neighbor distance	MED	m	LL, CL	Measures minimum edge to edge distance to the nearest neighbouring patch of the same type. It explains connected or isolation in landscape or habitat class
	Mean proximity index	MPI	--	CL	Measure of connectedness of habitat class, considers size and proximity of all patches with the same habitat type inside a specified search radius
<b>Diversity and Texture</b>					
Diversity and Texture	interspersion and juxtaposition index	IJI	%	LL	Measure evenness of patch adjacencies, and presents intermixing of different patch types. At landscape level, decrease in IJI suggests reduced degree of mixture of vegetation communities
	Shannon's diversity index	SHDI	--	LL	Measure diversity in landscape by taking into account the abundance of habitat categories. It increases as the number of categories increase or the equitability of distribution of land amongst the various classes increases

LL = Landscape Level, CL = Class Level

## 5.3. Results

### 5.3.1. Change in spatial structure of the landscape

As vegetation succession proceeded, significant changes in spatial patterns were observed. In the earliest landscape in 1945, many tiny patches of bare ground and open shrubland around the minimum ground mapping unit of 50 m<sup>2</sup> 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 5.2). However, the shrub patches within the matrix, having lowest mean patch size (MPS), as well as connectivity within patches (denoted by the Mean Radius of Gyration (MRG) 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 diversity 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, NP and PD, which by 2014 had decreased drastically to approximately one third of the 1945 levels (table 4.2), 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 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 moving within a patch. Since the forest climax trees are mostly restricted to the original forest remnants of 1945 in steep valleys and protected places near villages (figure 4.3), the improved connectivity within patches 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 patterns simplifies. For example, between 1989 and 2002 MPAR was greatly reduced because the main increase in forest was by infilling across interfluves, between adjacent linear valleys (figure 4.3), rather than by advance along a broad front, as front advance

would not affect MPAR significantly. This infilling may be related to the dispersal distances for forest seeds, as the main patches of forest in 1989 may have been too far apart for effective seed dispersal by birds such as bulbuls, but distances across interfluves between adjacent parallel valleys are generally below 200 m. Accordingly, in the final stage from 2002 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 interfluves merged into upper slopes (table 5.2).

Diversity and texture in the landscape was measured through SHDI and IJI. Both parameters increased steadily after 1945 and both were highest in 2001. 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 neighboring habitats, and would favor 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 (table 5.2).

Most spatial metrics show steady uni-directional change from the earliest to latest landscape, but two parameters, patch density (PD) and mean patch size (MPS), appear to show a reversal following 1963, before resuming the overall downward (PD) and upward (MPS) trend (figure 5.2). The establishment of large exotic plantations in the southwest of the study area before 1963, interrupting the natural succession, can explain this (table 5.2).

### **5.3.2. Change in spatial patterns of structural classes**

Class level metrics helped in quantification of spatial structure of the vegetation communities and conveyed the extent of changes and their effects on the landscape. The gradual consolidation and simplification of the landscape indicated by reductions in the landscape metrics NP, PD, MPAR and increase in MED over the study period are not

replicated by the class level metrics (table 5.3). 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 which have been observed to disperse seeds <100 m, and hwamei <50 m in 10-minute periods (Weir and Corlett, 2006).

Changes in spatial structure of grassland were opposite to changes in structure of forest - as most of the landscape has converted from earlier successional stage to late 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. 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 5.3), in this otherwise dynamic landscape.

### **5.3.3. Topographic patterns of vegetation successional stages over time**

Forest is seen advancing towards elevated areas in the landscape and away from watercourses (figure 5.7). The mean elevation of forest increased from 248m in 1945 to 394m in 2014 (figure 5.3), reflecting the confinement of forest remnants in the earlier 1945 landscape, to topographic ravines in valley bottoms, where steep slopes would have prevented tree extraction as well as fire penetration. Feng shui woods being adjacent to villages would also be at lower levels. 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 (figure 5.5). 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. Increase in mean elevation of grassland (462 m to 649 m) and decrease in proportion of grassland in the landscape (78.62 % to

7.86 %), indicates proportion of later successional stages of vegetation was rising along elevation - as a result, the current grassland habitat was confined to top of the mountains (figure 5.7).

Proximity of shrubland to channels has decreased over time indicating colonization of earlier successional stages along the water channels (figure 5.3). The increased distance of forest from water channels during 1945 to 1989, indicates that succession of shrubland into forest originally occurred within distance of 100 m around water channels that was expanded to higher distances in later years (figure 5.5, figure 5.7). A similar pattern of change was observed along the rising slopes, i.e., forest change rate increased on higher slopes in later years (figure 5.5). Plot of annual change rate in forest cover along aspect (figures 5.5) indicates that the change rate was higher along eastern and south eastern aspect during 1945-1963 and 1963 - 1989, while during the following period (1989-2001) the change rate was significantly higher along western (NW, W, SW) and south facing slopes (figures 5.5, 5.7). It is significant that increase in both in forest and shrubland between 1989 - 2001 was higher along northern, north western and north eastern aspects, but from 2001 to 2014 forest and shrubland encroached along all aspects indicating that forest was initially established along cooler aspects but is now expanding to warmer aspects (figure 5.4). The reason could be occurrence of hill fires in earlier periods on warmer and drier southern aspects as south-facing slope receive more solar radiations than flat area and north-facing slopes. Also traditionally, Chinese people prefer to locate villages on south-facing slopes, where activities of rural habitants result in fire. As a result, intensity of fire and occurrence was (or is) higher on drier and warmer south-facing slopes as compared to colder and wet north-facing slope (Chau, 1994). However, increase in shrubland and open shrubland along southern, south-western, and south-eastern slopes was significant during 2001-2014 while from 1989 to 2001 and 1963 to 1989, succession of grassland into later successional stages was less along the warmer aspect, probably due to the occurrence of hill fires along southern slopes, which burnt three to six times in the 1980s (Chau, 1994).

## 5.4. Discussion

The highest rate of increase in forest, of 11% a year between 1989 and 2002, 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 MPAR 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 2001-2014, the net gain in forest was greatest at this period. However, the infilling and consolidation of forest habitats up to 2001 also resulted in decreased landscape diversity, as indicated by reductions in SHDI and IJI. This may be a cause for concern, given that natural succession to forest in the study area appears to be dominated by a restricted number of hardy native pioneers as well as invasive exotic species (Dudgeon and Corlett, 2011), and many of the climax trees are absent. Moreover, the main seed dispersers in the study area are birds which favour the 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 within forest. Since these forest remnants had now, by 2014, become connected to regenerated secondary forest, the improved connectivity within forest patches as indicated by increased MRG appears promising if forest dispersers are present. Thus the reduced diversity at landscape level is now perhaps compensated by better internal connectivity within patches, enabling better seed dispersal by forest fauna in the future. However, since the birds known to disperse seeds in the study area (bulbuls, the Japanese white eye and hwamei) are not essentially forest birds and most of the original forest mammals disappeared long ago, this situation requires further research.

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 grassland habitat for these species, 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. 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.

In the earlier successional stages before 2001, when forest reached 20 % of the landscape, diversity and juxtapositioning of habitats at landscape level was high. Thus, up to 2001, SHDI and IJI achieved maximum values offering opportunities for species which move between open and closed 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 bulbuls and hwamei known to disperse seeds in the study area. However, knowledge of dispersal distance for other species is not available and requires further research.

## **5.5. 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 biodiversity remains low because of restricted distribution and dispersal limitations of climax trees. Significantly, as forest patches consolidate, the birds of open habitats including bulbuls and hwamei known to disperse most of the seeds in open and semi-open areas, will become less effective since the seeds of most of the climax trees are not part of their natural diet and this is a concern, given the loss of many seed dispersing forest mammals and large forest birds. To manage natural succession and to guarantee enough genetic diversity in the absence of late successional dispersal agents, climax trees should be planted in strategically selected plots over the territory, assisted by spatial metrics to locate larger forest patches with simpler shapes and lesser edge to edge distances from nearby similar forest patches. 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 will also encourage the natural recolonisation by mobile dispersal agents such as forest birds from neighbouring areas in South China. For example, 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 interfluves, making it unlikely that seeds can be dispersed by natural forces such as gravity, flash floods and surface wash.

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 biodiversity recovery may also depend on the reintroduction of specialised forest dispersal organisms (McConkey et al., 2012) such as Edwards's long-tailed giant rat (*Leopoldamys edwardsi*). This has to be balanced by the recognition that long absence from an ecosystem may be disruptive to the new ecological equilibrium (Corlett, 2013).

**Table 5.2** Spatiotemporal patterns of landscape indices in the landscape, at landscape level

Year	Patch Density and Size					Shape and Edge		Proximity / Isolation		Diversity and Texture	
	NP	PD	LPI	MPS	MRG	MSI	MPAR	ED	MED	IJI	SHDI
<b>1945</b>	6224	222.46	76.56	0.45	7.95	1.75	16193.46	89.3	9.82	30.48	0.75
<b>1963</b>	4012	143.40	58.75	0.70	13.76	2.01	13460.64	101.1	18.11	65.17	1.20
<b>1989</b>	4585	163.88	46.80	0.61	15.40	2.03	10894.13	123.0	20.59	71.22	1.47
<b>2001</b>	3459	123.66	27.96	0.81	22.07	2.22	6273.16	128.9	24.90	74.13	1.76
<b>2014</b>	2266	80.99	19.84	1.23	26.58	2.35	8359.23	118.7	28.26	65.97	1.67

**Table 5.3** Spatiotemporal patterns of landscape indices in the landscape, at class level

Structural Stage	Patch Density and Size					Shape and Edge			Proximity / Isolation	
	Year	NP	LPI	MPS	MRG	ED	MSI	MPAR x 10 <sup>3</sup>	MPI	MED
<b>Forest</b>										
	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
<b>Open Forest</b>										
	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
<b>Shrubland</b>										
	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
<b>Open Shrubland</b>										
	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
<b>Grassland</b>										
	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
<b>Plantations</b>										
	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

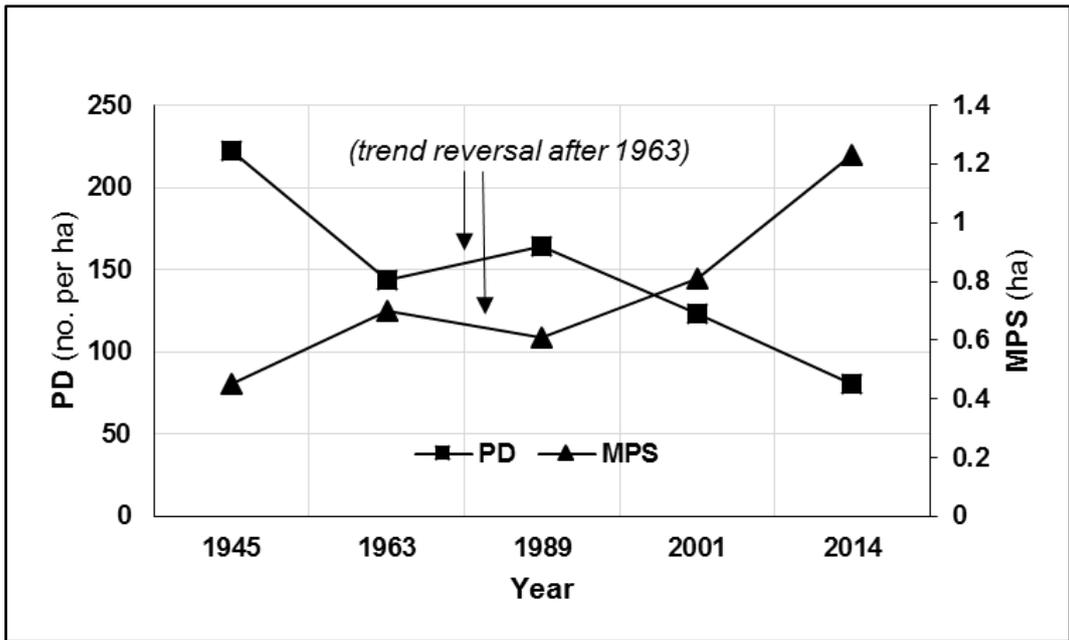


Figure 5.2 Change in Path Density (PD) and Mean Patch Size (MPS) over the years

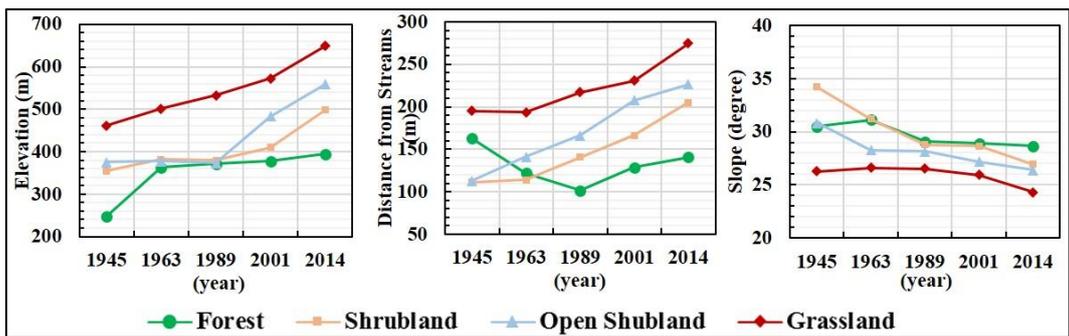


Figure 5.3 Mean topographic characteristics of structural classes over the years

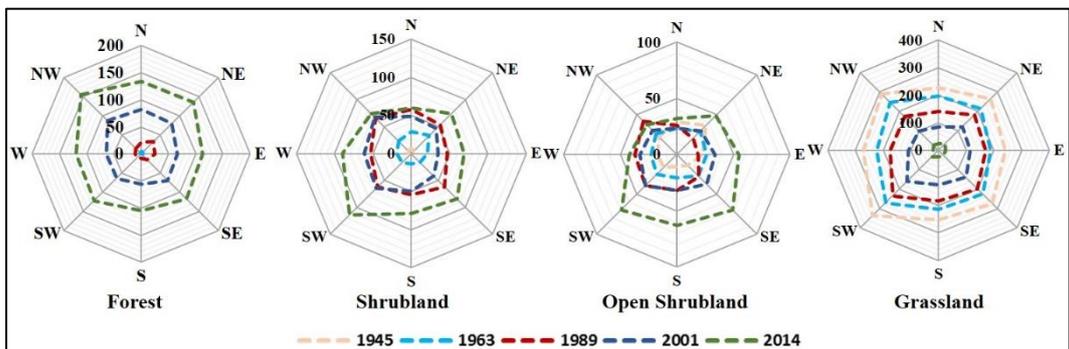
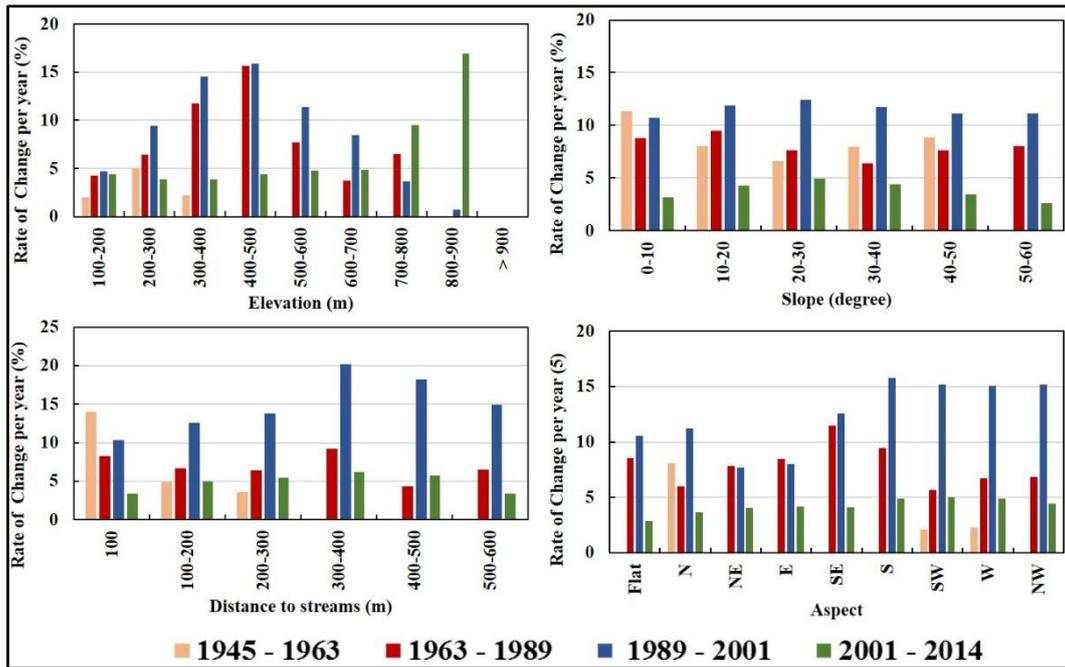
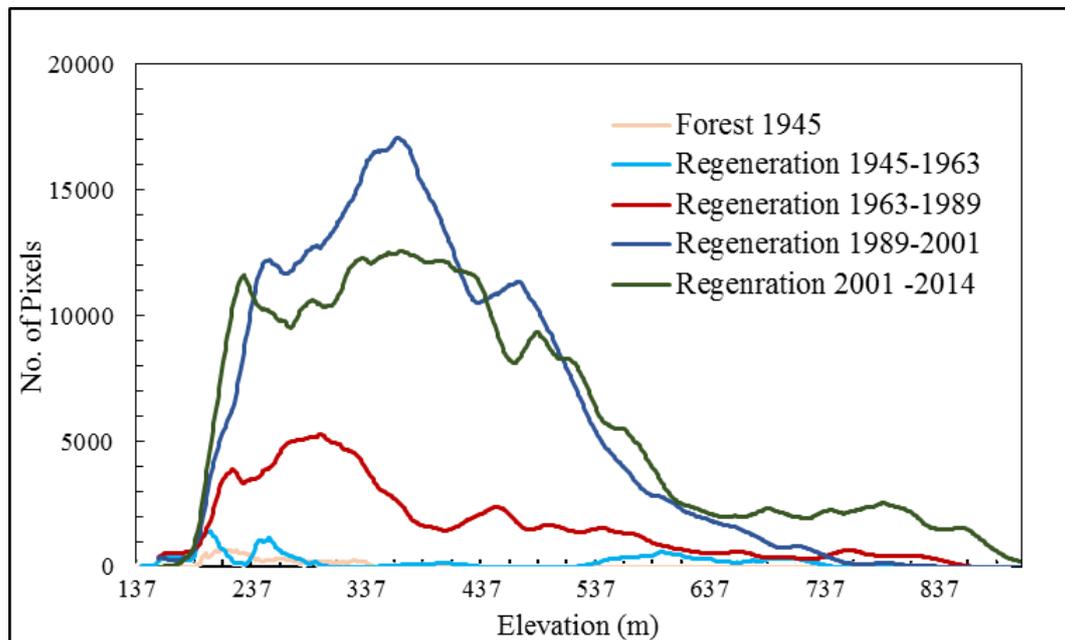


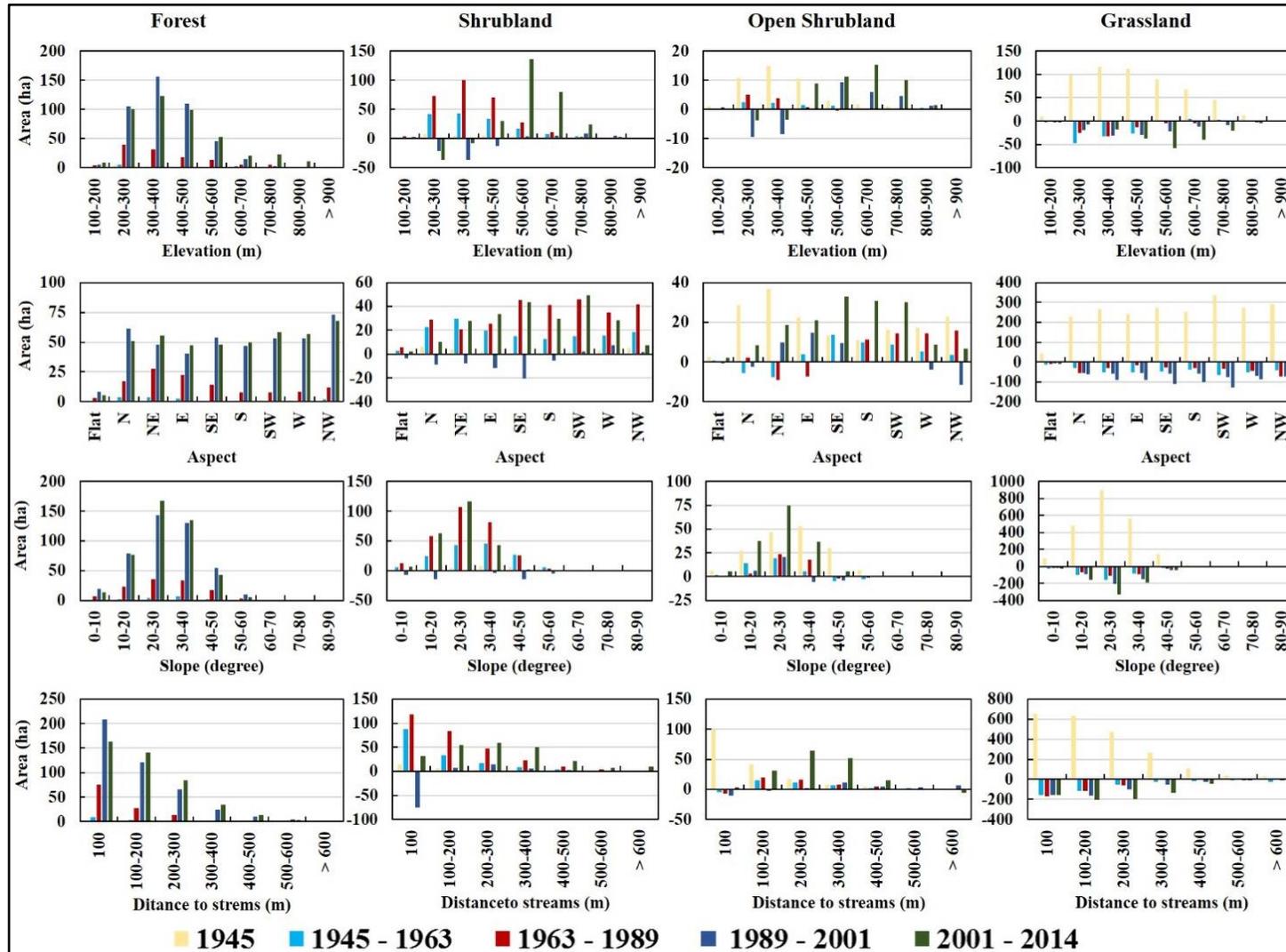
Figure 5.4 Structural changes in vegetation communities along aspects



**Figure 5.5** Annual rate of change (%) of forest along the topographic variable



**Figure 5.6** Histogram distribution of increase in forest along elevation



**Figure 5.7** Increase or decrease in area of structural stages during the each period of time

## Chapter 06

### Diversity and Compositional Traits of Forest Succession

#### 6.1. Introduction

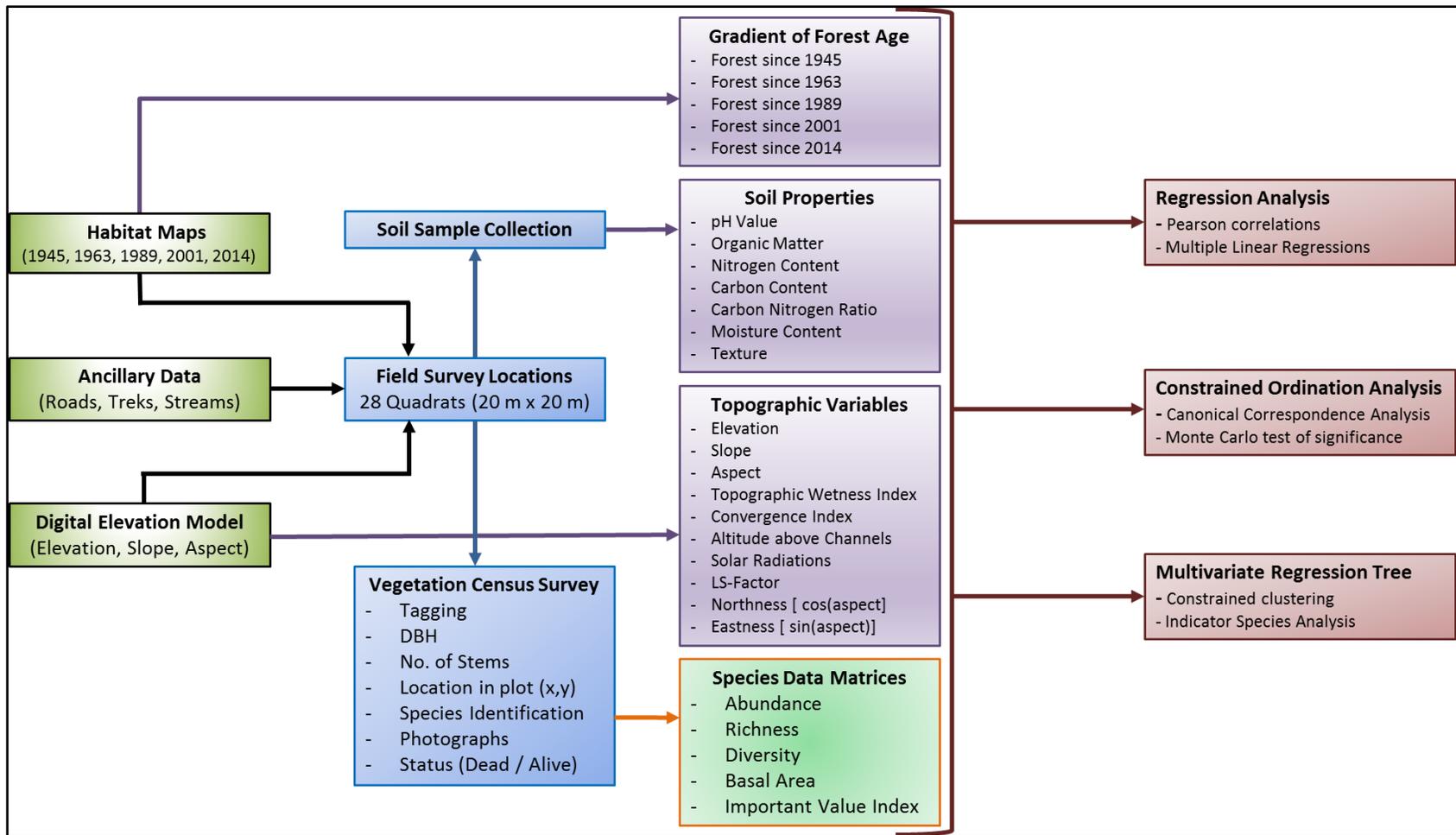
Secondary forests can serve as carbon sinks, as well as enhance regional biodiversity, environmental services, and forest-based economies. Secondary vegetation succession occurs on previously vegetated landscapes that have been abandoned after natural disturbances or anthropogenic activities. The succession process in a secondary forest starts from regeneration of scattered patches of different ages and sizes in the most favourable sites (Honnay et al., 2005) and leads to becoming the predominant patch type in the landscape over a certain period of time (Rocchini et al., 2006). Forest is the last structural stage in the vegetation structural gradient in most terrestrial ecosystems (Chaplin et al., 2011). However, forest patches at different stages of succession differ in total their biomass, net primary production, diversity and species composition, and all of these affect their relative contribution to global carbon cycle (Hartter et al., 2008; Honnay et al., 2005). Therefore, in these transforming landscapes, characterization of changes in shape, size and spatial patterns of regenerated forest patches are essential for understanding ecological functioning, and for devising spatially explicit conservation and/or restoration policies. In this perspective, assessment and monitoring of structure and diversity in the changing patterns of the landscapes at multiple time steps of vegetation recovery has significant importance for ecologists and policy makers for effective restoration of biodiversity and conservation (Braumoh, 2006; Roy, 2013).

In addition, microhabitats associated with environmental conditions serve as a proxy for environmental resource availability and determine the composition and structure of ecological communities (Bohlman et al., 2008; Costa et al., 2005; Punchi-Manage et al., 2013; Segura et al., 2003). Among the environmental conditions, topographic factors (Lovett et al., 2001; Vasquez and Givnish, 1998) and soil properties (Arekhi et al., 2010; Clark et al., 1999) are most associated with distribution of woody vegetation and floristic diversity in a landscape (Eilu et al., 2004; Nguyen et al., 2015). In general, the structure and composition of a forest community tend to increase in complexity and

stability with the progressive succession (Guariguata et al., 1997; Wang et al., 2006). For example, at a local scale, topography may define soil moisture conditions (Engelbrecht et al., 2007; Sukri et al., 2012) and distribution of nutrients (John et al., 2007), such that valley bottoms and flatter areas are found to be moister and richer in nutrients than areas near ridge tops and on steeper slopes (Balvanera et al., 2011; Gibbons and Newbery, 2003) and this can influence the distribution of species in a landscape. Also, topographic control on solar irradiance may affect the diversity of light demanding and shade tolerant species at a location (Larsen and Speckman, 2004). The physical and chemical properties of soil in a degraded landscape are also likely to influence the growth and species composition of recovering secondary forests. However, since the soil characteristics dramatically change after deforestation and the recovery of soil to its previous functions depends upon forest type, soil type, and intensity of past land use (Allen, 1985; Neill et al., 1997). Therefore, knowledge of the relative impact of environmental variables on the diversity and composition of forest communities is important for developing biodiversity conservation policies and informed forest management practices in disturbed tropical landscapes (Baldeck et al., 2016; Liu et al., 2014)

Secondary forest in Hong Kong is recovering after the last clear cutting during WWII. (Dudgeon and Corlett, 2011). In the study area, forest cover was only about 0.17 % of the landscape in 1945, primarily confined to feng shui woods around Shing Mun Reservoir, but in the intervening 70 years, has recovered to about 36% by 2014 as a result of natural regeneration of secondary forest. The structural changes associated with this forest recovery over the past 70 years can be documented and mapped by sequential analysis of aerial photographs and satellite images. Thus it is possible to record and study the changes in species composition along the successional and environmental gradients and thereby understand the process of ecosystem recovery in the degraded tropical landscape of Hong Kong. In Hong Kong, information about the spatial patterns of forest recovery and the influence of these patterns on species composition and forest structure is unknown to-date. Therefore the general objective of this part of the study is to analyze patterns of species composition in secondary forest succession and to explain the influence of topography, soil properties, and age of forest on the species assemblages using forest inventory data collected from the study area. The specific objectives are to:

- understand the influence of topography on changes in species composition and structural traits.
- determine how the patterns of species composition and forest structure are related to the age of the forest stand?
- what extent is the composition of plant communities is explained by physical and chemical properties of soil?



**Figure 6.1** Process of analysing diversity and compositional traits of forest succession

## **6.2. Materials and Methods**

A brief illustration of the methodology is given in figure 6.1, which is explained in the following text.

### **6.2.1. Vegetation survey**

The spatial pattern of forest recovery in terms of the amount and distribution of various successional stages (forest, shrubland, open shrubland, and grassland) was determined through remotely sensed datasets. However, field investigation was required to measure the composition and structural diversity along the successional and topographic gradient. Therefore, a floristic survey of vegetation was conducted between March 2015 and May 2016. Within the constraints of man power and time, 28 temporary plots were established and surveyed which cover a total area of 1.12 hectares. Only woody plant species were recorded and identified; and herbs, grasses and ferns were ignored.

#### ***Sampling approach***

Vegetation census data was collected by establishing 28 quadrats (20m x 20m) distributed along the elevation gradient and by considering the age of forest stands in the study area (figure 6.2). The minimum age of forest patches was determined from the five habitat maps (figure 4.3). Considering the heterogeneity in the landscape and accessibility, it was difficult to find continuous vegetation cover with similar types through random selection, therefore, a stratified random sampling method was used to select plot location. Initially, a total of 44 potential sites were selected, but only 28 were surveyed according to accessibility, man power and time. The sites were subjectively selected to maximize the range of vegetation types sampled and to occupy the geographic extent of the study area. Plots were located in different forest patches of the five vegetation communities (forest since 1945, forest since 1963, forest since 1989, forest since 2001, and forest since 2014). It was attempted to sample each vegetation community at an altitudinal interval of 200m, and further divided into cardinal slope directions (N, NE, E, SE, S, SW, W, and NW), as well as slope (flat, gentle, moderate, and steep), whenever possible.

#### ***Plot size***

Plot sizes for vegetation survey usually vary based on type of vegetation, environmental gradients and, primarily, the objectives of research. Researchers have used different plot sizes such as 100m by 100m in humid forests (Pyke et al., 2001), 500m by 5m in the western Amazonian forest (Tuomisto et al., 2003), 40m by 10m in the fragmented forests of Hong Kong during (Zhuang and Corlett, 1997), and 20m by 20m to the record natural woody plant understory of monocultural plantations stands in Hong Kong (Lee et al., 2007, 2005). Considering the fragmented nature of the forest in the study area, a sampling size of 20m by 20m was used, to ensure physiognomic uniformity of each plot as demonstrated by Lee et al., (2007, 2005), and Zhuang and Corlett, (1997). Each square plot was further divided into sixteen subplots of 5m × 5m (figure 6.3). Splitting a plot into subplots and recording vegetation census data in each sub-plot gives the possibility of converting the data into other quadrats of different sizes (for example, 10m × 10m, 20m × 10m, or 20m × 5m), which is useful when comparing with other survey data sets (Kindt and Coe, 2010). In order to keep the directional synchronization among all the plots, the orientation of every plot was kept towards North i.e, subplot 1 was always in north-west of a plot (figure 6.3).

### ***Measurements***

A temporary sample plot method was used to tag, measure, identify and record every individual taller than or equal to breast height (1.3m) in each sample plot. Within each sample plot, measurements included the d.b.h (diameter at breast height), number of stems, Cartesian coordinate (X5-Easting, Y5 – Northing) - location of a plant in a subplot, its status (Dead or Alive), and photographs of plants for species identification. Each plant was further categorized as single or multi-stemmed individual. A tree was recorded as single-stemmed individual if its bole was not forked at or below the breast height. In case of multi-stemmed trees, a separate diameter was measured for each stem and the number of stems were noted but the tree was recorded as a single individual.

### ***Species identification***

High quality digital photographs were taken for identification of specimens unidentified in the field. These photographs were identified by the ecologists from Kadoorie Farm & Botanic Garden Corporation (KFBG), Hong Kong. The nomenclature of the plant species followed the Angiosperm Phylogeny Group classification for the orders and families of flowering plants (APGIII, 2009). The life forms and seed dispersal agents of the woody

species were also determined with reference to local literature (Corlett, 1996; Zhuang, 1993).

### **6.2.2. Soil sampling**

Soil sample collection was done in May/June, 2016. Due to limitation of manpower, time and resources, only one representative soil sample was collected from the middle of each of the 28 plots at the depth of 0-20 cm after removal of the surface litter. Physical and chemical characteristics of the topsoil layer provide a vital source of nutrients that play an important role in composition and structure of vegetation communities (Nguyen et al., 2015). The samples were analyzed by ALS-lab (ALS, 2016) to determine the physical and chemical properties of the soil samples. The measured soil characteristics included; texture (sand, silt, clay), pH, organic matter, soil carbon content, soil nitrogen content, and soil moisture.

#### ***Soil pH***

Soil samples were air-dried and sieved through a 2mm test sieve before the analysis and 30g of each sample was weighed in a 100ml beaker. Then 75ml of distilled water was added to the beaker and the suspension stirred for few minutes. The suspension was allowed to stand for at least 8 hours and stirred again before measurement. The pH value was measured by a calibrated pH meter with temperature sensor. The calibrated range of the meter was pH 4.0 to 10.0. pH value of the meter is corrected to 25°C with the temperature measured by the temperature sensor of the meter. The limit of reporting was 0.1 pH unit.

#### ***Soil texture***

The soil samples were washed in water, in different sizes of sieve by water and content of each sieve was dried in an oven. The particle size distribution was determined by weighing soil retained at different sieve sizes. The limit of reporting was 1 %.

#### ***Organic matter***

This procedure covers the determination of the percentage by dry mass of organic matter present in a soil. Potassium dichromate was used to oxidize the organic matter in the sample and the amount of dichromate consumed was used to calculate the

organic matter concentration. The result was reported as % organic matter with reporting limit of 0.1 %.

### ***Carbon content***

The organic carbon content was determined as the proportion of the sample lost by ignition under an elevated temperature of 440°C. The result was reported as % carbon content with reporting limit of 0.1 %.

### ***Nitrogen content***

Organic nitrogen and ammonium nitrogen are reduced to ammonia by using sulfuric acid and presence of copper as a catalyst in the process known as Kjeldahl digestion, and the result is Total Kjeldahl Nitrogen (TKN) and reported as N (%) with reporting limit of 0.01 %.

### ***Moisture content***

The moisture content was determined by drying the soil sample at 105-110°C. The proportion of water lost by mass was reported as the moisture content of the sample. The results were reported as % with reporting limit of 0.1%

### **6.2.3. Topographic variables**

Habitat patterns in mountainous terrain are often influenced by regional climate coupled with micro-climatic conditions induced by topographic factors (Leempoel et al., 2015). Digital Elevation Models (DEM) and DEM-derived topographic variables have been used in many studies as relevant variables in mountain areas to understand ecosystem structure, biophysical processes, and species distribution in a variety of ecosystems (Lassueur et al., 2006; Pumijumnong and Payomrat, 2013; Punchi-Manage et al., 2013; Sann et al., 2016; Sørensen et al., 2006). In order to determine the influence of topography on species distribution patterns in this study, nine topographic variables were computed using the DEM (spatial resolution - 2m), including; elevation, slope, aspect, convergence index, curvature, horizontal curvature, vertical curvature, length of slope factor, topographic wetness index, solar radiation, and altitude above channels.

### ***Slope and Aspect***

Slope is the rate of change in elevation in the direction of steepest descent, and aspect is the orientation of the line of steepest descent (Wilson and Gallant, 2000). Both are the most standard metrics used to explain species distribution patterns. Aspect was computed in degrees clockwise from North, and slope was calculated in degrees from the horizon (Lassueur et al., 2006). Aspect being a circular land surface parameter, it was converted into two continuous gradients, “eastness” and “northness”, by applying sine and cosine transformations. Both transformed variables range from 1 to -1. In “eastness”, values closer to 1 indicate east-facing slopes and values closer to -1 indicate west-facing slopes, while for “northness”, values closer to 1 represent north-facing slopes and values closer to -1 indicate south-facing slopes (Lassueur et al., 2006; Piedallu and Gégout, 2008; Teferi et al., 2013). The trigonometric transformations are critical for using aspect in model development because in a circular variable large values are closer to small values, such as 360° and 0°, which both indicate North (Lassueur et al., 2006).

### ***Solar Radiation***

Solar radiation contributes to the distribution and composition of species or communities through regulating photosynthetic activity, evapotranspiration, surface and air temperatures. Although aspect and slope are considered as proxies to solar radiation (Wilson and Gallant, 2000), they do not incorporate the effects of latitude and sunshine duration, and the same radiation level could occur from different arrangements of slope and aspect (Piedallu and Gégout, 2008). Therefore, incoming total solar radiation was computed for an entire year (Piedallu and Gégout, 2008), as an environmental variable affecting the physiology of plants (Austin, 2002).

### ***Curvature***

Curvatures are second order derivatives that measure the rate of change of first order derivatives, such as slope and aspect, in a particular direction. The two most frequently computed curvature measures are profile curvature (vertical curvature) and plan curvature (horizontal curvature), which are used to define convexity and concavity of surface. Plan curvature measures the rate of change of aspect along a contour which

describes topographic convergence (concave plan curvature) or divergence (convex plan curvature) of water flow across the landscape. Profile curvature measures the rate of change of slope down a flow line which characterizes the relative acceleration (convex profile curvature) or deceleration (concave profile curvature) of flow velocity and material transport processes. A plethora of methods exist to compute curvature from a DEM, however the method of Zevenbergen and Thorne, (1987) was applied to derive profile and curvature raster as this method is considered to be one of the best in many studies (Lassueur et al., 2006). The unit of curvature is  $m^{-1}$ , which means a curvature of 0.01 indicates a curvature radius of 100m, and the sign of curvature is positive for convex surface (ridge) and negative for a concave surface (valley). In this study three curvature measurements, general curvature, vertical curvature and plan curvature were calculated using SAGA, a free open source software (Conrad et al., 2015).

### ***Convergence Index***

The convergence index describes the structure of the relief as a set of convergent areas (streams) and divergent areas (ridges). It is similar to plan curvature but does not depend upon height differences and gives smoother results (Hengl and Reuter, 2009). It calculates the degree to which surrounding cells point to the middle pixel. Negative values correspond to convergent, and positive to divergent flow conditions. The convergence index was also computed using SAGA (Conrad et al., 2015).

### ***Topographic Wetness Index***

The topographic Wetness index (TWI) quantifies the role of topographic control in redistribution of water in a landscape and describes the tendency of a cell to accumulate water, and hence describes the wetness of surface. It is calculated as the ratio of the upslope area from a point to the local slope at that point. Many studies have demonstrated correlation between TWI and soil moisture, soil pH, structure and distribution of species (Pumijumnong and Payomrat, 2013; PUNCHI-MANAGE et al., 2013; SANN et al., 2016; SØRENSEN et al., 2006). Low TWI values represent convex conditions whereas high TWI values represent concave conditions like coves or hill slope bases. The TWI is a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction. It is defined as equation 6.1 (Hengl and Reuter, 2009), and was calculated using Raster calculator in ArcGIS 10.

$$TWI = \ln \frac{A}{\tan(\beta)} \quad \text{Equation 6.1}$$

where,  $A$  is the catchment contributing area at the specific cell, and  $\beta$  is local slope angle expressed in radians.

### ***Length of slope factor***

The length of slope factor (LS factor) describes the combined influence of slope length (L factor) and slope angle (S factor) on soil erosion and deposition in the landscape (Hengl and Reuter, 2009). The S-factor measures the effect of slope steepness, and the L-factor defines the impact of slope length. LS factor is a dimensionless index calculated as a divergence of sediment flow transport capacity (Panagos et al., 2015). The LS factor was calculated using SAGA (Conrad et al., 2015).

### ***Altitude above channel***

The altitude above channel describes the vertical distance to stream network, lines which quantifies topographic control on hydrological processes (Hengl and Reuter, 2009) and is commonly used as a land surface parameter to explain tropical forest assemblages (Kanagaraj et al., 2011; Punchi-Manage et al., 2013). ACH was calculated using SAGA (Conrad et al., 2015).

### ***Selection of Independent Topographic Variables***

A correlation matrix was computed to examine the correlation between each pair of topographic and soil variable (figure 6.4 and figure 6.5) and the specific variables  $|r| > 0.60$  were omitted, primary topographic variables were given preference over the secondary topographic variables, for subsequent analysis to avoid multicollinearity. Finally five independent topographic variables were retained: elevation, northness (cos [aspect]), slope, curvature, and convergence index.

#### **6.2.4. Vegetation data analysis**

Two species data matrices consisting of the species' basal area metrics and species' density metrics were computed from the survey data.

Descriptive statistics of the communities were measured by computing species abundance, richness, diversity, evenness, and important value index (IVI).

### ***Abundance***

Species abundance is referred to the total number of plants occurring in a community.

### ***Richness***

Species richness is represented by the total number of plant species occurring in a community.

### ***Diversity***

Species diversity describes the components of richness and abundance of species in a plant community. It was computed for each site by Shannon's Diversity Index  $H'$  (Magurran, 1988). The equation is

$$H' = -\sum_{i=1}^S (P_i \ln (P_i)) \quad \text{Equation 6.2}$$

where  $P_i$  is the proportion of individuals or the abundance of the  $i$ th species,  $S$  is number of species.

### ***Evenness***

Evenness is a measure of uniformity of species abundance. Evenness indices are used to standardize abundance, and ranges from near 0 when most individuals belong to a few species, to close to 1, when species are almost equally abundant (Smith and Wilson, 1996). The Pielou's evenness index ( $J$ ) was applied to quantify the evenness component of diversity. The equation is

$$J = (-\sum_{i=1}^S (P_i \ln (P_i))) \div \ln S \quad \text{Equation 6.3}$$

where  $P_i$  is the proportion of individuals or the abundance of the  $i$ th species,  $S$  is number of species.

The indices were calculate using 'vegan' package in R (R Core Team, 2016)

### ***Important Value Index (IVI)***

The important Value Index (IVI) determines the overall importance of each species in the community structure. It is calculated by summing the values of relative density, relative dominance, and relative frequency (Curtis, 1959).

Relative density is the study of numerical strength of a species in relation to the total number of individuals of all the species and can be calculated as

$$\text{Relative Density} = \frac{\text{Number of Individuals of Species}}{\text{Total Number of Individuals}} \times 100 \quad \text{Equation 6.4}$$

Dominance of a species is determined by the value of the basal cover. Relative dominance is the coverage value of a species with respect to the sum of coverage of the rest of the species in the area.

$$\text{Relative Dominance} = \frac{\text{Total basal area of the Species}}{\text{Total basal area of all Species}} \times 100 \quad \text{Equation 6.5}$$

Relative frequency refers to dispersion of individual species in an area in relation to the number of all the species which occur.

$$\text{Relative Frequency} = \frac{\text{Frequency of a Species}}{\text{Frequency of all Species}} \times 100 \quad \text{Equation 6.6}$$

### ***Regression Analysis***

Pearson's correlation coefficient was calculated to assess the influence of environmental variables (Topographic variables (table 6.1) , Soil variables (table 6.2), and Age) on species abundance, richness and diversity (table 6.3). Variables having skewed distributions were transformed prior to regression modelling (Bellemare et al., 2002). Furthermore, all possible multiple linear regression models were calculated to investigate the response of each diversity trait (response variables: abundance, richness, diversity and evenness) to the three different categories of the explanatory variables and their combinations. For each category the most parsimonious model was selected using the Akaike Information Criterion (AIC) (Liu et al., 2014). For the combination of the categories (e.g., soil and topography), if the best model was identical to the parsimonious model of the either single category (e.g., topography), then the second best model was chosen for subsequent investigation of the combined effect of the variables. The analysis was performed in R (R Core Team, 2016).

### ***Canonical Correspondence Analysis (CCA)***

Constrained ordination was performed using the canonical correspondence analysis (CCA) to investigate associations of species with the environmental variables (ter Braak and Verdonschot, 1995). CCA determines significant relationship between environmental variables and community distribution by combining direct (regression) and indirect (ordination) gradient analysis that relates community variation, composition and abundance, to the environmental variation (Legendre, 1989). CCA was performed by forward selection of the variables followed by the Monte Carlo permutation test to evaluate additional variance explained by each variable, the significance of the variable and the pseudo F -value (Jongman et al., 1995; Oksanen, 2013). Furthermore, to avoid the multi collinearity problem, the environmental variables with larger variance inflation factors (VIFs),  $VIF > 10$ , were omitted prior to performing the CCA (Oksanen, 2013). The analysis was executed using the 'vegan' package in R (R Core Team, 2016).

### ***Variation Partitioning***

Variation partitioning (Borcard et al., 1992) was performed to quantify the relative importance of each subset of reduced environmental variables explaining the proportion of variation in the species distribution (Baldeck et al., 2016; Lan et al., 2011). The topographic variables include elevation, aspect, slope, convergence index, and curvature, soil variables including carbon content, carbon-nitrogen ratio, and the age variable. Variation partitioning splits the total variation in the species composition into the fractions uniquely explained by each set of variables (for our analysis - topography, soil and age), as well as variance explained by each combination of the explanatory variable set. Variation partitioning can provide insight into the relative contribution of topographic filtering, the effect of soil fertility, and age-dependent ecological processes in shaping community structure (Baldeck et al., 2016). The analysis was performed using the variation partition function, varpart, of the 'vegan' package in R (R Core Team, 2016).

### ***Multivariate Regression Tree (MRT)***

A multivariate regression tree (MRT) approach was used to group the sites with similar species composition (i.e. species assemblage) according to the environmental variables (De'ath, 2002). The MRT is a constrained clustering method based on a recursive

algorithm that explores the relationship among the multi-species data and the influencing environment characteristics (De'ath, 2002). The algorithm determines the threshold of the environmental gradient that splits the sites into two groups by minimizing the within-group species dissimilarity (Larsen and Speckman, 2004). The species abundance matrix was square-root transformed and the sum of squares (Euclidean distance) MRT (SS-MRT) was used for splitting (De'ath, 2002; DeVantier et al., 2006). The tree was pruned by minimizing the cross-validated relative error with the 1-SE rule (De'ath, 2002) that resulted in a tree size of seven. Furthermore, indicator species analysis (Dufrêne and Legendre, 1997) was performed to investigate the statistically significant indicator species (Legendre et al., 2009) which best characterized the groups (De'ath, 2002). The indicator value is defined as the product of relative frequency of occurrence and relative dominance of species within a group (De'ath, 2002). A minimum value of 0 is assigned when a species does not occur in a group, and a maximum value of 1 is assigned when a species occurs in all sites within a particular group and does not occur in any other group (Punchi-Manage et al., 2013). The analysis was performed using the 'mvpart', 'labdsv', and 'MVPARTwrap' packages in R (R Core Team, 2016).

### **6.3. Results**

A total of 8,575 plants of  $\geq 1$ cm DBH belonging to 229 species and 63 families were tagged, measured, identified and recorded in the 28 plots.

#### **6.3.1. Regression analysis**

The Pearson's correlation analysis of species richness with individual environmental gradients showed that richness was highly associated with slope ( $r = 0.31$ ), but the relationship was not statistically significant (table 6.5; figure 6.6). However, species abundance was inversely correlated with elevation ( $r = -0.49$ ,  $p \leq 0.01$ ) and the carbon-nitrogen ratio ( $r = -0.37$ ,  $p \leq 0.1$ ), i.e., abundance decreases towards higher elevations as well as with increasing carbon- nitrogen ratio (table 6.5; figure 6.6). Diversity and evenness were positively affected by elevation ( $r = 0.328$ ,  $p \leq 0.1$ ;  $r = 0.516$ ,  $p \leq 0.01$ ) and carbon-nitrogen ratio ( $r = 0.34$ ,  $p \leq 0.1$ ;  $r = 0.42$ ,  $p \leq 0.05$ ; table 6.5; figure 6.6). However, evenness also showed a significantly positive link with soil organic matter ( $r = 0.33$ ,  $p \leq 0.1$ ; table 6.5; figure 6.6).

Analysis of multiple linear regressions also indicated a strong topographic control on species diversity (table 6.6). Results showed that species richness and abundance were also associated with the age of plots (table 6.4, table 6.6, figure 6.7), and although the contribution was not significant, the overall explanatory power of the models improved (i.e.,  $R^2$  improved from 0.10 to 0.35 for richness ( $p \leq 0.1$ ), and 0.24 to 0.42 for abundance ( $p \leq 0.05$ )). Diversity and evenness were better explained by the addition of soil moisture content to the elevation variable ( $R^2 = 0.24, p \leq 0.1$ ;  $R^2 = 0.34, p \leq 0.05$ ; table 6.6).

### 6.3.2. Canonical Correspondence Analysis (CCA)

Prior to the ordination analysis, the following environmental variables were forward selected based on significance and variance inflation factors: five topographic variables - elevation (Elv), aspect (AspN), slope (slp), convergence index (CI), and curvature (Curv), two soil variables - carbon (C), and carbon-nitrogen ratio (C:N), and one categorical variable - age of sample sites (Age). This combination of variables explained 56.48 % of the total variance in the species composition (table 6.7) and a Monte Carlo permutation test (with 1000 permutations) showed that the vegetation - environment relationships distinguished by all axes were highly significant ( $F$ -value = 1.888,  $p = 0.009$ ; table 6.7). The first axis of the CCA explained 11.73 % of the total variance ( $p = 0.009$ : the Monte Carlo permutation test with 1000 permutations) and was strongly positively correlated with elevation, while the second axis of CCA explained an additional 10.4 % of the variance and showed a positive correlation with aspect and negative correlation with convergence index and curvature (table 6.7). The environmental variables were shown with vectors in the ordination graphs (figures 6.8, 6.9 and 6.10). The length of the vector is proportional to its importance. The angles between the vector and ordination axis indicates its correlation with the axis and the angle between the vectors indicates the correlation between the variables. In addition, age of the forest was positively related to the first axis and negatively associated to the second axis (figure 6.10; table 6.7).

The sample sites at high elevation were clearly distinguishable by their placement at the top right corner of the ordination diagram and are differentiated from rest of the sites due to abundance of species such as *Myrsine sequinii*, *Camela caudate*, *Ligustrum japonicum*, *Eurya nitida*, *Eurya macartneyi*, and *Ilex viridis*. The oldest sites located, at

lower elevation, on the top left side of the diagram are distinguished by abundance of late successional tree species such as, *Cryptocarya chinensis*, *Elaeocarpus chinensis*, and *Choerospondias axillaris*(figures 6.8, 6.9 and 6.10). The remaining sites located in the middle and bottom of the diagram are marked by early or mid-successional species such as, *Psychotria asiatica*, *Aporosa octandra*, *Machilus gamblei*, *Machilus chekiangensis*, *Diospyros morrisiana*, *Machilus breviflora*, *Schefflera heptaphylla*, *Acronychia pedunculata*, *Desmos chinensis*, *Sterculia lanceolate*, *Syzygium hancei*, *Daphniphyllum calycinum*, *Ilex asprella*, and *Garcinia oblongifolia*(figures 6.8, 6.9 and 6.10). Only the abbreviation of the species' name are shown in the diagrams for space limitations, and full names are given Appendix 1.

### **6.3.3. Variation partitioning**

The Venn diagram indicating variation partitioning in species composition among the environmental variables is given in (figure 6.11). The variation partitioning showed that topography and age explained 44 % of the total variation in species composition, whereas, 10 % of the variance is explained by the combination of soil and topographic variables. Soil alone explained only 1 % of the variation in the species composition and the residual variance was 44 % (figure 6.11).

### **6.3.4. Multivariate Regression Tree**

Sites were grouped by MRT based on species composition of the sites and the environmental variable. A tree with seven terminal nodes was selected with splits based on the four explanatory variables (elevation, age, convergence index and curvature (table 6.13, figure 6.12)). Cross-validation relative error of the MRT was 0.86 and the tree explained 64.5 % of the standardized species variance (figure 6.13). Splits were primarily governed by elevation and the age categories. Elevation governed the first split (break point = 467.5) accounting for the 20.88% of species variance. The second major split was determined by the age at the node-3 that explained additional 24.63 % of variance in the species composition (table 6.13, figure 6.12). The total additional variance explained by the other splits was 18.99%. The discriminant species for the first split was *Psychotria Asiatica*, which was the dominant species in the right hand branch of the tree along with *Aporosa octandra* and *Garcinia oblongifolia*. These species also had minimum presence in the left hand branch of the tree (Elv > 467.5 m) and thus did not

contribute to the subsequent splits in that formed groups A and B. Conversely, the left hand branch of the tree was dominated by *Machilus thunbergii*, *Machilus chekiangensis*, and *Myrsine seguinii*, and *Machilus chekiangensis*, with dominant presence on the left hand branch, became the discriminant species to form groups A and B. Similarly, the right hand branch of the tree was split to form the five groups C, D, E, F and G (table 6.13, figure 6.12). Furthermore, indicator species were analysed for all the groups forming the seven trinomial nodes of the tree. For example, group A consisted of two sites (P07 and P10) and three significant indicator species namely: *Melastoma malabathricum*, *Machilus chekiangensis*, and *Machilus pauhoi* (table 6.13), whereas group G contained 3 sites (P25, P26, and P28) and had five significant indicator species namely: *Pavetta hongkongensis*, *Ficus variolosa*, *Rhodomyrtus tomentosa*, *Glochidion wrightii* and *Diospyros morrisiana* (table 6.13 ).

## 6.4. Discussion

The sample sites in this study were very diverse, with elevations ranging from 205 m to 822 m above sea level and a chronosequence of five successional stages ranging from less than fourteen years to greater than seventy years old. For each site, species abundance (the total number of plants occurring in a community), species richness (the total number of plant species occurring in a community), species diversity (Shannon's Diversity Index - describes the components of richness and abundance of species in a plant community) and species evenness (Pielou's evenness index - a measure of uniformity of species abundance) were calculated and their relationships with the environmental variables were analysed. Canonical correspondence analysis (CCA) and multivariate regression tree (MRT) analysis were performed to determine the influence of the environmental variables on species composition. In addition, variation partitioning was computed to investigate the relative importance of the environmental variables in explaining the variation in the species distribution.

Environmental conditions can influence species diversity positively, negatively or the association can follow a unimodal relationship. Strong evidence of topographic control on species abundance, richness, diversity, and composition was observed. Notably, species abundance decreased towards the higher elevation due to presence of large boulders and exposed soil but species diversity increased with elevation although the species richness did not vary significantly. Zhuang and Corlett, (1996) also documented higher species diversity of secondary forest in the uplands of Hong Kong and attributed the higher species diversity to inaccessibility and least effect of human impact.

A number of studies have shown the influence of topographic variables on species distribution (Eilu et al., 2004; Lan et al., 2011; Liu et al., 2014; Lovett et al., 2001; PUNCHI-MANAGE et al., 2013). In this study, elevation and curvature among the topographic variables were the main drivers of distribution patterns of species. Species richness and diversity were significantly influenced by topography indicating an impact of habitat filtering at local community scale, supporting the fundamental hypothesis of environmental filtering in community assemblage in tropical forests (Taylor et al., 1990). Similar observations were also documented by Liu et al., (2014) in tropical forest in southwest China. During the re-colonization process of secondary succession, different environmental conditions can lead towards different combinations of species

composition that can be further filtered by seed dispersion processes or seed competition (Hubbell, 2001; Lebrija-trejos et al., 2015).

Among the topographic variables, species richness appeared to be related to terrain slope although the relationship was not significant. During the field observations it was observed that the gentle slopes had been used for agriculture as indicated by presence of terraces, whereas the steeper slopes were not suitable for agricultural practices and therefore were more diverse in species richness. However, richness followed the 'hump-backed curve' as richness reached a maximum at an intermediate time interval since the last disturbance i.e., since 1945, and declined to the present time. Lugo and Helmer, (2004) also observed lower species richness in abandoned shade coffee than in secondary forest regenerating from previous cut over or disturbed stands. These observations are also supported by an experimental study on effect of disturbance frequency by Collins et al., (1995) that showed a significant monotonic decay in species diversity with rising frequency in the experimental disturbance.

Species diversity also tended to increase as the C:N ratio increased, as observed from the significant positive relation between species diversity and C:N. The observed increase in species diversity as well as C:N was also noted by Nadeau and Sullivan, (2015), who documented an increase in plant biodiversity with rising C:N in a mature tropical forest of Costa Rica. Generally, tropical forest ecosystems with higher species diversity tend to have poor soil and lower fertility (Huston, 1980; Peña-Claros et al., 2012). In these ecosystems, highest species richness occurs under poor growth conditions (Huston, 1980) as nutrient-poor soil (leached due to the chemical weathering under high temperature and rainfall (Tilman et al., 1996)) does not allow dominance of a few species. Instead, opportunistic competition is set up, whereby the fittest species to survive the impoverished environment, compete for survival (Huston, 1979). On the other hand, nutrient rich soil enables faster growth rates that allow a rapid competitive exclusion and thus species diversity is reduced due to a dominance of fewer species (Huston, 1979). Furthermore, in poor soil condition, a species-rich decomposer web of bacteria, fungi and soil mesofauna acts as an effective filter retaining the nutrients being leached by rainwater and thus avoiding nutrient loss (Tilman et al., 1996). The plants also retain and recycle nutrients, minimizing nutrient loss and so the leaf litter is usually poor in N and other nutrients. This suggests that most

of the nitrogen and nutrients are taken up by the plants as they are intercepting and taking up nutrients at the moment they are released by decomposition (Terborgh, 1992). Therefore carbon, being a product of plant decomposition, will thus be high relative to the nitrogen (Nadeau and Sullivan, 2015).

The chronosequence of basal area along successional stages can increase asymptotically or peak at an intermediate stage (Guariguata and Ostertag, 2001). In this study the increase in basal area followed the asymptotic pattern (figure 6.6; table 6.4), which is similar to the pattern observed by Denslow, (2000) during the secondary forest succession in Panama. On the other hand species richness and abundance were positively correlated, and followed the 'intermediate disturbance hypothesis' of Connell, (1978) which is indicated by a 'hump-backed curve (Pausas and Austin, 2001)' in figure 6.6. The curve is marked by a steady increase in basal area during earlier successional stages to a maximum value at an intermediate stage (when the site age was ~ 50 years), it then fell in later successional stages (figure 6.6; table 6.4). This chorosequence pattern of basal area is contrary to 'succession models (Peet, 1992)' which suggest an asymptotic increase to maximum species diversity as observed by Saldarriaga et al., (1988) in the recovering forest of Colombia and Venezuela.

On the other hand, Zhuang, (1993) documented the highest species richness in Hong Kong's oldest sites of feng shui woods (maximum species richness was 40). In this study, species richness of the single site studied in fung shui woods was found to be similar that reported by Zhuang, (1993) but seven sites in lowland and highland secondary forests had species richness above 40 out of which three had more than 50 species (table 6.3). Also, the species richness in the other three sites in the oldest forest patches, more than seventy years older, was significantly lower than the sites at intermediate successional stages (table 6.3). These difference could arise due to change in successional stage over a period of ~ 25 years, the time difference between this study and Zhuang's, (1993) study, or due to differences in locations of sampling sites and study area.

Elevation did not appear to have a significant effect on the recovery of forest structure, but it had a strong influence on species composition. Both the constrained ordination and the regression tree classifications indicate that elevation (break point at elevation of 467.5 m) clearly define two different types of flora within similar successional stages.

There are two parallel successional trajectories clearly divided by elevation and the two different types of floristic composition are evident in the constrained ordination and the regression tree. At lower elevations species ordination (figure 6.8) shows a floristic trend from light-demanding pioneers, such as *Aporosa octandra*, *Sterculia lanceolate*, *Acronychia pedunculata*, *Daphniphyllum calycinum*, *Schefflera heptaphylla*, *Sapium discolor*, *Diospyros morrisiana*, *Ficus variolosa*, *Psychotria asiatica*, and *Ardisia quinquegona*, to the large dominant species in older sites such as, *Sarcosperma laurinum*, *Bischofia jananica*, *Cryptocarya chinensis*, *Elaeocarpus chinensis*, and *Choerospondias axillaris*. Whereas the higher elevations were first colonized with species such as, *Machilus chekiangensis*, *Gordonia axillaris*, *Melastoma malabathricum*, and *Eurya chinensis*, and later dominated by species such, as *Myrsine seguinii*, *Machilus breviflora*, *Ilex viridis*, *Camellia caudata*, *Symplocos sumuntia*, and *Ligustrum japonicum*. Similar patterns of parallel forest recovery along the elevational gradient were also observed by Aide et al., (1996) in the abandoned pastures of northeastern Puerto Rico.

The floral classification in the study area is mainly due to the absence or enormous decrease in diversity of tropical families, such as Rubiaceae, Myrtaceae, Malvaceae and Araliaceae, and several notable tropical species such as, *Aporosa octandra*, *Sterculia lanceolate*, *Psychotria asiatica*, and *Ardisia quinquegona*, and *Acronychia pedunculata*, in the higher elevation forests. The altitudinal break point of floristic composition of Hong Kong's mountain flora may have been defined by the damage caused by frost events. During a recent cold spell in January 2016, the temperature dropped to  $-6^{\circ}\text{C}$  recorded at 950m on Hong Kong's highest mountain, Tai Mo Shan. Coincidentally, during the time when the frost event occurred, field data collection for this study was on-going and an exclusive field visit was undertaken to perceive impacts of frost on the vegetation. Field observations during mid-February and in April/May 2016 revealed extensive damage to the vegetation beginning at 400 m and increasing with altitude. Above 600 m even large and mature individuals of *Mallotus paniculatus*, *Litsea ssp.*, *Canarium album*, *Schefflera heptaphylla*, *Ficus ssp.*, *Garcinia oblongifolia*, *Carallia brachiata* and exotic trees such as *Acacia confusa*, *Eucalyptus ssp* and, *Lophostemon confertus* were being partly or completely defoliated, and suffered major branch die-back to the main branches. On exposed sites they were either completely killed or died back to the root system. The high degree of frost damage observed above 600 m and a high return frequency of frost explains the absence of tropical taxa and the presence of more temperate floristic

elements including deciduous species at this altitude, and indicates a transition zone from tropical to subtropical between 400 m to 600 m in Hong Kong's vegetation (Ge et al., 2015). Corlett, (1992) also documented the impacts of a cold spell in December 1991 on Hong Kong's mountain flora, when temperatures at Tai Mo Shan fell to  $-4.7^{\circ}\text{C}$  for a period of 26 hours. He also observed extensive frost damage in species whose main distribution was in tropical lowlands south of Hong Kong, although these were actually native species. As outlined previously by Ge et al., (2015) a higher frequency of frosts would favour deciduous species, which are more resilient to frost and in the long run would eliminate evergreen forests above 600 m in Hong Kong.

After the major division by the elevation and successional stages, the composition of lowland forest was further explained by elevation and terrain curvature as indicated by ordination and the regression tree (figure 6.8 and figure 6.12). The combination of elevation and curvature explained  $\sim 15\%$  of the total variance in species composition (figure 6.2). This is comparable to 25 % variance in species composition which was explained by topography in a 25 ha plot at Sinharaja tropical rain forest in Srilanka (Punchi-Manage et al., 2013).

Although environmental factors partially explained the species composition, it was interesting to note that topography and the age of sites exclusively explain 44 % of the variation in species composition. The association of topography with species composition is also reported in the Xishuangbanna tropical forests in southwest China (Lan et al., 2011; Liu et al., 2014) and wet lowland tropical forest in Amazonian Ecuador (Valencia et al., 2004). In this study, elevation determines the major split between low elevation and high elevation flora while age explain the changes in species composition along the successional gradient. However, neither the regression tree nor the variation partitioning indicated that soil was exclusively responsible for species distribution, as soil alone explained only 1 % of the variance in the species composition. Therefore, elevation followed by successional stage remain the main determining factors of changes in species composition. However, the residual variation i.e. 44 % of the variation in species composition, was not explained by either topography, soil or successional stage, which indicates an influence of unknown elements on ecological processes that may be attributed to deterministic variation caused by unmeasured environmental constraints (Jones et al., 2008), spatially controlled biological processes

limited by seed dispersal mechanisms (Karst et al., 2005; Lan et al., 2011) or extensive land use history (Bellemare et al., 2002)

## 6.5. Conclusion

Vegetation community data at species level from 28 sample sites were analysed along topographic, soil and successional gradients to examine the importance of different environmental factors on species assemblages in the secondary forest in the tropical degraded landscape of Hong Kong. Successional stages and elevation played an important role in the distribution of species in the study area which should be taken into account while designing management strategies for secondary forest restoration. Although the secondary forest has attained a species richness comparable to or greater than the old growth forest sites, their composition is very different from the old growth forest stands in the study area. Almost all the secondary forest sites lack the presence of late successional tree species, such as *Cryptocaria chinensis* and *Sarcosperma laurinum* which can grow under shade. Such results clearly show that there is an urgent need to introduce the late successional species either by facilitating natural succession or by artificial enhancement planting. Indeed, common forestry practices of planting low diversity stands of cash crops on a landscape scale can not provide the required diversity and may be in need of urgent reconsideration. Large parts of the tropics and subtropics have suffered badly from deforestation over recent decades, resulting in depauperate vegetation communities often without sufficient seed sources available for natural recovery into diversity-rich ecosystems (MacDicken et al., 2015). In such cases, there is an urgent need to artificially enhance diversity by planting pockets of high diversity, which will act as seed sources for natural recovery in the future. As forest is the climax vegetation of Hong Kong, the inevitable decline in habitat diversity observed in this study, as succession proceeds to closed forest, may be viewed as a natural and desirable first step in restoration of the ecosystem. However, the absence of specialist forest fauna may be an issue in the future structure of this regenerated landscape, especially since the shade-tolerant, later successional forest species have poor dispersal abilities. Therefore, to manage natural succession and to guarantee enough genetic diversity in Hong Kong's newly establishing forests, climax trees may be planted strategically in carefully selected plots where the oldest forest pioneers are established. Although it may not be possible to restore the ecosystem to pre-disturbance conditions

or the original species composition, the ecosystem may follow a different pathway of equilibrium, particularly in the absence of native fauna, seed dispersal agents and the altered surrounding environment. For examples, Lugo and Helmer (2004) observed new species composition dominated by alien species in the naturally recovering secondary forest on abandoned lands in Puerto Rico and the soil in the emerging forest was characterised with lower carbon content and higher bulk density. In New England, species compositions of recovering secondary forests on post-agriculture abandoned lands were observed to be persistently different from primary forests (Bellemare et al., 2002). Thus, restoration efforts can be directed towards developing a functional and sustainable secondary forest ecosystem that requires further in-depth studies such as this, to determine and understand the functions and successional trajectories of recovering forest.

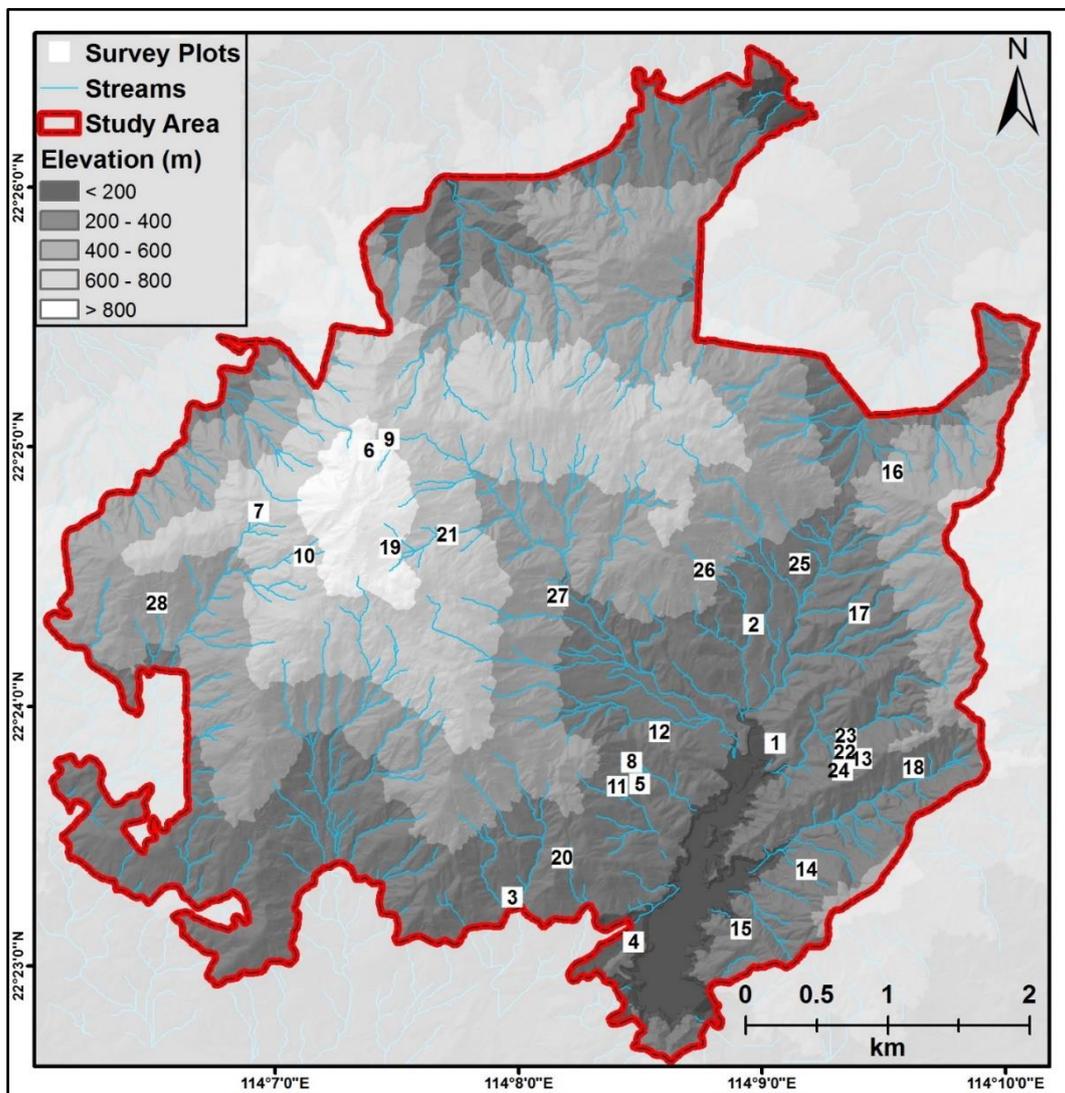
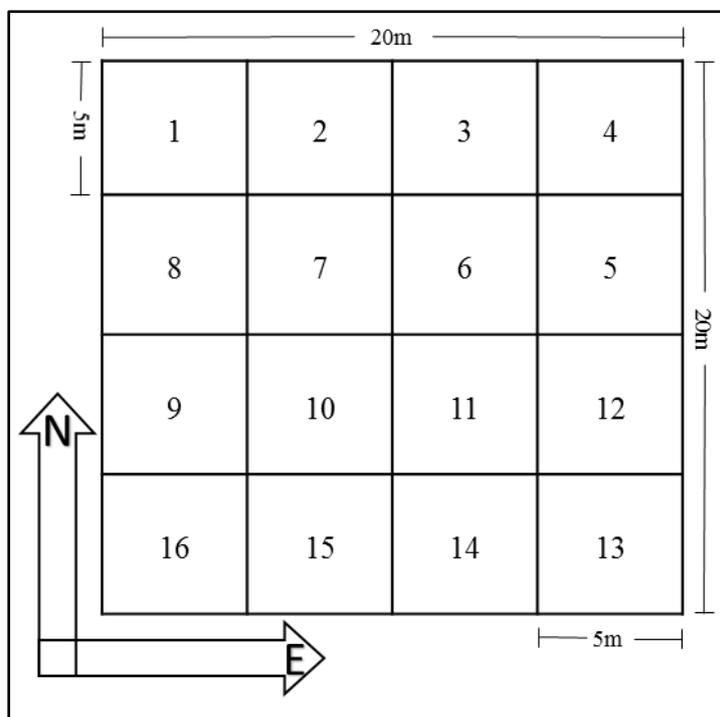
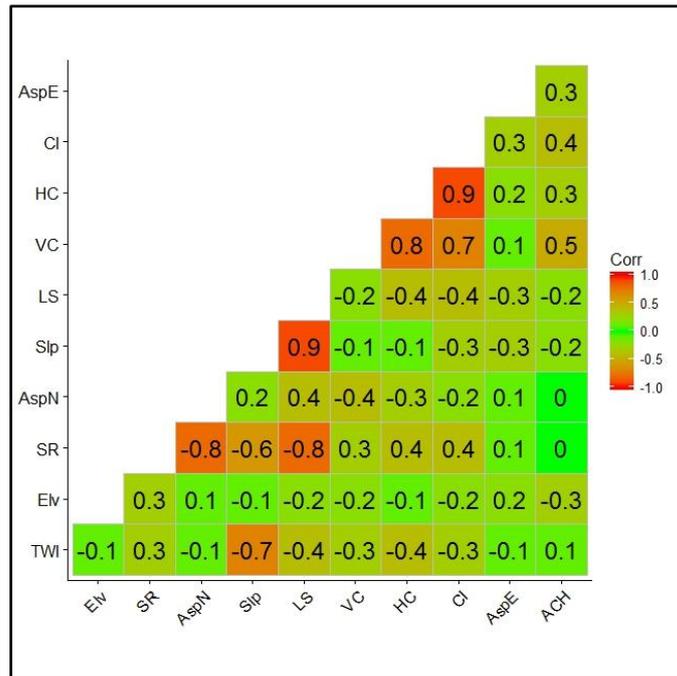


Figure 6.2 Locations of sample sites

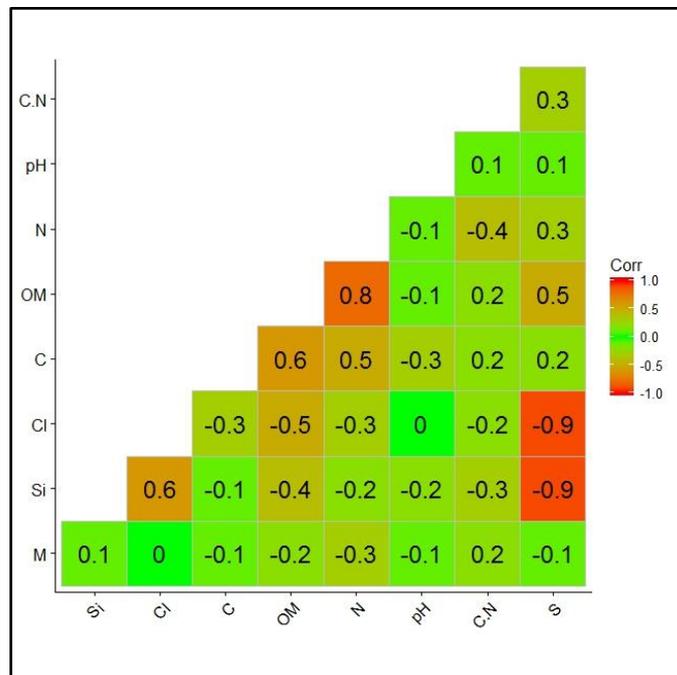


**Figure 6.3** Layout design of each sample site (20m × 20m) with 16 subplots (5m × 5m)



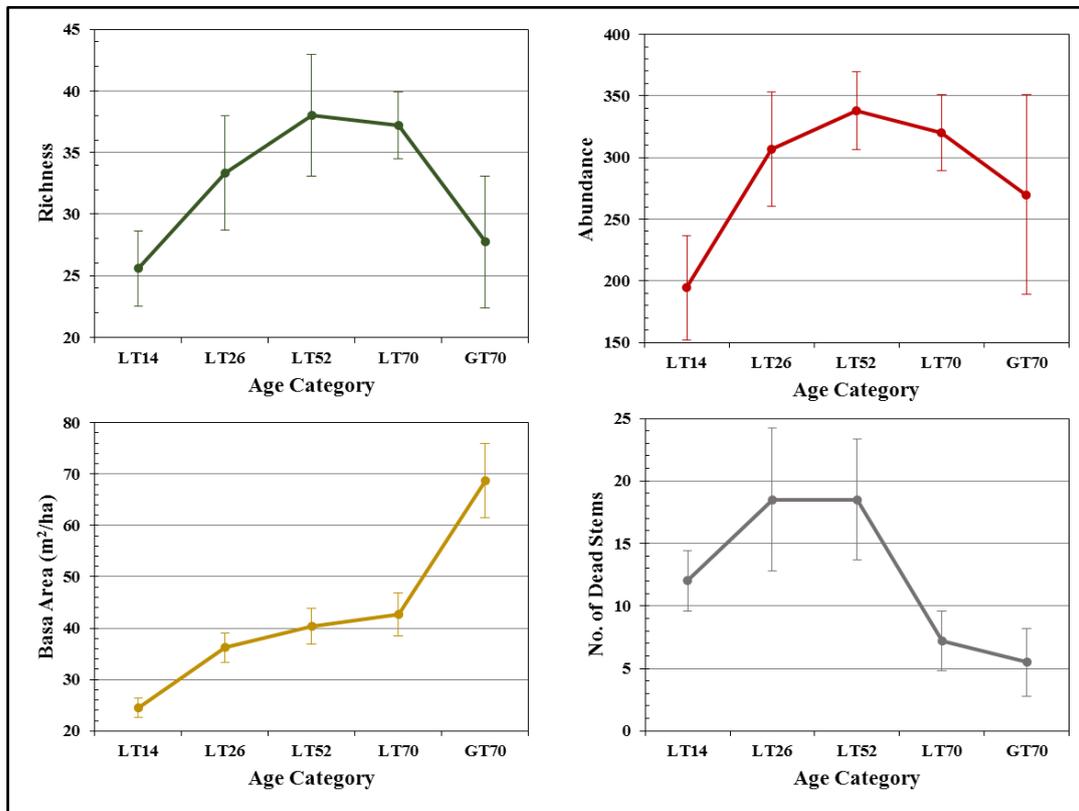
**Figure 6.4** Pair-wise correlation matrix plot of topographic variables

*AspN = northness (cos of aspect), AspE = eastness (sin of aspect), ACH = altitude above channels, Slp = slope, Elv = elevation, LS = length of slope factor, SR = solar radiations, TWI= topographic wetness index, VC= vertical curvature, HC = horizontal curvature, CI = convergence index*



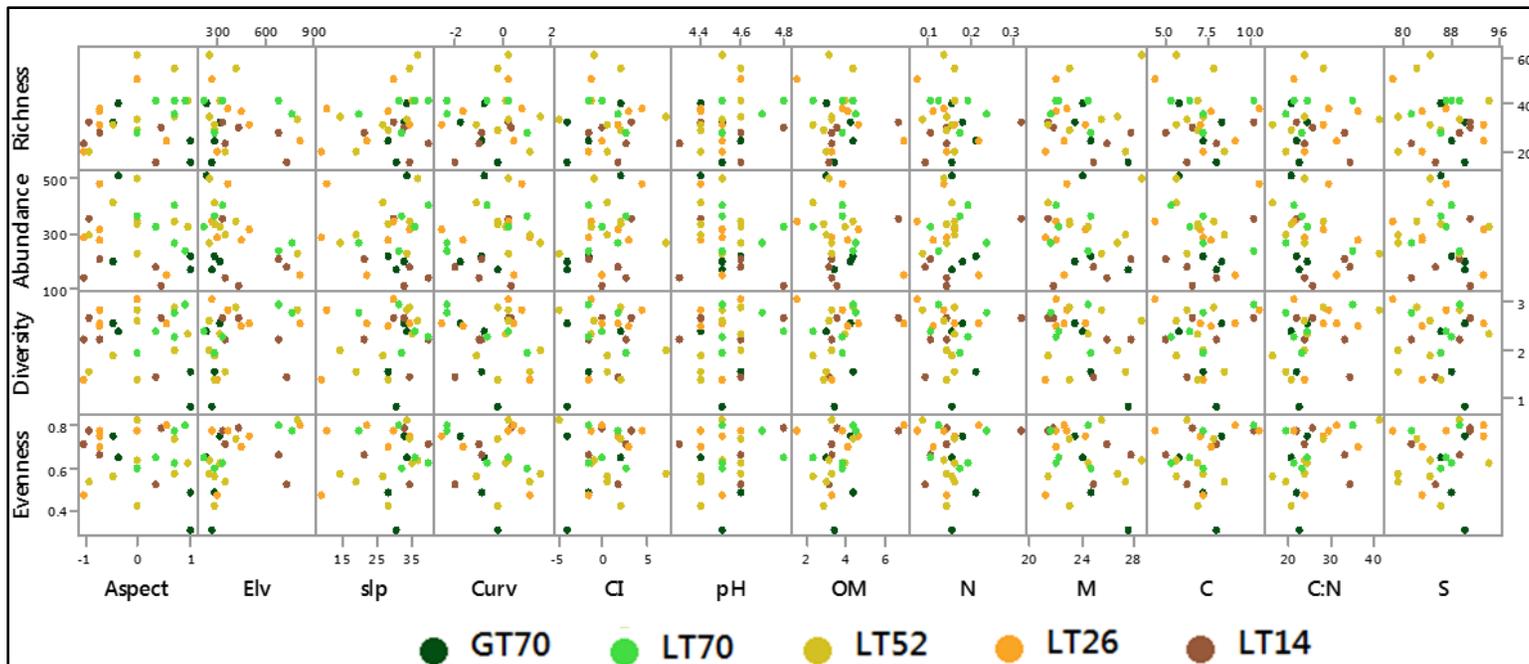
**Figure 6.5** Pair-wise correlation matrix plot of soil variables

*OM= organic matter, N = nitrogen content, C = carbon content, C:N = Carbon Nitrogen ratio, M = moisture content, S = sand, Si= Silt, Cl = Clay*



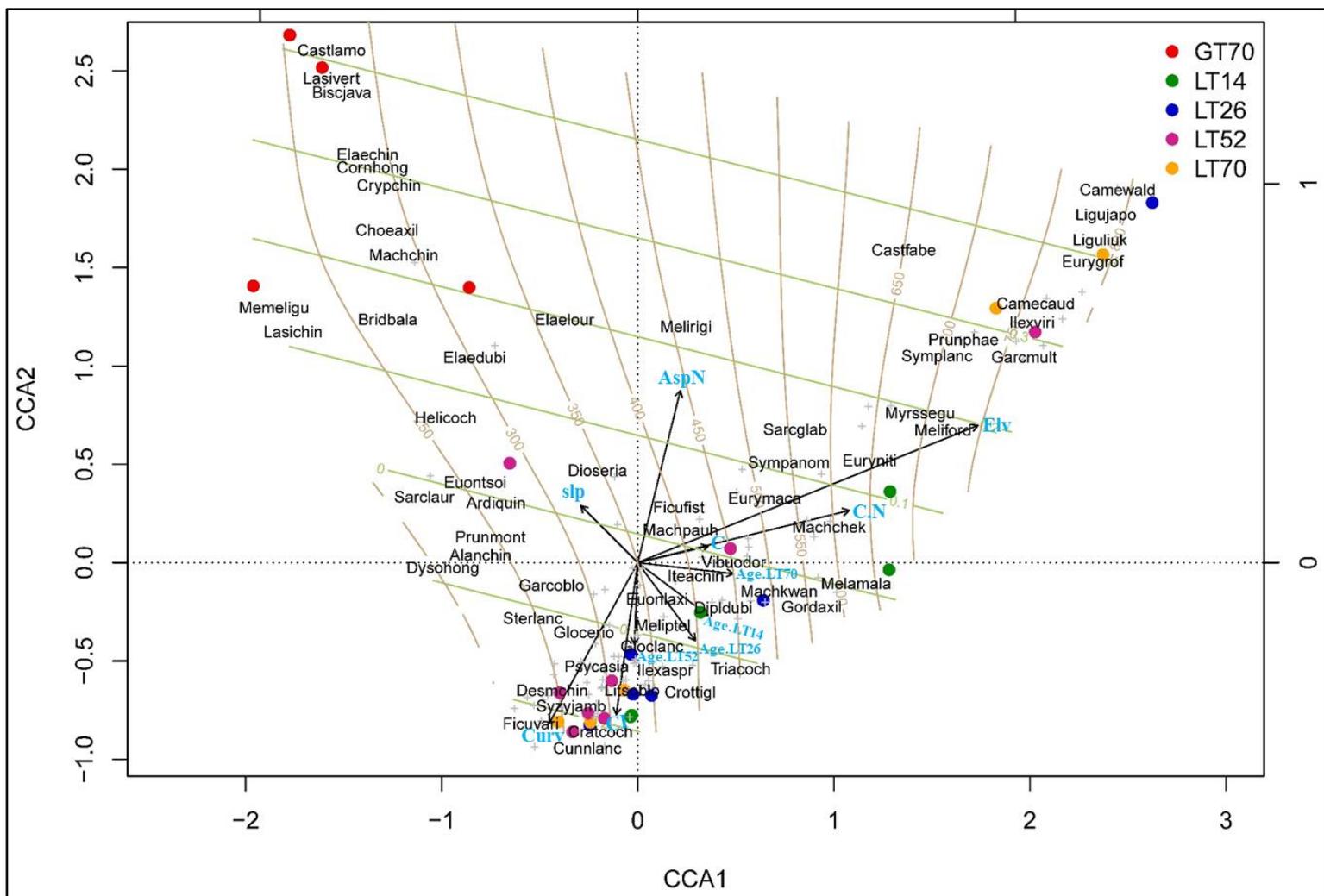
**Figure 6.6**Chronosequence of species richness, abundance, Basal Area and No of dead stems

*GT70 = greater than 70-year old forest (forest since 1945), LT70 = less than 70-year old forest (forest since 1963) LT52 = less than 52-year old forest (forest since 1989), LT26 = less than 26-year old forest (forest since 2001), and LT14 = less than 14-year old forest (forest since 2014)*



**Figure 6.7** Matrix plot between community traits and the environmental variables

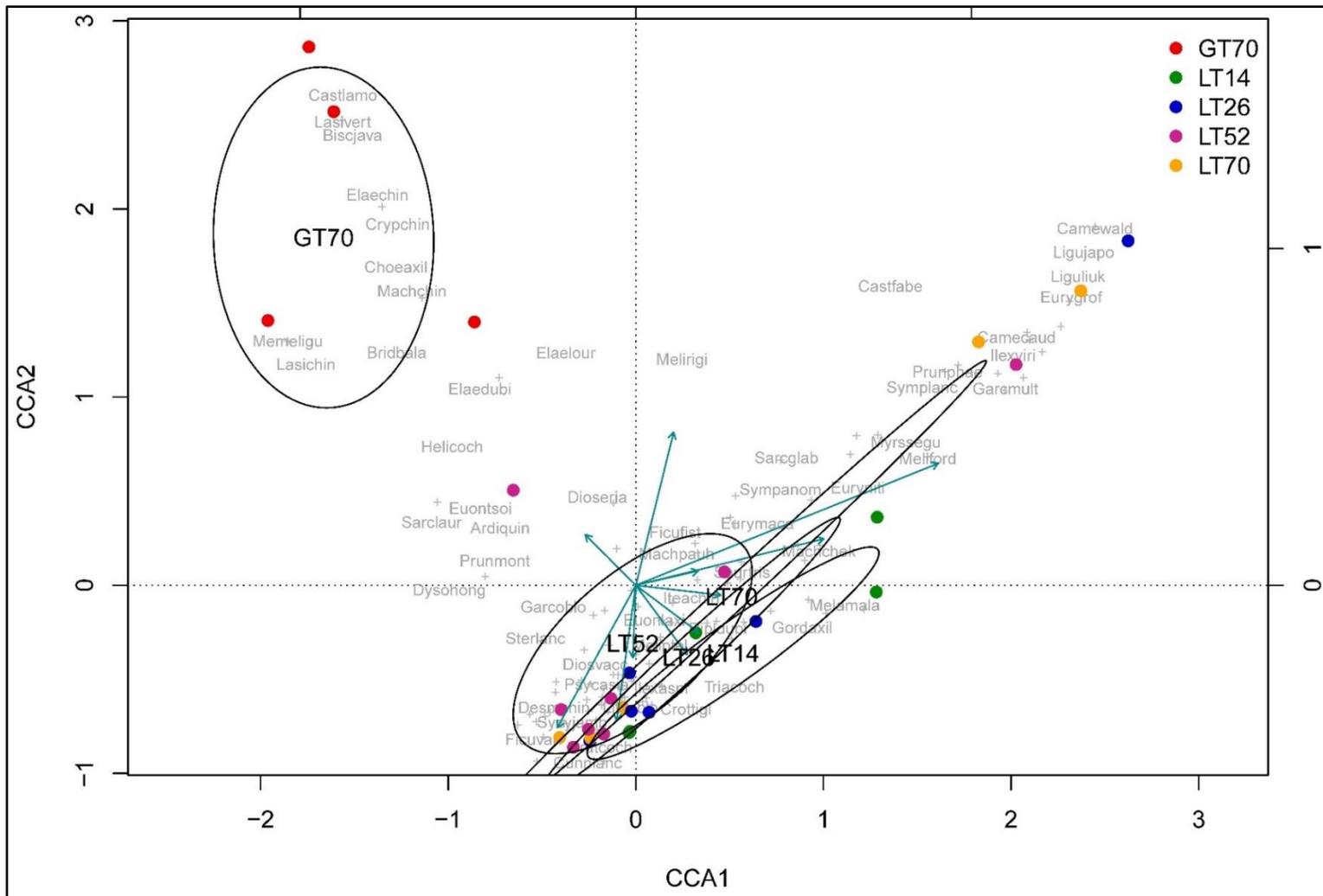
*Diversity = Shannon Diversity Index, Evenness = Pielou's Evenness Index. Aspect = northerness (cos of aspect), slp = slope, Elv = elevation, Curv = Curvature, CI = convergence index, OM= organic matter, N = nitrogen content, C = carbon content, C:N = Carbon Nitrogen ratio, M = moisture content, S = sand, GT70 = greater than 70-year old forest (forest since 1945), LT70 = less than 70-year old forest (forest since 1963) LT52 = less than 52-year old forest (forest since 1989), LT26 = less than 26-year old forest (forest since 2001), and LT14 = less than 14-year old forest (forest since 2014)*



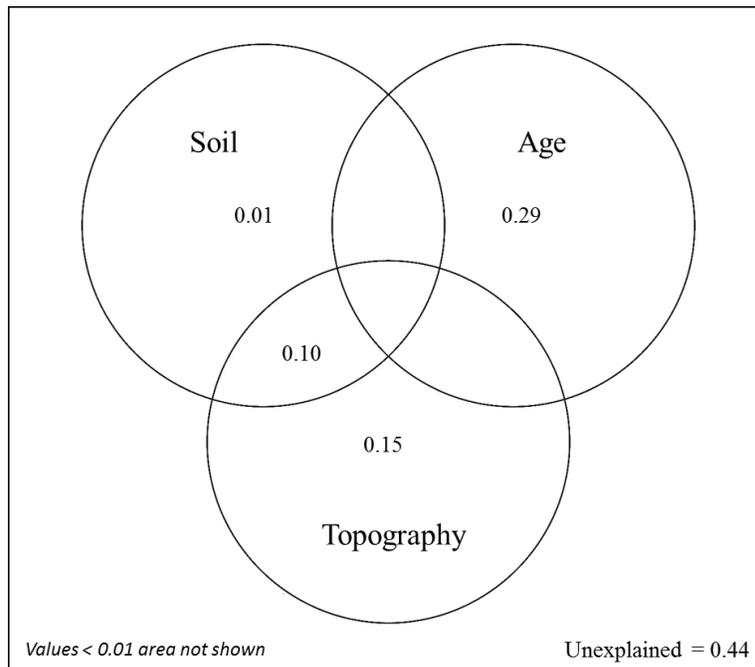
**Figure 6.8** CCA ordination diagram-1 showing the relationship of species with the environmental variables

Green horizontal lines indicate Aspect surface whereas vertical brown lines indicate elevation surface. Sites are shown with filled circles of different colors corresponding to age of the site, and species are shown by "+" sign in grey color overlaid with abbreviated names of dominant species. A complete list of full names and abbreviations is given in Appendix 1.

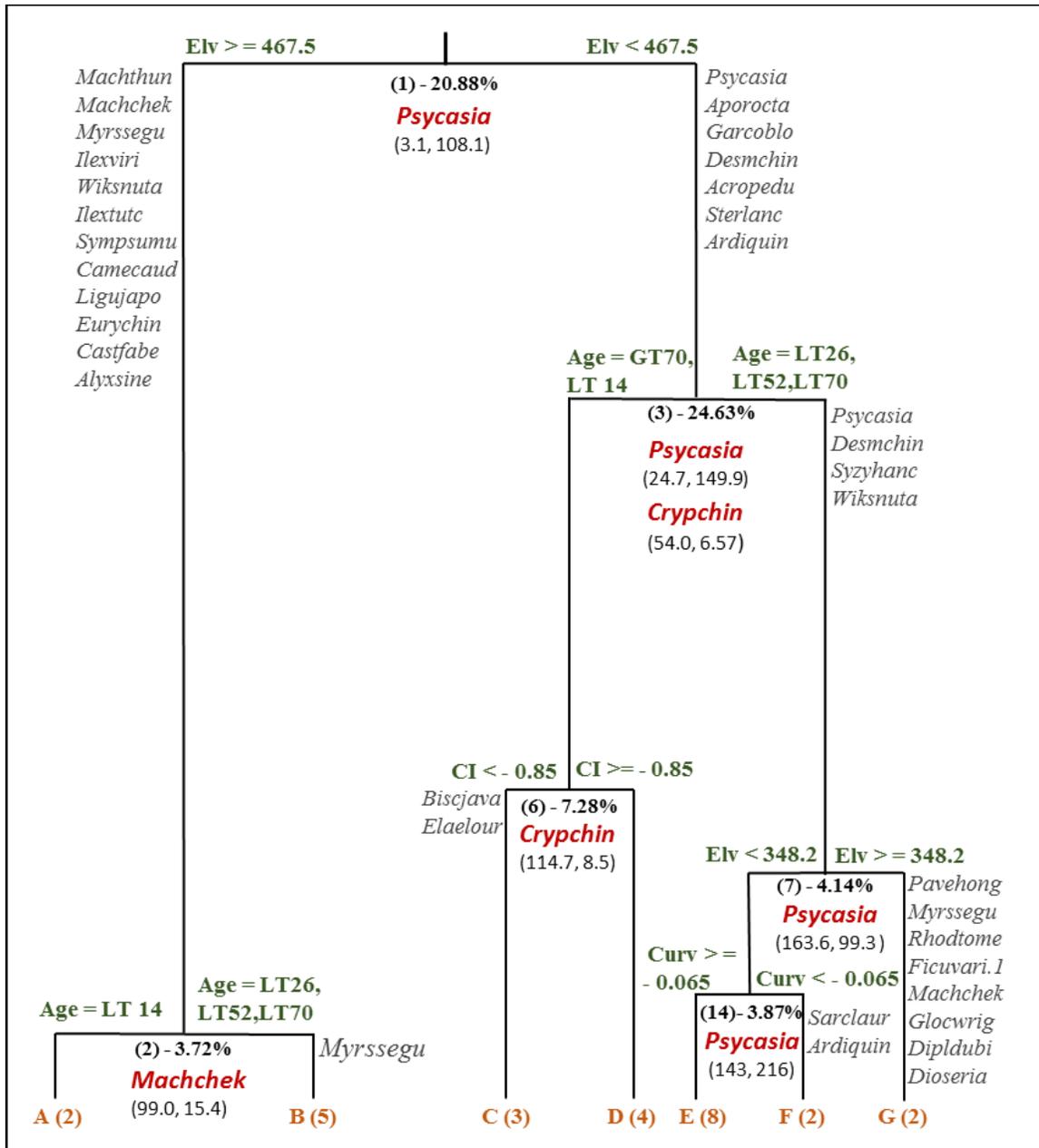




**Figure 6.10** CCA ordination diagram-3 showing the relationship of species with the environmental variables, with sites names ellipsoids of age categories

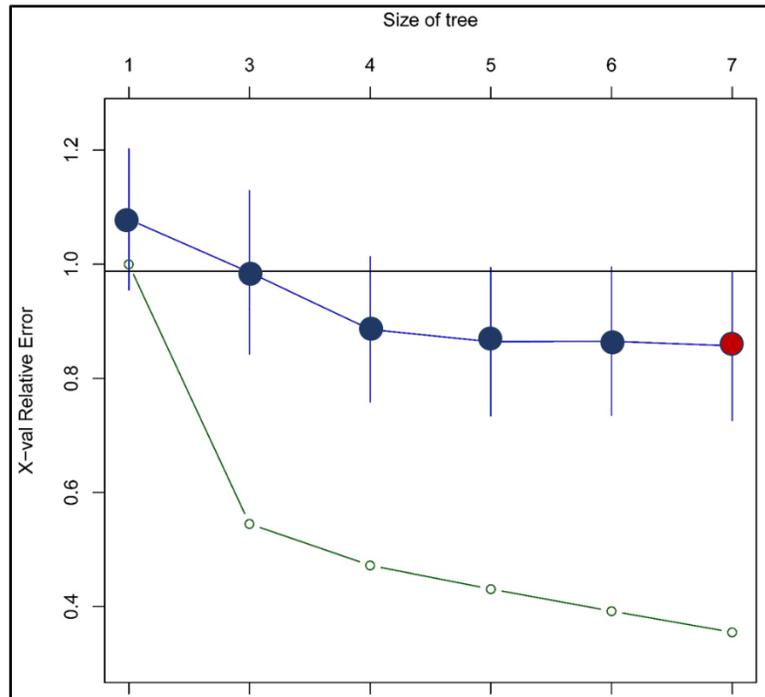


**Figure 6.11** Portioning of the variation of species explained by topography, soil and Age



**Figure.6.12** Multivariate regression tree analysis

The species abundance matrix was square-root transformed and Euclidean distance was used for splitting. Variation explained by each node is given under the node, breakpoints of explanatory variable at every leaf of the node are in green font, significant indicator species at each node are mentioned on the left and the right of the node and discriminant species at the node is also given in italic and red font. Final partitioning cluster are indicated with letter A to G with number of site in bracket. (Variation Explained (R<sup>2</sup>): 64.5 % ; Variation not Explained (Error): 35.5 %; Cross Validation Relative Error (CVRE) : 0.857 ; Standard Error (SE) : 0.131.A complete list of full names and abbreviations is given in Appendix 1



**Figure.6.13** Selection of the tree was made by 1-SE rule.

The relative error (green line with open circles) decreases with the tree size, whereas the cross-validated relative error (filled circles) decreases to a minimum for a tree size of seven. The solid black line indicates one standard error above the minimum cross-validated relative error.

**Table 6.1** Topographic characteristics of the sample sites

<b>Plot No</b>	<b>AspN</b>	<b>AspE</b>	<b>ACH</b>	<b>Slp</b>	<b>Elv</b>	<b>LS</b>	<b>SR</b>	<b>TWI</b>	<b>VC</b>	<b>HC</b>	<b>CI</b>
	--	--	m	degree	m	--	Wh/m2	--	m <sup>-1</sup>	m <sup>-1</sup>	--
P01	-0.37	-0.93	2.37	33.78	215.46	6.59	1506860	2.51	-0.01	0.03	1.91
P02	-1.00	0.00	13.16	8.90	292.96	1.32	1671920	6.23	0.00	-0.01	-1.74
P03	0.71	0.71	12.17	14.37	241.68	3.19	1537290	3.48	0.01	0.03	7.02
P04	0.37	-0.93	16.34	35.55	205.12	8.12	1300560	2.79	0.00	0.00	-0.18
P05	0.00	1.00	6.75	31.94	266.01	6.37	1334850	2.45	0.02	0.05	2.53
P06	0.55	0.83	5.57	21.56	822.56	5.20	1589870	2.97	-0.02	0.00	-0.09
P07	-0.71	-0.71	1.53	21.37	682.45	2.92	1749210	3.87	-0.01	-0.02	-1.55
P08	-0.45	0.89	3.77	26.54	265.53	5.20	1556200	3.05	-0.01	0.00	0.44
P09	0.71	0.71	1.70	19.65	776.25	3.37	1553360	3.12	0.01	0.02	1.70
P10	0.37	-0.93	2.03	34.24	746.55	6.87	1400560	2.37	-0.01	0.03	1.75
P11	0.71	0.71	13.51	39.50	328.44	10.89	1158790	2.86	0.01	-0.04	-1.78
P12	0.00	1.00	5.50	28.37	271.18	5.09	1465750	3.05	0.01	0.03	2.12
P13	-0.45	-0.89	1.32	33.07	313.19	10.49	1403860	4.04	-0.01	-0.06	-3.92
P14	0.00	-1.00	3.11	29.62	260.23	7.75	1429680	3.34	-0.01	-0.02	-1.22
P15	0.00	-1.00	5.70	36.35	245.49	9.75	1342120	3.39	-0.02	-0.03	-1.17
P16	0.45	-0.89	0.89	32.85	433.93	8.15	1289160	2.71	-0.01	0.00	-0.13
P17	-1.00	0.00	8.33	39.44	337.27	7.65	1485430	1.79	0.03	0.06	2.47
P18	-0.89	-0.45	4.09	29.68	319.82	6.52	1636960	2.67	0.01	0.06	3.34
P19	0.00	1.00	1.84	33.81	815.45	6.56	1550440	3.42	-0.06	-0.07	-4.87
P20	-0.89	0.45	11.04	18.86	336.66	3.34	1691800	3.24	0.00	0.01	0.48
P21	0.93	0.37	3.01	30.97	686.64	8.59	1266130	3.44	-0.03	-0.03	-1.56
P22	1.00	0.00	2.84	28.28	269.92	7.51	1188110	3.73	-0.04	-0.03	-1.57
P23	1.00	0.00	1.09	30.33	254.08	8.68	1174000	3.69	-0.05	-0.06	-3.94
P24	0.95	0.32	5.70	34.90	309.32	8.27	1122910	2.61	-0.03	-0.03	-1.31
P25	-0.71	0.71	14.99	10.29	359.75	2.14	1695270	4.35	0.00	0.04	4.48
P26	-0.71	0.71	5.05	28.48	446.12	5.92	1581260	2.27	0.02	0.04	2.93
P27	0.71	0.95	17.97	34.40	415.75	7.68	1331730	2.41	0.02	0.05	2.13
P28	-0.71	0.71	3.17	33.96	488.96	7.22	1599330	2.55	0.01	0.03	1.69

*AspN = northness (cos of aspect), AspE = eastness (sin of aspect), ACH = altitude above channels, Slp = slope, Elv = elevation, LS = length of slope factor, SR = solar radiations, TWI= topographic wetness index, VC= vertical curvature, HC = horizontal curvature, CI = convergence index*

**Table 6.2** Soil characteristics of the sample sites

Plot No	pH	OM	N	C	C:N	M	S	Si	Cl
	pH unit	%	%	%	--	%	%	%	%
P01	4.4	3	0.15	5.7	19.9	24	86	6	8
P02	4.5	3.3	0.14	7.2	23	21.1	83	10	7
P03	4.6	3.2	0.14	7.2	23	26.6	79	12	9
P04	4.8	2.3	0.1	6.4	24	22.1	87	6	7
P05	4.5	3.8	0.17	7.1	22.4	24.6	86	6	8
P06	4.5	6.9	0.22	9.1	31	22.6	93	4	3
P07	4.6	3.2	0.1	4.9	33	27.8	89	4	7
P08	4.4	2.3	0.15	5.5	15.7	21.3	84	8	8
P09	4.7	4.5	0.24	7.2	19	21.5	81	8	11
P10	4.6	3.1	0.09	6.2	34	24.8	85	8	7
P11	4.5	3.8	0.19	5.2	20.5	22	88	6	6
P12	4.4	2.8	0.14	6.9	20.2	23	86	8	6
P13	4.5	4.2	0.18	8.3	23.6	23.3	90	6	4
P14	4.6	1.5	0.07	4.3	20.9	21.9	78	8	14
P15	4.5	3.1	0.13	5.5	23.4	28.5	84	8	8
P16	4.8	3.5	0.14	6.5	25	21.7	91	4	5
P17	4.3	3.2	0.14	8	23	25.9	81	10	9
P18	4.4	6.7	0.32	10.3	21	21.3	91	4	5
P19	4.5	3.2	0.08	6.2	41	25.5	89	4	7
P20	4.4	2.9	0.16	8.4	19	27.2	79	10	11
P21	4.5	4.3	0.12	10.2	35	24.5	89	4	7
P22	4.6	4.4	0.21	7.2	21.4	24.6	88	6	6
P23	4.5	3.4	0.15	8	22.1	27.6	90	6	4
P24	4.6	3.9	0.16	6.9	23.7	24.3	94	2	4
P25	4.4	3.8	0.13	10.5	29	22.8	87	6	7
P26	4.4	4.1	0.11	7.7	36	21.9	83	8	9
P27	4.6	4.3	0.16	7.8	27.7	22.9	82	8	10
P28	4.5	4.6	0.16	7	28	24.1	93	2	5

*OM= organic matter, N = nitrogen content, C = carbon content, C:N = Carbon Nitrogen ratio, M = moisture content, S = sand, Si= Silt, Cl = Clay*

**Table 6.3** Community traits of the sample site.

Sites	Richness	Abundance	Diversity	Evenness	Basal Area (m <sup>2</sup> /ha)	No. of Dead Stems	Age - Category
P01	40	511	2.41	0.65	87.83	13	GT70
P02	19	285	1.38	0.47	49.10	4	LT26
P03	34	261	2.00	0.57	52.45	0	LT52
P04	41	328	2.41	0.65	27.26	1	LT70
P05	27	362	1.96	0.60	44.26	4	LT70
P06	24	142	2.58	0.81	28.65	0	LT26
P07	28	208	2.22	0.67	31.29	13	LT14
P08	31	415	1.91	0.56	25.13	1	LT52
P09	36	267	2.79	0.78	53.54	11	LT70
P10	15	170	1.41	0.52	23.54	15	LT14
P11	41	408	2.29	0.62	44.15	6	LT70
P12	29	334	1.40	0.42	49.75	25	LT52
P13	32	190	2.59	0.75	52.75	0	GT70
P14	51	345	3.07	0.78	37.66	24	LT26
P15	61	510	2.63	0.64	49.53	16	LT52
P16	30	107	2.69	0.79	19.25	6	LT14
P17	23	136	2.24	0.71	24.61	7	LT14
P18	32	351	2.68	0.77	23.83	19	LT14
P19	33	225	2.88	0.83	41.16	35	LT52
P20	19	292	1.58	0.54	39.93	27	LT52
P21	41	237	2.97	0.80	44.23	14	LT70
P22	24	212	1.54	0.49	66.37	4	GT70
P23	15	166	0.82	0.30	68.20	5	GT70
P24	42	322	2.32	0.62	34.38	11	LT52
P25	38	489	2.84	0.78	34.36	36	LT26
P26	37	269	2.52	0.70	33.34	19	LT26
P27	55	345	2.95	0.74	30.86	33	LT52
P28	31	311	2.58	0.75	34.19	28	LT26

*Diversity = Shannon Diversity Index, Evenness = Pielou's Evenness Index, GT70 = greater than 70-year old forest (forest since 1945), LT70 = less than 70-year old forest (forest since 1963) LT52 = less than 52-year old forest (forest since 1989), LT26 = less than 26-year old forest (forest since 2001), and LT14 = less than 14-year old forest (forest since 2014)*

**Table 6.4** Descriptive statistics of community traits

Variable	Age	n	M	MSE	SD	CoV	Min	Med	Max
<b>Richness</b>									
	GT70	4	28	5	11	39	15	28	40
	LT70	5	37	3	6	16	27	41	41
	LT52	8	38	5	14	37	19	34	61
	LT26	6	33	5	11	34	19	34	51
	LT14	5	26	3	7	27	15	28	32
	<b>Total</b>	<b>28</b>	<b>33</b>	<b>2</b>	<b>11</b>	<b>34</b>	<b>15</b>	<b>32</b>	<b>61</b>
<b>Abundance</b>									
	GT70	4	270	81	162	60	166	201	511
	LT70	5	320	31	69	22	237	328	408
	LT52	8	338	32	90	27	225	328	510
	LT26	6	307	46	113	37	142	298	489
	LT14	5	194	43	95	49	107	170	351
	<b>Total</b>	<b>28</b>	<b>293</b>	<b>21</b>	<b>110</b>	<b>38</b>	<b>107</b>	<b>289</b>	<b>511</b>
<b>Diversity</b>									
	GT70	4	1.84	0.41	0.82	44.49	0.82	1.98	2.59
	LT70	5	2.49	0.18	0.40	16.12	1.96	2.41	2.97
	LT52	8	2.21	0.21	0.58	26.41	1.40	2.16	2.95
	LT26	6	2.50	0.24	0.59	23.43	1.38	2.58	3.07
	LT14	5	2.25	0.23	0.52	23.23	1.41	2.24	2.69
	<b>Total</b>	<b>28</b>	<b>2.27</b>	<b>0.11</b>	<b>0.58</b>	<b>25.59</b>	<b>0.82</b>	<b>2.41</b>	<b>3.07</b>
<b>Evenness</b>									
	GT70	4	0.55	0.10	0.20	35.70	0.30	0.57	0.75
	LT70	5	0.69	0.04	0.09	13.71	0.60	0.65	0.80
	LT52	8	0.61	0.04	0.13	20.61	0.42	0.59	0.83
	LT26	6	0.72	0.05	0.13	17.71	0.47	0.77	0.81
	LT14	5	0.69	0.05	0.11	15.63	0.52	0.71	0.79
	<b>Total</b>	<b>28</b>	<b>0.65</b>	<b>0.03</b>	<b>0.13</b>	<b>20.51</b>	<b>0.30</b>	<b>0.66</b>	<b>0.83</b>
<b>Basal Area (m<sup>2</sup>/ha)</b>									
	GT70	4	68.79	7.22	14.45	21.00	52.75	67.28	87.83
	LT70	5	42.69	4.26	9.52	22.30	27.26	44.23	53.54
	LT52	8	40.40	3.48	9.84	24.35	25.13	40.55	52.45
	LT26	6	36.21	2.84	6.95	19.18	28.65	34.27	49.10
	LT14	5	24.50	1.94	4.33	17.68	19.25	23.83	31.29
	<b>Total</b>	<b>28</b>	<b>41.13</b>	<b>2.95</b>	<b>15.62</b>	<b>37.97</b>	<b>19.25</b>	<b>38.80</b>	<b>87.83</b>
<b>No. of Dead Stems</b>									
	GT70	4	6	3	5	99	0	5	13
	LT70	5	7	2	5	73	1	6	14
	LT52	8	19	5	14	74	0	21	35
	LT26	6	19	6	14	76	0	22	36
	LT14	5	12	2	5	46	6	13	19
	<b>Total</b>	<b>28</b>	<b>13</b>	<b>2</b>	<b>11</b>	<b>84</b>	<b>0</b>	<b>12</b>	<b>36</b>

*N* = No of samples, *M* = Mean, *MSE* = Mean Standard Error, *SD* = Standard Deviation, *CoV* = Coefficient of Variation, *Min* = Minimum, *Med* = Median, *Max* = Maximum Diversity = Shannon Diversity Index, *Evenness* = Pielou's Evenness Index *GT70* = greater than 70-year old forest (forest since 1945), *LT70* = less than 70-year old forest (forest since 1963) *LT52* = less than 52-year old forest (forest since 1989), *LT26* = less than 26-year old forest (forest since 2001), and *LT14* = less than 14-year old forest (forest since 2014)

**Table 6.5** Pearson correlation of among the community variables and the environmental variables

	<b>Richness</b>	<b>Abundance</b>	<b>Diversity</b>	<b>Evenness</b>
AspN	0.19	-0.11	-0.01	-0.15
Elv	-0.19	-0.49***	0.328*	0.516***
slp	0.31	0.05	0.17	0.10
Curv	0.01	0.19	-0.14	-0.18
CI	0.05	0.26	0.01	0.02
pH	0.17	-0.278	0.16	0.12
OM	-0.14	-0.22	0.18	0.333*
N	-0.14	0.03	-0.06	0.03
M	-0.12	-0.13	-0.29	-0.29
C	-0.24	-0.19	0.09	0.21
C:N	0.02	-0.369*	0.335*	0.419**
S	-0.14	-0.19	0.08	0.19

Significance levels: \*\*\* ( $p \leq 0.01$ ), \*\* ( $p \leq 0.05$ ), \* ( $p \leq 0.1$ )

AspN = Cos [Aspect], Elv = Elevation, slp = Slope, Curv = Curvature, CI = Convergence Index, OM = Organic Matter, N = Nitrogen, M = Moisture Content, C = Carbon, C:N = Carbon Nitrogen Ratio, S = Sand. Diversity = Shannon Diversity Index, Evenness = Pielou's Evenness Index.

**Table 6.6** Results of linear regression model of community traits with three different categories of explanatory variables and their combinations

Response Variable	Explanatory Variables Category	Best AIC Model	R <sup>2</sup>	F	p	AIC
<b>Richness</b>						
	Topographic	+slp	0.10	2.74	0.11	-79.15
	Soil	-C	0.06	1.61	0.22	-78.02
	Age	+Age	0.20	1.44	0.25	-76.58
	Topographic+Soil	AspN + slp* - S	0.19	1.88	0.16	-78.26
	Topographic+Age	+slp**+ Age	0.35	2.32	0.08	-80.19
	Soil+Age	-C + Age	0.25	1.43	0.25	-76.24
	Topographic+Soil+Age	+slp**+ Age	0.35	2.32	0.08	-80.19
<b>Abundance</b>						
	Topographic	-Elv***	0.24	8.21	0.01	-77.57
	Soil	-OM*+N	0.14	2.01	0.16	-72.05
	Age	Age	0.22	1.62	0.20	-70.84
	Topographic+Soil	-Elv + CI + C	0.09	0.75	0.53	-74.85
	Topographic+Age	-Elv**+ Age	0.42	3.18	0.03	-77.20
	Soil+Age	-OM*+N	0.14	2.01	0.16	-72.05
	Topographic+Soil+Age	-AspN - Elv ***+ CI* -C + S + Age*	0.55	2.40	0.05	-75.97
<b>Shannon</b>						
	Topographic	Elv*	0.11	3.13	0.09	-72.26
	Soil	OM-N-M	0.23	2.39	0.09	-72.40
	Age	Age	0.13	0.87	0.50	-67.02
	Topographic+Soil	Elv* - M + slp	0.24	2.56	0.08	-72.86
	Topographic+Age	Elv*	0.11	3.13	0.09	-72.26
	Soil+Age	-M	0.08	2.29	0.14	-71.74
	Topographic+Soil+Age	Elv* - M + slp	0.24	2.56	0.08	-72.86
<b>Evenness</b>						
	Topographic	Elv***	0.27	9.43	0.00	-77.53
	Soil	OM*** + N** - M*	0.33	3.95	0.02	-76.09
	Age	Age	0.19	0.19	0.29	68.68
	Topographic+Soil	Elv *** - M*	0.34	6.53	0.01	-78.63
	Topographic+Age	Elv***	0.27	9.43	0.00	-77.53
	Soil+Age	OM*** + N** - M*	0.33	3.95	0.02	-76.09
	Topographic+Soil+Age	Elv *** - M*	0.34	6.53	0.01	-78.63

Significance levels: \*\*\* ( $p \leq 0.01$ ), \*\* ( $p \leq 0.05$ ), \* ( $p \leq 0.1$ )

AspN = Cos [Aspect], Elv = Elevation, slp = Slope, Curv = Curvature, CI = Convergence Index, OM = Organic Matter, N = Nitrogen, M = Moisture Content, C = Carbon, C:N = Carbon Nitrogen Ratio, S = Sand. Diversity = Shannon Diversity Index, Evenness = Pielou's Evenness Index.

**Table 6.7** Statistics of CCA analysis and variation explained by the first six CCA-axis

<b>Analysis of Inertia</b>						
	Inertia	Proportion				
Total	5.845	1				
Constrained	3.301	0.5648				
Unconstrained	2.543	0.4352				
Significance						
<b>Permutation Test for Significance</b>						
F-value of All Axis	1.887855					
Significance	0.009901					
F-value of First-Axis	4.311443					
Significance	0.009901					
<b>Proportion explained by axis</b>						
	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Eigenvalue	0.6854	0.608	0.45497	0.367	0.27327	0.25876
Proportion Explained	0.1173	0.104	0.07784	0.0628	0.04676	0.04427
Cumulative Proportion	0.1173	0.2213	0.29914	0.3619	0.4087	0.45297
<b>Biplot Scores of Variables</b>						
	CCA1	CCA2	CCA3	CCA4	CCA5	CCA6
Elv***	0.893532	0.38765	0.17086	0.03212	-0.03624	0.05981
AspN**	0.104008	0.4626	-0.39574	0.01583	-0.03078	-0.23526
CI*	-0.05366	-0.41609	0.21093	-0.17812	-0.08039	0.52336
Curv*	-0.2236	-0.43021	-0.13638	-0.15146	0.03287	-0.53667
slp	-0.15369	0.14888	0.01948	0.03166	0.07068	-0.1328
C**	0.186693	0.05095	-0.44446	-0.01428	-0.08753	0.45974
Age[T.LT14]	0.194364	-0.12277	0.39136	0.68652	-0.10173	0.01828
Age[T.LT26]	0.151741	-0.2148	0.04502	-0.01002	0.61128	0.38699
Age[T.LT52]	-0.00059	-0.21024	-0.2293	-0.27088	-0.06272	-0.57664
Age[T.LT70]	0.252122	-0.02529	-0.24204	-0.19239	-0.43121	0.17734
C:N	0.081047	0.07521	-0.24059	-0.03232	0.10535	0.32054

*GT70 = greater than 70-year old forest (forest since 1945), LT70 = less than 70-year old forest (forest since 1963) LT52 = less than 52-year old forest (forest since 1989), LT26 = less than 26-year old forest (forest since 2001), and LT14 = less than 14-year old forest (forest since 2014). AspN = Cos [Aspect], Elv = Elevation, slp = Slope, Curv = Curvature, CI = Convergence Index, C = Carbon, C:N = Carbon Nitrogen Ratio*

**Table 6.8** Results of MRT analysis

Cluster	No of Sites	Sites	No. of Indicator Species	Indicator Species	Abbr.	Indicator Value	p	Breakpoints
MRT Group A	2	P07, P10	3	<i>Melastoma malabathricum</i>	Melamala	0.935	0.004	Elv >= 467.5; Age =LT14
				<i>Machilus chekiangensis</i>	Machchek	0.668	0.004	
				<i>Machilus pauhoi</i>	Machpauh	0.431	0.047	
MRT Group B	5	P06, P09, P19, P21, P28	6	<i>Symplocos sumuntia</i>	Sympsumu	0.800	0.005	Elv > 467.5; Age =LT26, LT52, LT70
				<i>Machilus thunbergii</i>	Machthun	0.752	0.015	
				<i>Ilex viridis</i>	Ilexviri	0.733	0.029	
				<i>Camellia caudata</i>	Camecaud	0.717	0.017	
				<i>Myrsine seguinii</i>	Myrssegu	0.625	0.015	
				<i>Ligustrum japonicum</i>	Ligujapo	0.600	0.033	
MRT Group C	3	P13, P22, P23	7	<i>Bischofia javanica</i>	Biscjava	1.000	0.001	Elv < 467.5; Age =GT70; CI < - 0.85
				<i>Cryptocarya chinensis</i>	Crypchin	0.846	0.001	
				<i>Elaeocarpus chinensis</i>	Elaechin	0.667	0.025	
				<i>Elaeagnus loureiroi</i>	Elaelour	0.611	0.015	
				<i>Elaeocarpus dubius</i>	Elaedubi	0.608	0.028	
				<i>Turpinia montana</i>	Turpmont	0.561	0.036	
				<i>Choerospondias axillaris</i>	Choeaxil	0.513	0.034	
MRT Group F	3	P08, P11 P12	2	<i>Daphniphyllum macropodum</i>	Daphmacr	0.6667	0.031	Elv < 467.5; Age =LT26, LT52, LT70; Elv < 348.2; Curv < -0.065
				<i>Psychotria asiatica</i>	Psycasia	0.4252	0.001	
MRT Group G	3	P25, P26 P28	5	<i>Pavetta hongkongensis</i>	Pavehong	0.9362	0.001	Elv < 467.5; Age =LT26, LT52, LT70; Elv >=348.2
				<i>Ficus variolosa</i>	Ficuvvari.1	0.5944	0.018	
				<i>Rhodymyrtus tomentosa</i>	Rhodtome	0.5685	0.038	
				<i>Glochidion wrightii</i>	Glocwrig	0.5301	0.031	
				<i>Diospyros morrisiana</i>	Diosmorr	0.4691	0.046	

The indicator values for the 23 significant indicator species found in five of the MRT groups: Groups A, B, C, F and G. MRT group D and E did not have statistically significant indicator species at the Sidak-corrected 5 % significance level (Legendre et al., 2009).

## Chapter 07

### Conclusions and Recommendations

A semi-automated multiscale object based approach was applied to sequential aerial photographs and recent high-resolution satellite images to map structural changes in natural vegetation over the last 70 years, from 1945 to 2014. An important aspect of object-based approach is the segmentation process which appeared as an automated digitizing of habitat boundaries which is a good alternative to manual digitizing of habitat patches, especially when using single channel remote sensing data. In addition to the automatic delineation of habitat boundaries based, image objects delineated through multiscale segmentation also provided additional features related to structural characteristics of vegetation which combines texture and tonal characteristics of image object primitives resulted in a precise semi-automatic classification of high resolution panchromatic (single channel) aerial photographs. The object-based approach, with an additive advantage of observations at multiple time steps, resulted in mapping accuracies of more than 92 %. And the methodology is abatable elsewhere in the world for similar studies using long-term remote sensing observation, especially over time periods longer than the operational period of earth resource (sun-synchronized) satellites i.e. the last four decades, as it allows efficient inclusion of landscape concepts by segmenting a digital image into meaningful geographic entities

Forest has increased from 0.17% (4.82 ha) to 36.44 % (1019.23 ha) in the landscape at an annual rate 7.7 % over the 70-year period of forest regeneration in the study area. The structural succession of natural vegetation, from open grass and shrubland, to open, then closed canopy forest, is very fast (e.g., 10.8% a year between 1989 and 2001), if the landscape is protected from fire. Fire is a major barrier to natural succession in the landscape. A comparison of structural changes between the areas which burnt consistently and the areas which did not burn consistently indicates the fire as a pertinent limiting factor of structural succession in the Hong Kong's Country Parks. Natural forest succession can be encouraged by preventing or controlling hill fires and constructing fire breaks to isolate frequently burnt areas from the fire source.

Forest is expanding along the altitudinal gradient and away from the streams, from valley bottoms to up along the slopes. Furthermore, with fire protection, all aspects will succeed to forest irrespective of soil conditions, as from 2001 to 2014, the growth rate of the forest was the same on all aspects.

Plantations appeared detrimental to the natural shrub to forest succession. The practice of afforestation as a nursery stage on degraded hillsides, for the establishment of forest seedlings by natural invasion, is not supported by the evidence, as when disease eliminated the native *Pinus massoniana* plantations during the 1970s, no forest or woody species were observed in the areas affected. In fact, there was a reversion to grassland, which persisted there for almost three decades, until recent shrub invasion. Also, poor regeneration of native species is reported in exotic plantations. Thus, monoculture plantations are suitable for assisting natural forest recovery in the degraded landscape as they are susceptible to disease and generates spatially homogenous conditions which result in by poor regeneration of native species.

The highest rate of increase in forest, of 11% per year between 1989 and 2001, appears to be due to a process of infilling across interfluves between linear valley patches, rather than across a broad forest front. And this rapid regeneration occurred when the distances between forest edges became proportional to optimal seed dispersal distance of bulbul (<100 m) and hwamei (<50m). Therefore, to facilitate structural succession to forest, broad scale plantation can be replaced with direct seeding of native tree and/or shrubs in linear shape patches extending outwards from existing forest. This will increase the natural seed rain and accelerate forest succession by providing new food sources to forest dwelling animals.

The changing morphology of landscape's spatial structure indicated a gradual consolidation of the landscape and improved internal connectivity of forest patches, as most of the landscape has converted from an earlier to the later successional stage with the dominance of forest, which enables easier traversability and movement of organisms in habitat patches. However, improved connectivity and increasing size of forest patches indicate better opportunities as well as urgent needs of forest specialist seed dispersal agents.

Significantly, the birds of open 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, 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 dispersal agents other than those which have operated over recent decades

At the landscape scale, elevation partitioned the species composition into two parallel successional trajectories (break point at the elevation of 467 m) which were further

distinguished by the successional stage of forest stands. A majority of the higher elevation forest species belongs to subtropical families while lowland forest belonged to tropical families. The altitudinal break point of the floristic composition of Hong Kong's mountain flora may have been defined by the damage caused by frequent frost events.

Accumulation of stand basal area showed a consistent increase, but it is slower, as the stand basal area of the secondary forests had only reached half of the old-growth forest stands after 70 years of succession. The number of dead stems were higher during 15 to 50 years of succession. This increased density is related to the stem exclusion phase, when fewer species, in the absence of late-successional species, outcompetes and becomes stand-dominating due to limited resource availability and the trees may start to die after reaching to a maximum age. This phenomenon is also evident in hump-backed curves of species richness and abundance. The curve is marked by a steady increase during earlier successional stages to a maximum value at an intermediate stage (when the site age was ~ 50 years), it then fell in later successional stages which may be attributed to increasing tree gaps as well as absences of the understory of late successional forest species.

Although the secondary forest has attained a species richness comparable to or greater than the old growth forest sites, their composition is very different from the few old-growth forest stands in the study area. Almost all secondary forest sites lack the presence of late successional tree species which can grow under shade, such as *Cryptocaria chinensis* and *Sarcosperma laurinum*. To assist ecosystem restoration in the landscape, late successional species can be planted to assist natural succession, particularly in the absence of native fauna, seed dispersal agents, and the altered surrounding environment. Therefore, pockets of high diversity plantations can be planted near established forests to artificially enhance the species diversity, which will act as seed sources for natural recovery in the future.

Also, large parts of the tropics and subtropics have suffered badly from deforestation over recent decades, resulting in depauperate vegetation communities often without sufficient seed sources available for natural recovery into diversity-rich ecosystems (MacDicken et al., 2015). As forest is the climax vegetation in Hong Kong, the inevitable decline in habitat diversity as succession proceeds to closed forest may be viewed as a natural and desirable first step in the restoration of the ecosystem. However, the absence of specialist forest fauna may be an issue in the future structure of this regenerated landscape, especially since the shade-tolerant, later successional forest species have poor dispersal abilities. Therefore, to manage natural succession and to guarantee enough genetic diversity in Hong Kong's newly establishing forests, climax trees may be planted strategically in carefully selected plots, such as those mapped in 1989, where the oldest forest pioneers are established.

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 biodiversity recovery may also depend on the reintroduction of specialised forest dispersal organisms (McConkey et al., 2012) such as Edwards's long-tailed giant rat (*Leopoldamys edwardsi*). This has to be balanced by the recognition that long absence from an ecosystem may be disruptive to the new ecological equilibrium (Corlett, 2013).

This study also demonstrated the significance of remote sensing and GIS based analysis for landscape level assessment of trends in species composition. In this study, sequential analysis of time series remote sensing data permitted mapping of forest patches at several successional stages, which enabled chronosequence analysis of floristic traits and successional trajectories of the recovering forest. Furthermore, composite maps of forest cover patches with different successional stages can also help for site-specific management of the recovering forest, for example, introduction of late successional tree species where forest pioneers have been established.

## References

- Abel, C., 1818. narrative of a journey in the interior of china and of a voyage to and from that country 1816-1817. London.
- AFCD, 2013. Agriculture, Fisheries and Conservation Department of Hong Kong. Departmental Annual Report 2012 -2013.
- AFCD, 2012. Agriculture, Fisheries and Conservation Department of Hong Kong. Department Annual Report 2011-2012.
- Aide, T.M., Grau, H.R., 2004. ECOLOGY: Enhanced: Globalization, Migration, and Latin American Ecosystems. *Science* (80-. ). 305, 1915–1916. doi:10.1126/science.1103179
- Aide, T.M., Zimmerman, J.K., Rosario, M., Marcano, H., 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in northeastern Puerto Rico. *Biotropica* 28, 537–548. doi:10.2307/2389095
- Allard, A., 2003. Vegetation changes in mountainous area - a monitoring methodology based on aerial photographs, high-resolution satellite images, and field investigation. Stockholm University.
- Allen, J.C., 1985. Soil Response to Forest Clearing in the United States and the Tropics: Geological and Biological Factors. *Biotropica* 17, 15. doi:10.2307/2388373
- ALS, 2016. ALS Global [WWW Document]. URL <http://www.alsglobal.com/>
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. doi:10.1111/j.1461-0248.2010.01552.x
- APGIII, 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161, 105–121. doi:10.1111/j.1095-8339.2009.00996.x
- Araujo, L.S., Komonen, A., Lopes-Andrade, C., 2015. Influences of landscape structure on

- diversity of beetles associated with bracket fungi in Brazilian Atlantic Forest. *Biol. Conserv.* 191, 659–666. doi:10.1016/j.biocon.2015.08.026
- Arekhi, S., Heydari, M., Pourbabaei, H., 2010. Vegetation-Environmental Relationships and Ecological Species Groups of the Ilam Oak Forest Landscape, Iran. *Casp. J. Environ. Sci.* 8, 115–125.
- Au, A.Y.Y., Corlett, R.T., Hau, B.C.H., 2006. Seed rain into upland plant communities in Hong Kong, China. *Plant Ecol.* 186, 13–22. doi:10.1007/s11258-006-9108-5
- Austin, M.P., 2002. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. *Ecol. Modell.* 157, 101–118. doi:10.1016/S0304-3800(02)00205-3
- Baldeck, C.A., Tupayachi, R., Sinca, F., Jaramillo, N., Asner, G.P., 2016. Environmental drivers of tree community turnover in western Amazonian forests. *Ecography (Cop.)*. 1–11. doi:10.1111/ecog.01575
- Balvanera, P., Quijas, S., Perez-Jimenez, a, 2011. Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. *Biotropica* 43, 414–422. doi:DOI 10.1111/j.1744-7429.2010.00712.x
- Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: An assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29, 1401–1420. doi:10.1046/j.1365-2699.2002.00762.x
- Bohlman, S. a, Laurance, W.F., Laurance, S.G., Nascimento, H.E.M., Fearnside, P.M., Andrade, A., 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. *J. Veg. Sci.* 19, 863–874. doi:10.3170/2008-8-18463
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the Spatial Component of Ecological Variation. *Ecology* 73, 1045–1055. doi:10.2307/1940179
- Braimoh, A.K., 2006. Random and systematic land-cover transitions in northern Ghana. *Agric. Ecosyst. Environ.* 113, 254–263. doi:10.1016/j.agee.2005.10.019
- Cao, H., Wu, L., Wang, Z., Huang, Z., Li, L., Wei, S., Lian, J., Ye, W., 2013. Dinghushan Lower Subtropical Forest Dynamics Plot: Tree Species and Their Distribution Patterns. China Forestry Press, Beijing.

- Catterall, C.P., McKenna, S., Kanowski, J., Piper, S.D., 2008. Do cyclones and forest fragmentation have synergistic effects? A before-after study of rainforest vegetation structure at multiple sites. *Austral Ecol.* 33, 471–484. doi:10.1111/j.1442-9993.2008.01902.x
- Chandrakanth, M., Romm, J., 1991. Sacred Forests , Secular Forest Policies and People ' s Actions. *Nat. Resour. J.* 31, 741–756.
- Chaplin, F.S.I., Matson, P. a., Vitousek, P.M., 2011. Principles of Terrestrial Ecosystem Ecology. doi:10.1007/978-1-4419-9504-9
- Chau, K.-C.L., 1994. The ecology of fire in Hong Kong. The University of Hong Kong.
- China, J.D., Helmer, E.H., 2003. Diversity and composition of tropical secondary forests recovering from large-scale clearing: Results from the 1990 inventory in Puerto Rico. *For. Ecol. Manage.* 180, 227–240. doi:10.1016/S0378-1127(02)00565-0
- Chiu, T.N., So, C.L., Catt, P., 1986. A Geography of Hong Kong, 2nd ed. Oxford University Press, Hong Kong .
- Cihlar, J., 2000. Land cover mapping of large areas from satellites: Status and research priorities. *Int. J. Remote Sens.* 21, 1093–1114. doi:10.1080/014311600210092
- Clark, D.B., Palmer, M.W., Clark, D.A., 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* 80, 2662–2675. doi:10.1890/0012-9658(1999)080[2662:EFATLS]2.0.CO;2
- Clark, J.S., 2001. Ecological Forecasts: An Emerging Imperative. *Science* (80-. ). 293, 657–660. doi:10.1126/science.293.5530.657
- Cole, L.E.S., Bhagwat, S. a, Willis, K.J., 2014. Recovery and resilience of tropical forests after disturbance. *Nat. Commun.* 5, 3906. doi:10.1038/ncomms4906
- Collins, S.L., Glenn, S.M., Gibson, D.J., 1995. Experimental Analysis of Intermediate Disturbance and Initial Floristic Composition: Decoupling Cause and Effect. *Ecology* 76, 486–492.
- Congalton, R., Gu, J., Yadav, K., Thenkabail, P., Ozdogan, M., 2014. Global Land Cover Mapping: A Review and Uncertainty Analysis. *Remote Sens.* 6, 12070–12093. doi:10.3390/rs61212070

- Connell, J.H., 1978. Diversity in Tropical Rain Forests. *Science* (80- ). doi:10.1126/science.199.4335.1302
- Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. *Geosci. Model Dev.* 8, 1991–2007. doi:10.5194/gmd-8-1991-2015
- Coppin, P., Jonckheere, I., Nackaerts, K., Muys, B., Lambin, E., 2004. Review Article Digital change detection methods in ecosystem monitoring: a review. *Int. J. Remote Sens.* 25, 1565–1596. doi:10.1080/0143116031000101675
- Corlett, R.T., 2011. Seed dispersal in Hong Kong, China: past, present and possible futures. *Integr. Zool.* 6, 97–109. doi:10.1111/j.1749-4877.2011.00235.x
- Corlett, R.T., 1999. Environmental forestry in Hong Kong: 1871 - 1997. *For. Ecol. Manage.* 116, 93–105.
- Corlett, R.T., 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. *J. Trop. Ecol.* 12, 819–833. doi:10.1017/S0266467400010075
- Corlett, R.T., 1995. Tropical secondary forests. *Prog. Phys. Geogr.* 19, 159–172. doi:10.1177/030913339501900201
- Corlett, R.T., 1992. The impact of cold and frost on terrestrial vegetation in Hong Kong. . *Memoirs of the Hong Kong Natural History Society.*
- Corlett, R.T., Turner, I.M., 1997. Long-Term Survival in Tropical Forest Remnants in Singapore and Hong Kong, in: William F. Laurance and Richard O. Bierregaard, J. (Ed.), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities.* The University of Chicago Press, Chicago, pp. 333–345.
- Costa, F.R.C., Magnusson, W.E., Luizao, R.C., 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. *J. Ecol.* 93, 863–878. doi:10.1111/j.1365-2745.2005.01020.x
- Curtis, J.T., 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities.* University of Wisconsin Press.
- Cusack, D., Montagnini, F., 2004. The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *For. Ecol. Manage.* 188, 1–15. doi:10.1016/S0378-1127(03)00302-5

- De'ath, G., 2002. Multivariate regression trees: A new technique for modeling species-environment relationships. *Ecology* 83, 1105–1117. doi:10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2
- Delang, C.O., Hang, Y.Y., 2009. Remote Sensing-Based Estimation of Carbon Sequestration in Hong Kong Country Parks from 1978 to 2004. *Open Environ. Sci.* 3, 97–115.
- Denslow, J., 2000. Patterns of structure and diversity across a tropical moist forest chronosequence. *Proc. IAVS Symp.* 237–241.
- DeVantier, L.M., De'ath, G., Turak, E., Done, T.J., Fabricius, K.E., 2006. Species richness and community structure of reef-building corals on the nearshore Great Barrier Reef. *Coral Reefs* 25, 329–340. doi:10.1007/s00338-006-0115-8
- Dissanska, M., Bernier, M., Payette, S., 2009. Object-based classification of very high resolution panchromatic images for evaluating recent change in the structure of patterned peatlands. *Can. J. Remote Sens.* 35, 189–215. doi:10.5589/m09-002
- Dudgeon, D., Corlett, R., 2011. *The Ecology and Biodiversity of Hong Kong* (revised ed.). Hong Kong: Cosmos Books & Lions Nature Education Foundation.
- Dudgeon, D., Corlett, R., 1994. *Hills and Streams: An Ecology of Hong Kong*. Hong Kong University Press. doi:10.2307/j.ctt2jc0hg
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. doi:10.2307/2963459
- Eilu, G., Hafashimana, D.L.N., Kasenene, J.M., 2004. Density and species diversity of trees in four tropical forests of the Albertine rift, western Uganda. *Divers. Distrib.* 10, 303–312. doi:10.1111/j.1366-9516.2004.00089.x
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, 80–82. doi:10.1038/nature05747
- Etter, A., McAlpine, C., Pullar, D., Possingham, H., 2005. Modeling the age of tropical moist forest fragments in heavily-cleared lowland landscapes of Colombia. *For. Ecol. Manage.* 208, 249–260. doi:10.1016/j.foreco.2004.12.008

- Evan, J., 1992. *Plantation forestry in the tropics*, 2nd ed. Clarendon Press, OXFORD, UK.
- Faber-Langendoen, D., 1992. Ecological constraints on rain forest management at Bajo Calima, western Colombia. *For. Ecol. Manage.* 53, 213–244. doi:10.1016/0378-1127(92)90044-A
- FAO, 2015. *Global Forest Resources Assessment 2015. How are the world's forests changing?* Room.
- FAO, 2010. *Global forest resource assessment*. Rome.
- Flanders, D., Hall-Beyer, M., Pereverzoff, J., 2003. Preliminary evaluation of eCognition object-based software for cut block delineation and feature extraction. *Can. J. Remote Sens.* 29, 441–452. doi:10.5589/m03-006
- Frelich, E.L., Reich, B.P., 1999. Minireviews: Neighborhood Effects, Disturbance Severity, and Community Stability in Forests. *Ecosystems* 2, 151–166. doi:10.1007/s100219900066
- Fukui, A., 2003. Relationship between seed retention time in bird's gut and fruit characteristics. *Ornithol. Sci.* 2, 41–48. doi:10.2326/osj.2.41
- Gadgil, M., Vartak, V., 1976. The sacred groves of Western Ghats in India. *Econ. Bot.* 30, 152–160.
- Galo, A.J.J., 2016. Acquisition, Characteristics and Preprocessing of Passive Remote Sensing Images in Tropical Forestry, in: Pancel, L., Köhl, M. (Eds.), *Tropical Forestry Handbook*. Springer Berlin Heidelberg, Berlin, Heidelberg, Heidelberg, pp. 1–30. doi:10.1007/978-3-642-41554-8\_108-2
- Gao, J., Liu, Y., 2012. Deforestation in Heilongjiang Province of China, 1896–2000: Severity, spatiotemporal patterns and causes. *Appl. Geogr.* 35, 345–352. doi:10.1016/j.apgeog.2012.08.001
- Ge, J., Xiong, G., Wang, Z., Zhang, M., Zhao, C., Shen, G., Xu, W., Xie, Z., 2015. Altered dynamics of broad-leaved tree species in a Chinese subtropical montane mixed forest: The role of an anomalous extreme 2008 ice storm episode. *Ecol. Evol.* 5, 1484–1493. doi:10.1002/ece3.1433
- Geist, H.J., Lambin, E.F., 2002. Proximate Causes and Underlying Driving Forces of Tropical Deforestation. *Bioscience* 52, 143. doi:10.1641/0006-

3568(2002)052[0143:PCAUDF]2.0.CO;2

- Geri, F., Rocchini, D., Chiarucci, A., 2010. Landscape metrics and topographical determinants of large-scale forest dynamics in a Mediterranean landscape. *Landsc. Urban Plan.* 95, 46–53. doi:10.1016/j.landurbplan.2009.12.001
- Gibbons, J.M., Newbery, D.M., 2003. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. *Plant Ecol.* 164, 1–18. doi:10.1023/A:1021210532510
- Grainger, A., 1988. Estimating Areas of Degraded Tropical Lands Requiring Replenishment of Forest Cover. *Int. Tree Crop. J.* 5, 31–61. doi:10.1080/01435698.1988.9752837
- Gregorio, A.D., Janson, J.M.L., 2005. Land Cover Classification System concepts and user manual software version 2. Rome.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M., Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecol.* 132, 107–120. doi:10.1023/A:1009726421352
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: Changes in structural and functional characteristics. *For. Ecol. Manage.* 148, 185–206. doi:10.1016/S0378-1127(00)00535-1
- Guevara, S., Laborde, J., 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* 107, 319–338. doi:10.1007/BF00052232
- Guida Johnson, B., Zuleta, G.A., 2013. Land-use land-cover change and ecosystem loss in the Espinal ecoregion, Argentina. *Agric. Ecosyst. Environ.* 181, 31–40. doi:10.1016/j.agee.2013.09.002
- Halle, S., Fattorini, M., 2004. Advances in restoration ecology: insights from aquatic and terrestrial ecosystems ., in: Temperton, V., Hobbes, R., Nuttle, T., Halle, S. (Eds.), *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. Washington (DC): Island Press;, pp. p. 10–33.
- Hartshorn, G.S., 1980. Neotropical Forest Dynamics. *Biotropica* 12, 23. doi:10.2307/2388152

- Hartter, J., Lucas, C., Gaughan, A.E., Lizama Aranda, L., 2008. Detecting tropical dry forest succession in a shifting cultivation mosaic of the Yucatán Peninsula, Mexico. *Appl. Geogr.* 28, 134–149. doi:10.1016/j.apgeog.2007.07.013
- Hau, B.C.H., Corlett, R.T., 2003. Factors affecting the early survival and growth of native tree seedlings planted on a degraded hillside Grassland in Hong Kong, China. *Restor. Ecol.* 11, 483–488.
- Hau, H.C., 1997. Tree seed predation on degraded hillsides in Hong Kong. *For. Ecol. Manage.* 99, 215–221. doi:10.1016/S0378-1127(97)00207-7
- Hay, G.J., Castilla, G., Wulder, M. a., Ruiz, J.R., 2005. An automated object-based approach for the multiscale image segmentation of forest scenes. *Int. J. Appl. Earth Obs. Geoinf.* 7, 339–359. doi:10.1016/j.jag.2005.06.005
- Helmer, E.H., 2000. The landscape ecology of tropical secondary forest in montane Costa Rica. *Ecosystems* 3, 98–114. doi:10.1007/s100210000013
- Hengl, T., Reuter, H.I., 2009. *Geomorphometry : concepts, software, applications*, 1st ed. Elsevier, Amsterdam .
- HK-Landsd, 2014. Lands Department: The Government of the Hong Kong Special Administrative Region [WWW Document]. URL <http://www.landsd.gov.hk/en/about/welcome.htm>
- Holl, K.D., 1999. 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. doi:10.1046/j.1526-100x.2000.80049.x
- Honnay, O., Jacquemyn, H., Bossuyt, B., Hermy, M., 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytol.* 166, 723–736. doi:10.1111/j.1469-8137.2005.01352.x
- Howe, H.F., Miritti, M.N., 2004. When Seed Dispersal Matters. *Bioscience* 54, 651. doi:10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2
- Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, N.J.

- Huston, M., 1980. Soil Nutrients and Tree Species Richness in Costa Rican Forests. *J. Biogeogr.* 7, 147–157.
- Huston, M.A., 1979. A general hypothesis of species diversity. *Am. Nat.* 113, 81–101. doi:10.1086/283366
- Jingyun, F., Yide, L., Biao, Z., Guohua, L., Guangyi, Z., 2004. Community structures and species richness in the montane rain forest of Jianfengling, Hainan island, China. *Biodivers. Sci.*
- John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., Foster, R.B., 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proc. Natl. Acad. Sci.* 104, 864–869. doi:10.1073/pnas.0604666104
- Johst, K., Brandl, R., Eber, S., 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Ecology* 83, 263–270.
- Jones, M.M., Tuomisto, H., Borcard, D., Legendre, P., Clark, D.B., Olivas, P.C., 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. *Oecologia* 155, 593–604. doi:10.1007/s00442-007-0923-8
- Jongman, C.J.F., Ter Braak, O.F.R., van Tongeren, R.H.G., 1995. *Data Analysis in Community and Landscape Ecology*. publisherNameCambridge University Press.
- Kanagaraj, R., Wiegand, T., Comita, L.S., Huth, A., 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage. *J. Ecol.* 99, 1441–1452. doi:10.1111/j.1365-2745.2011.01878.x
- Karst, J., Gilbert, B., Lechowicz, M.J., 2005. Fern community assembly: the roles of chance and the environment at local and intermediate scales. *Ecology* 86, 2473–2486. doi:10.1890/04-1420
- Kim, D., Sexton, J.O., Townshend, J.R., 2015. Accelerated deforestation in the humid tropics from the 1990s to the 2000s. *Geophys. Res. Lett.* 42, 1–7. doi:10.1002/2014GL062777.Received
- Kindt, R., Coe, R., 2010. *Tree diversity analysis, Training*. doi:10.1198/tas.2008.s264
- King, D.A., Davies, S.J., Tan, S., Noor, N.S.M., 2006. The role of wood density and stem

- support costs in the growth and mortality of tropical trees. *J. Ecol.* 94, 670–680. doi:10.1111/j.1365-2745.2006.01112.x
- Körner, C., 2004. Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philos. Trans. R. Soc. B Biol. Sci.* 359, 493–498.
- Kwok, H.K., Corlett, R.T., 2000. The bird communities of a natural secondary forest and a *Lophostemon confertus* plantation in Hong Kong, South China. *For. Ecol. Manage.* 130, 227–234. doi:10.1016/S0378-1127(99)00178-4
- Kwok, H.K., Corlett, R.T., 1999. Seasonality of forest birds community in hong kong, south china. *Ibis (Lond. 1859)*. 141, 70–79.
- Lan, G., Hu, Y., Cao, M., Zhu, H., 2011. Topography related spatial distribution of dominant tree species in a tropical seasonal rain forest in China. *For. Ecol. Manage.* 262, 1507–1513. doi:10.1016/j.foreco.2011.06.052
- Larsen, D.R., Speckman, P.L., 2004. Multivariate Regression Trees for Analysis of Abundance Data. *Biometrics* 60, 543–549.
- Lassueur, T., Joost, S., Randin, C.F., 2006. Very high resolution digital elevation models: Do they improve models of plant species distribution? *Ecol. Modell.* 198, 139–153. doi:10.1016/j.ecolmodel.2006.04.004
- Lausch, A., Blaschke, T., Haase, D., Herzog, F., Syrbe, R.-U., Tischendorf, L., Walz, U., 2015. Understanding and quantifying landscape structure – A review on relevant process characteristics, data models and landscape metrics. *Ecol. Modell.* 295, 31–41. doi:10.1016/j.ecolmodel.2014.08.018
- Lebrija-trejos, A.E., Pérez-garcía, E.A., Meave, J.A., Bongers, F., Ecology, S., February, N., Meave, A., 2015. Functional traits and environmental filtering drive community assembly in a species-rich tropical system Published by: Ecological Society of America Functional traits and environmental drive community filtering in a species-rich tropical system assembly 91, 386–398. doi:10.1890/08-1449.1
- Lee, E.W.S., Hau, B.C.H., Corlett, R.T., 2007. Seed rain and natural regeneration in *Lophostemon confertus* plantations in Hong Kong, China. *New For.* 35, 119–130. doi:10.1007/s11056-007-9065-4
- Lee, E.W.S., Hau, B.C.H., Corlett, R.T., 2005. Natural regeneration in exotic tree

- plantations in Hong Kong, China. *For. Ecol. Manage.* 212, 358–366. doi:10.1016/j.foreco.2005.03.057
- Leempoel, K., Parisod, C., Geiser, C., Daprà, L., Vittoz, P., Joost, S., 2015. Very high resolution digital elevation models: are multi-scale derived variables ecologically relevant? *Methods Ecol. Evol.* n/a–n/a. doi:10.1111/2041-210X.12427
- Legendre, P., 1989. *Data Analysis in Community and Landscape Ecology.* Ecology.
- Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.F., He, F., 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology* 90, 663–674. doi:10.1890/07-1880.1
- Leung, G.P.C., Hau, B.C.H., Corlett, R.T., 2008. Exotic plant invasion in the highly degraded upland landscape of Hong Kong, China. *Biodivers. Conserv.* 18, 191–202. doi:10.1007/s10531-008-9466-5
- Lillesand, T.M., Kiefer, R.W., Chipman, J.W., 2008. *Remote sensing and image interpretation*, 6th ed. John Wiley & Sons, Hoboken, NJ.
- Liu, J., Yunhong, T., Slik, J.W.F., 2014. Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. *For. Ecol. Manage.* 330, 75–81. doi:10.1016/j.foreco.2014.06.045
- Lovett, J.C., Clarke, G.P., Moore, R., Morrey, G.H., 2001. Elevational distribution of restricted range forest tree taxa in eastern Tanzania. *Biodivers. Conserv.* 10, 541–550. doi:10.1023/A:1016610526242
- Lucas, P.W., Corlett, R.T., 1998. Seed Dispersal by Long-Tailed Macaques 44, 29–44. doi:10.1002/(SICI)1098-2345(1998)45
- Lucas, R.M., Honzák, M., do Amaral, I., Curran, P.J., Foody, G.M., 2002. Forest regeneration on abandoned clearances in central Amazonia 37–41. doi:10.1080/01431160110069791
- Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *For. Ecol. Manage.* 190, 145–161. doi:10.1016/j.foreco.2003.09.012
- MacDicken, K., Reams, G., de Freitas, J., 2015. Introduction to the Changes in Global Forest Resources from 1990 to 2015. *For. Ecol. Manage.* 352, 1–2. doi:10.1016/j.foreco.2015.06.018

- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Springer Netherlands, Dordrecht. doi:10.1007/978-94-015-7358-0
- Marceau, D.J., Gratton, D.J., Fournier, R.A., Fortin, J.P., 1994. Remote sensing and the measurement of geographical entities in a forested environment. 2.The optimal spatial resolution. *Remote Sens. Environ.* 49, 105–117. doi:10.1016/0034-4257(94)90047-7
- Mathieu, R., Aryal, J., Chong, A.K., 2007. Object-Based Classification of Ikonos Imagery for Mapping Large-Scale Vegetation Communities in Urban Areas. *Sensors* 7, 2860–2880. doi:10.3390/s7112860
- McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., Santamaria, L., 2012. Seed dispersal in changing landscapes. *Biol. Conserv.* 146, 1–13. doi:10.1016/j.biocon.2011.09.018
- Mcgarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps.
- Meachem, W., 1994. Archaeological investigation on Chek Lap Kok Island, Hong Kong.
- Middleton, M., Närhi, P., Sutinen, M.L., Sutinen, R., 2008. Object based change detection of historical aerial photographs reveals altitudinal forest expansion, in: *GEOBIA 2008 - Pixels, Objects, Intelligence: GEOgraphic Object Based Image Analysis for the 21st Century*. p. 6.
- Möller, M., Lymburner, L., Volk, M., 2007. The comparison index: A tool for assessing the accuracy of image segmentation. *Int. J. Appl. Earth Obs. Geoinf.* 9, 311–321. doi:10.1016/j.jag.2006.10.002
- Munsi, M., Malaviya, S., Oinam, G., Joshi, P.K., 2010. A landscape approach for quantifying land-use and land-cover change (1976-2006) in middle Himalaya. *Reg. Environ. Chang.* 10, 145–155. doi:10.1007/s10113-009-0101-0
- Nadeau, M.B., Sullivan, T.P., 2015. Relationship between plant biodiversity and soil fertility in a mature tropical forest, Costa Rica. *Int. J. For. Res.* 2015, 1–13. doi:10.1155/2015/732946
- Neill, C., Melillo, J.M., Steudler, P.A., Cerri, C.C., De Moraes, J.F.L., Piccolo, M.C., Brito, M., 1997. Soil carbon and nitrogen stocks following forest clearing for pasture in the

- southwestern Brazilian Amazon. *Ecol. Appl.* doi:10.1890/1051-0761(1997)007[1216:SCANSF]2.0.CO;2
- Nepstad, D.C., Uhl, C., Serrao, E.A.S., 1991. Recuperation of a degraded Amazonian landscape - forest recovery and agricultural restoration. *Ambio* 20, 448–255.
- Nguyen, T. Van, Mitlohner, R., Bich, N. Van, Do, T. Van, 2015. Environmental Factors Affecting the Abundance and Presence of Tree Species in a Tropical Lowland Limestone and Non-limestone Forest in Ben En National Park, Vietnam. *J. For. Environ. Sci.* 31, 177–191. doi:10.7747/JFES.2015.31.3.177
- Nichol, J., Wong, M.S., 2008. Habitat Mapping in Rugged Terrain Using Multispectral Ikonos Images. *Photogramm. Eng. Remote Sens.* 74, 1325–1334. doi:10.14358/PERS.74.11.1325
- Nobre, C.A., Sellers, P.J., Shukla, J., 1991. Amazonian Deforestation and Regional Climate Change. *J. Clim.* 4, 957–988. doi:10.1175/1520-0442(1991)004<0957:ADARCC>2.0.CO;2
- Oksanen, J., 2013. Multivariate analysis of ecological communities in R: vegan tutorial.
- Onojeghuo, A.O., Blackburn, G.A., 2011. Forest transition in an ecologically important region: Patterns and causes for landscape dynamics in the Niger Delta. *Ecol. Indic.* 11, 1437–1446. doi:10.1016/j.ecolind.2011.03.017
- Osbeck, P., 1771. *A voyage to China and East Indies*. Printer for Benjamin White, London.
- Panagos, P., Borrelli, P., Meusburger, K., 2015. A New European Slope Length and Steepness Factor (LS-Factor) for Modeling Soil Erosion by Water. *Geosciences* 5, 117–126. doi:10.3390/geosciences5020117
- Parrotta, J. a, Turnbull, J.W., Jones, N., 1997. Catalyzing native forest regeneration on degraded tropical lands. *For. Ecol. Manage.* 99, 1–7. doi:10.1016/S0378-1127(97)00190-4
- Pausas, J.G., Austin, M.P., 2001. Patterns of Plant Species Richness in Relation to Different Environments: An Appraisal. *J. Veg. Sci.* 12, 153–166. doi:10.2307/3236601
- Pearson, R.G., Dawson, T.P., 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning

- under climate change. *Biol. Conserv.* 123, 389–401.  
doi:10.1016/j.biocon.2004.12.006
- Peet, R.K., 1992. Community structure and ecosystem function, in: *Plant Succession: Theory and Prediction*. Champion & Hall, London, pp. 103–151.
- Pellerin, S., Lavoie, C., 2003. Reconstructing the recent dynamics of mires using a multitechnique approach. *J. Ecol.* 91, 1008–1021. doi:10.1046/j.1365-2745.2003.00834.x
- Peña-Claros, M., Poorter, L., Alarcón, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano, M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L., Toledo, M., 2012. Soil Effects on Forest Structure and Diversity in a Moist and a Dry Tropical Forest. *Biotropica* 44, 276–283. doi:10.1111/j.1744-7429.2011.00813.x
- Perz, S., Skole, D., 2003. Secondary forest expansion in the Brazilian Amazon and the refinement of forest transition theory. *Soc. Nat. Resour.* 16, 277–294. doi:10.1080/08941920390178856
- Piedallu, C., Gégout, J.C., 2008. Efficient assessment of topographic solar radiation to improve plant distribution models. *Agric. For. Meteorol.* 148, 1696–1706. doi:10.1016/j.agrformet.2008.06.001
- Pontius, R.G., Shusas, E., McEachern, M., 2004. Detecting important categorical land changes while accounting for persistence. *Agric. Ecosyst. Environ.* 101, 251–268. doi:10.1016/j.agee.2003.09.008
- Pringle, R.M., Syfert, M., Webb, J.K., Shine, R., 2009. Quantifying historical changes in habitat availability for endangered species: Use of pixel- and object-based remote sensing. *J. Appl. Ecol.* 46, 544–553. doi:10.1111/j.1365-2664.2009.01637.x
- Pumijumnong, N., Payomrat, P., 2013. The Effective Ecological Factors and Vegetation at Koh Chang Island, Trat Province, Thailand. *Open J. For.* 3, 41–48. doi:10.4236/ojf.2013.31007
- Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C. V., Nimal Gunatilleke, I.A.U., Wiegand, K., Huth, A., 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. *J. Ecol.* 101, 149–160. doi:10.1111/1365-2745.12017

- Puyravaud, J.-P., 2003. Standardizing the calculation of the annual rate of deforestation. *For. Ecol. Manage.* 177, 593–596. doi:10.1016/S0378-1127(02)00335-3
- Pyke, C.R., Condit, R., Aguilar, S., Lao, S., 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. *J. Veg. Sci.* 12, 553–566. doi:10.2307/3237007
- Qi, X., Wang, K., Zhang, C., 2013. Effectiveness of ecological restoration projects in a karst region of southwest China assessed using vegetation succession mapping. *Ecol. Eng.* 54, 245–253. doi:10.1016/j.ecoleng.2013.01.002
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabia, A.H., Terribile, F., 2013. Semi-Automated Classification of Gray Scale Aerial Photographs using Geographic Object Based Image Analysis ( GEOBIA ) Technique. *Geophys. Res. Abstr.* 15, 2013.
- Reddy, C.S., Jha, C.S., Dadhwal, V.K., 2013. Assessment and monitoring of long-term forest cover changes in Odisha, India using remote sensing and GIS. *Environ. Monit. Assess.* 185, 4399–4415. doi:http://dx.doi.org/10.1007/s10661-012-2877-5
- Rhemtulla, J.M., Mladenoff, D.J., Clayton, M.K., 2009. Historical forest baselines reveal potential for continued carbon sequestration. *Proc. Natl. Acad. Sci.* 106, 6082–6087. doi:10.1073/pnas.0810076106
- Rocchini, D., Perry, G.L.W., Salerno, M., Maccherini, S., Chiarucci, A., 2006. Landscape change and the dynamics of open formations in a natural reserve. *Landsc. Urban Plan.* 77, 167–177. doi:10.1016/j.landurbplan.2005.02.008
- Rocha-Santos, L., Pessoa, M.S., Cassano, C.R., Talora, D.C., Orihuela, R.L.L., Mariano-Neto, E., Morante-Filho, J.C., Faria, D., Cazetta, E., 2016. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. *Biol. Conserv.* 196, 1–9. doi:10.1016/j.biocon.2016.01.028
- Roy, P.S., 2013. Biodiversity Characterization at Landscape level using Geospatial Model Parth Sarathi Roy. *An. XVI Simpósio Bras. Sensoriamento Remoto - SBSR 95*, 3321–3328.
- Saldarriaga, J.G., West, D.C., Tharpt, M.L., Uhq, C., Tharp, M.L., Uhl, C., Tharpt, M.L., Uhq,

- C., Tharp, M.L., Uhl, C., 1988. Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. *J. Ecol.* 76, 938 – 958. doi:10.2307/2260625
- Sann, B., Kanzaki, M., Ohta, S., 2016. Vegetation patterns and species-filtering effects of soil in secondary succession in a tropical dry forest in central Myanmar. *J. Trop. Ecol.* 32, 116–124. doi:10.1017/S026646741600002X
- Segura, G., Balvanera, P., Durán, E., Pérez, A., 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. *Plant Ecol.* 169, 259–271. doi:10.1023/A:1026029122077
- Smith, B., Wilson, J.B., 1996. A Consumer's Guide to Evenness Indices. *Oikos* 76, 70. doi:10.2307/3545749
- Sodhi, N.S., Brook, B.W., 2008. Fragile Southeast Asian biotas. *Biol. Conserv.* 141, 883–884. doi:10.1016/j.biocon.2007.12.027
- Song, C., Woodcock, C.E., 2002. The spatial manifestation of forest succession in optical imagery The potential of multiresolution imagery 82, 271–284.
- Sørensen, R., Zinko, U., Seibert, J., 2006. On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrol. Earth Syst. Sci.* 10, 101–112. doi:10.5194/hess-10-101-2006
- Stott, P., 1991. Recent trends in the ecology and management of the world savanna formations. *Prog. Phys. Geogr.* 15, 18–28.
- Sukri, R.S., Wahab, R.A., Salim, K.A., Burslem, D.F.R.P., 2012. Habitat Associations and Community Structure of Dipterocarps in Response to Environment and Soil Conditions in Brunei Darussalam, Northwest Borneo. *Biotropica* 44, 595–605. doi:10.1111/j.1744-7429.2011.00837.x
- Taylor, D.R., Aarssen, L.W., Loehle, C., 1990. On the Relationship between r/K Selection and Environmental Carrying Capacity: A New Habitat Templet for Plant Life History Strategies. *Oikos* 58, 239. doi:10.2307/3545432
- Teferi, E., Bewket, W., Uhlenbrook, S., Wenninger, J., 2013. Understanding recent land use and land cover dynamics in the source region of the Upper Blue Nile, Ethiopia: Spatially explicit statistical modeling of systematic transitions. *Agric. Ecosyst.*

- Environ. 165, 98–117. doi:10.1016/j.agee.2012.11.007
- ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquat. Sci.* 57, 255–289. doi:10.1007/BF00877430
- Terborgh, J., 1992. *Diversity and the Tropical Rain Forest*. Scientific American Library, New York.
- Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest Resilience, Biodiversity, and Climate Change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems, Technical Series. doi:10.1007/978-3-642-10445-9\_5
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720. doi:10.1038/379718a0
- Tuomisto, H., Ruokolainen, K., Yli-Halla, M., 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241–244. doi:10.1126/science.1078037
- Turner, I.M., Corlett, R.T., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *TREE* 11, 330–333.
- Turner, I.M., Wong, Y.K., Chew, P.T., Ibrahim, A. Bin, 1996. Rapid assessment of tropical rain forest successional status using aerial photographs. *Biol. Conserv.* 77, 177–183. doi:10.1016/0006-3207(95)00145-X
- Turner, I.M., Wong, Y.K., Chew, P.T., Ibrahim, bin A., 1997. Tree species richness in primary and old secondary tropical forest in Singapore. *Biodivers. Conserv.* 6, 537–543. doi:10.1023/A:1018381111842
- Turner, M.G., Gardner, R.H., O'Neill, R. V, 2001. *Landscape ecology in theory and practice: Pattern and process*. Springer, New York.
- Uddin, K., Chaudhary, S., Chettri, N., Kotru, R., Murthy, M., Prasad, R., Ning, W., Man, S., Krishna, S., 2015. Landscape and Urban Planning The changing land cover and fragmenting forest on the Roof of the World : A case study in Nepal ' s Kailash Sacred Landscape. *Landsc. Urban Plan.* 141, 1–10.

doi:10.1016/j.landurbplan.2015.04.003

- Valencia, R., Foster, R.B., Villa, G., Condit, R., Svenning, J.-C., Hernandez, C., Romoleroux, K., Losos, E., Magard, E., Balslev, H., 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92, 214–229. doi:10.1111/j.0022-0477.2004.00876.x
- Vasquez, J.A., Givnish, T.J., 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *J. Ecol.* 86, 999–1020.
- Walker, L.R., Chapin, F.S., 1987. Interactions among Processes Controlling Successional Change. *Oikos* 50, 131–135. doi:10.2307/3565409
- Wang, D.P., Ji, S.Y., Chen, F.P., Xing, F.W., Peng, S.L., 2006. Diversity and relationship with succession of naturally regenerated southern subtropical forests in Shenzhen, China and its comparison with the zonal climax of Hong Kong. *For. Ecol. Manage.* 222, 384–390. doi:10.1016/j.foreco.2005.10.053
- Weir, J.E.S., 2004. Patterns of seed dispersal by flying frugivores in Hong Kong. The University of Hong Kong.
- Weir, J.E.S., Corlett, R.T., 2006. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landsc. Ecol.* 22, 131–140. doi:10.1007/s10980-006-9002-5
- Wilson, J.P., Gallant, J.C., 2000. *Terrain analysis : principles and applications*. John Wiley, New York.
- Wright, S.J., 2005. Tropical forests in a changing environment. *Trends Ecol. Evol.* 20, 553–560. doi:10.1016/j.tree.2005.07.009
- Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38, 287–301. doi:10.1111/j.1744-7429.2006.00154.x
- Wu, J., Loucks, O.L., 1995. From Balance of Nature to Hierarchical Patch Dynamics: A Paradigm Shift in Ecology. *Q. Rev. Biol.* 70, 439–466.
- Zevenbergen, L.W., Thorne, C.R., 1987. Quantitative analysis of land surface topography. *Earth Surf. Process. Landforms* 12, 47–56. doi:10.1002/esp.3290120107
- Zewdie, W., Csaplovics, E., 2016. Identifying Categorical Land Use Transition and Land

- Degradation in Northwestern Drylands of Ethiopia. *Remote Sens.* 8, 408.  
doi:10.3390/rs8050408
- Zhang, H., Jim, C.Y., 2013. Species adoption for sustainable forestry in Hong Kong's degraded countryside. *Int. J. Sustain. Dev. World Ecol.* 20, 484–503.  
doi:10.1080/13504509.2013.818590
- Zhao, M., Pan, B., Tan, Y., Corlett, R.T., 2015. Winners and losers among tree species in Xishuangbanna: which traits are most important? *Sci. Bull.* 60, 916–924.  
doi:10.1007/s11434-015-0799-7
- Zhuang, X., 1997. Rehabilitation and development of forest on degraded hills of Hong Kong. *For. Ecol. Manage.* 99, 197–201. doi:10.1016/S0378-1127(97)00205-3
- Zhuang, X., 1993. Forest succession in Hong Kong. The University of Hong Kong.
- Zhuang, X., Corlett, R.T., 1997. Forest and forest succession in Hong Kong, China. *J. Trop. Ecol.* 14, 857–866.
- Zhuang, X., Corlett, R.T., 1996. The Conservation status of Hong Kong's Tree Flora. *Chinese Biodivers.* 4, 36–43.
- Zhuang, X., Xing, F.W., Corlett, R.T., 1995. The tree flora of Hong Kong: distribution and status, in: *Memmoirs of the Hong Kong Natural History Society.* pp. 1–205.

## **Appendices**

**Appendix 1** List of species recorded during the survey, with abbreviations (Abbr.), APGIII Family, Author, and IVI (Important Value Index)

Species	Abbr.	Family	Author	IVI
<i>Acacia confusa</i>	Acacconf	Leguminosae	Merr.	0.19
<i>Acronychia pedunculata</i>	Acropedu	Rutaceae	(L.) Miq.	5.30
<i>Adina pilulifera</i>	Adinpilu	Rubiaceae	(Lam.) Franch. ex Drake	0.21
<i>Aidia canthioides</i>	Aidicant	Rubiaceae	(Champ. ex Benth.) Masam.	0.13
<i>Aidia pycnantha</i>	Aidipycn	Rubiaceae	(Drake) Tirveng.	0.12
<i>Alangium chinense</i>	Alanchin	Cornaceae	(Lour.) Harms	0.37
<i>Albizia corniculata</i>	Albicorn	Leguminosae	(Lour.) Druce	0.24
<i>Alyxia sinensis</i>	Alyxsine	Apocynaceae	Champ. ex Benth.	0.27
<i>Antidesma bunius</i>	Antibuni	Phyllanthaceae	(L.) Spreng.	0.13
<i>Antidesma fordii</i>	Antiford	Phyllanthaceae	Hemsl.	0.12
<i>Antidesma japonicum</i>	Antijapo	Phyllanthaceae	Siebold & Zucc.	0.14
<i>Antidesma montanum var. microphyllum</i>	Antimicr	Phyllanthaceae	(Hemsl.) Petra Hoffm.	0.12
<i>Antirhea chinensis</i>	Antichin	Rubiaceae	(Champ. ex Benth.) Benth. & Hook.f. ex F.B.Forbes & Hemsl.	0.24
<i>Aphananthe cuspidata</i>	Aphacusp	Cannabaceae	(Blume) Planch.	0.30
<i>Aporosa octandra</i>	Aporocta	Phyllanthaceae	(Buch.-Ham. ex D.Don) Vickery	9.48
<i>Aquilaria sinensis</i>	Aquisine	Thymelaeaceae	(Lour.) Spreng.	0.16
<i>Archidendron lucidum</i>	Archluci	Leguminosae	(Benth.) I.C.Nielsen	2.01
<i>Ardisia crenata</i>	Ardicren	Primulaceae	Sims	0.25
<i>Ardisia hanceana</i>	Ardihanc	Primulaceae	Mez	1.05
<i>Ardisia lindleyana</i>	Ardilind	Primulaceae	D.Dietr.	0.17
<i>Ardisia quinquegona</i>	Ardiquin	Primulaceae	Blume	2.26
<i>Artocarpus tonkinensis</i>	Artotonk	Moraceae	A.Chev. ex Gagnep.	0.29
<i>Beilschmiedia glandulosa</i>	Beilglan	Lauraceae	N.H.Xia, F.N.Wei & Y.F.Deng	0.37
<i>Bischofia javanica</i>	Biscjava	Phyllanthaceae	Blume	0.97
<i>Boehmeria nivea</i>	Boehnive	Urticaceae	(L.) Gaudich.	0.12
<i>Breynia fruticosa</i>	Breyfrut	Phyllanthaceae	(L.) Müll.Arg.	0.81
<i>Bridelia balansae</i>	Bridbala	Phyllanthaceae	Tutcher	5.19
<i>Bridelia tomentosa</i>	Bridtome	Phyllanthaceae	Blume	0.16
<i>Callicarpa cathayana</i>	Callcath	Lamiaceae	C.H.Chang	0.13
<i>Callicarpa dichotoma</i>	Calldich	Lamiaceae	(Lour.) K.Koch	0.12
<i>Callicarpa nudiflora</i>	Callnudi	Lamiaceae	Hook. & Arn.	0.33
<i>Callicarpa rubella</i>	Callrube	Lamiaceae	Lindl.	0.13
<i>Calophyllum membranaceum</i>	Calomemb	Clusiaceae	Gardner & Champ.	0.36
<i>Camellia caudata</i>	Camecaud	Theaceae	Wall.	2.14
<i>Camellia kissii</i>	Camekiss	Theaceae	Wall.	0.31
<i>Camellia oleifera</i>	Cameolei	Theaceae	Abel	0.26
<i>Camellia sinensis</i>	Camesine	Theaceae	(L.) Kuntze	0.26
<i>Camellia sinensis var. waldenae</i>	Camewald	Theaceae	(S.Y.Hu) H.T.Chang	0.12
<i>Canarium album</i>	Canaalbu	Burseraceae	(Lour.) DC.	0.15
<i>Canarium pimela</i>	Canapime	Burseraceae	K.D.Koenig	0.79
<i>Carallia brachiata</i>	Carabrac	Rhizophoraceae	(Lour.) Merr.	0.29
<i>Casearia glomerata</i>	Caseglom	Salicaceae	Roxb.	0.20
<i>Casearia velutina</i>	Casevelu	Salicaceae	Blume	0.24

<i>Castanopsis concinna</i>	Castconc	Fagaceae	(Champ. ex Benth.) A.DC.	1.93
<i>Castanopsis faberi</i>	Castfabe	Fagaceae	Hance	1.01
<i>Castanopsis fissa</i>	Castfiss	Fagaceae	(Champ. ex Benth.) Rehder & E.H.Wilson	3.94
<i>Castanopsis lamontii</i>	Castlamo	Fagaceae	Hance	0.14
<i>Celtis timorensis</i>	Celttimo	Cannabaceae	Span.	0.12
<i>Choerospondias axillaris</i>	Choeaxil	Anacardiaceae	(Roxb.) B.L.Burt & A.W.Hill	3.84
<i>Chrysophyllum roxburghii</i>	Chryroxb	Sapotaceae	G.Don	0.39
<i>Cinnamomum porrectum</i>	Cinnporr	Lauraceae	(Roxb.) Kosterm.	2.36
<i>Citrus japonica</i>	Citrjapo	Rutaceae	Thunb.	0.29
<i>Cornus hongkongensis</i>	Cornhong	Cornaceae	Hemsl.	0.26
<i>Cratoxylum cochinchinense</i>	Cratcoch	Hypericaceae	(Lour.) Blume	0.75
<i>Croton tiglium</i>	Crottigl	Euphorbiaceae	L.	0.12
<i>Cryptocarya chinensis</i>	Crypchin	Lauraceae	(Hance) Hemsl.	9.67
<i>Cunninghamia lanceolata</i>	Cunnlanc	Cupressaceae	(Lamb.) Hook.	1.11
<i>Dalbergia benthamii</i>	Dalbbent	Leguminosae	Prain	0.12
<i>Daphniphyllum calycinum</i>	Daphcaly	Daphniphyllaceae	Benth.	2.83
<i>Daphniphyllum macropodum</i>	Daphmacr	Daphniphyllaceae	Miq.	0.25
<i>Dendropanax proteus</i>	Dendprot	Araliaceae	(Champ. ex Benth.) Benth.	0.12
<i>Dendrotrophe varians</i>	Dendvari	Santalaceae	(Blume) Miq.	0.48
<i>Desmos chinensis</i>	Desmchin	Annonaceae	Lour.	2.93
<i>Dichroa febrifuga</i>	Dichfebr	Hydrangeaceae	Lour.	0.12
<i>Dimocarpus Longan</i>	DimoLong	Sapindaceae	Lour.	0.43
<i>Diospyros eriantha</i>	Dioseria	Ebenaceae	Champ. ex Benth.	0.57
<i>Diospyros morrisiana</i>	Diosmorr	Ebenaceae	Hance	6.86
<i>Diospyros tsangii</i>	Dioistsan	Ebenaceae	Merr.	0.13
<i>Diospyros tutcheri</i>	Dioistut	Ebenaceae	Dunn	0.70
<i>Diospyros vaccinioides</i>	Diosvacc	Ebenaceae	Lindl.	0.41
<i>Diplospora dubia</i>	Dipldubi	Rubiaceae	(Lindl.) Masam.	2.29
<i>Duranta erecta</i>	Duraerec	Verbenaceae	L.	0.19
<i>Dysoxylum hongkongense</i>	Dysohong	Meliaceae	(Tutcher) Merr.	0.30
<i>Elaeagnus loureiroi</i>	Elaelour	Elaeagnaceae	Champ.	0.91
<i>Elaeocarpus chinensis</i>	Elaechin	Elaeocarpaceae	(Gardner & Champ.) Hook.f. ex Benth.	2.65
<i>Elaeocarpus dubius</i>	Elaedubi	Elaeocarpaceae	DC.	4.03
<i>Elaeocarpus japonicus</i>	Elaejapo	Elaeocarpaceae	Siebold & Zucc.	0.73
<i>Elaeocarpus sylvestris</i>	Elaesylv	Elaeocarpaceae	(Lour.) Poir.	0.39
<i>Embelia laeta</i>	Embelaet	Primulaceae	(L.) Mez	0.25
<i>Embelia vestita</i>	Embevest	Primulaceae	Roxb.	0.12
<i>Endospermum chinense</i>	Endochin	Euphorbiaceae	Benth.	0.94
<i>Enkianthus quinqueflorus</i>	Enkiquin	Ericaceae	Lour.	0.35
<i>Eriobotrya fragrans</i>	Eriofrag	Rosaceae	Champ. ex Benth.	0.27
<i>Eucalyptus exserta</i>	Eucaexse	Myrtaceae	F.Muell.	0.36
<i>Euonymus laxiflorus</i>	Euonlaxi	Celastraceae	Champ. ex Benth.	0.30
<i>Euonymus tsoi</i>	Euontsoi	Celastraceae	Merr.	0.68
<i>Eurya chinensis</i>	Eurychin	Pentaphylacaceae	R.Br.	0.91
<i>Eurya groffi</i>	Eurygrof	Pentaphylacaceae	Merr.	0.51
<i>Eurya loquaiana</i>	Euryloqu	Pentaphylacaceae	Dunn	0.27

<i>Eurya macartneyi</i>	Eurymaca	Pentaphylacaceae	Champ.	3.64
<i>Eurya nitida</i>	Euryniti	Pentaphylacaceae	Korth.	2.36
<i>Ficus fistulosa</i>	Ficufist	Moraceae	Reinw. ex Blume	1.27
<i>Ficus formosana</i>	Ficuform	Moraceae	Maxim.	0.40
<i>Ficus hirta</i>	Ficuhirt	Moraceae	Vahl	0.40
<i>Ficus hispida</i>	Ficuhisp	Moraceae	L.f.	0.28
<i>Ficus nervosa</i>	Ficunerv	Moraceae	B.Heyne ex Roth	0.24
<i>Ficus subpisocarpa</i>	Ficusubp	Moraceae	Gagnep.	0.40
<i>Ficus variegata</i>	Ficuvvari	Moraceae	Blume	0.25
<i>Ficus variolosa</i>	Ficuvvari.1	Moraceae	Lindl. ex Benth.	1.20
<i>Garcinia multiflora</i>	Garcmult	Clusiaceae	Champ. ex Benth.	0.50
<i>Garcinia oblongifolia</i>	Garcoblo	Clusiaceae	Champ. ex Benth.	4.08
<i>Gardenia jasminoides</i>	Gardjasm	Rubiaceae	J.Ellis	0.50
<i>Glochidion eriocarpum</i>	Glocerio	Phyllanthaceae	Champ. ex Benth.	0.64
<i>Glochidion lanceolarium</i>	Gloclanc	Phyllanthaceae	(Roxb.) Voigt	0.31
<i>Glochidion wrightii</i>	Glocwrig	Phyllanthaceae	Benth.	1.39
<i>Gnetum luofuense</i>	Gnetluof	Gnetaceae	C.Y.Cheng	0.36
<i>Gordonia axillaris</i>	Gordaxil	Theaceae	(Roxb. ex Ker Gawl.) Endl.	1.12
<i>Grewia nervosa</i>	Grewnerv	Malvaceae	(Lour.) Panigrahi	0.69
<i>Helicia cochinchinensis</i>	Helicoch	Proteaceae	Lour.	0.24
<i>Homalium cochinchinense</i>	Homacoch	Salicaceae	(Lour.) Druce	0.92
<i>Huodendron biaristatum</i> var. <i>parviflorum</i>	Huodparv	Styracaceae	(Merr.) Rehder	0.20
<i>Ilex asprella</i>	Ilexaspr	Aquifoliaceae	(Hook. & Arn.) Champ. ex Benth.	4.20
<i>Ilex lohfaensis</i>	Ilexlohf	Aquifoliaceae	Merr.	0.15
<i>Ilex memecylifolia</i>	Ilexmeme	Aquifoliaceae	Champ. ex Benth.	0.12
<i>Ilex pubescens</i>	Ilexpube	Aquifoliaceae	Hook. & Arn.	2.35
<i>Ilex rotunda</i>	Ilexrotu	Aquifoliaceae	Thunb.	0.96
<i>Ilex triflora</i>	Ilextrif	Aquifoliaceae	Blume	0.27
<i>Ilex tutcheri</i>	Ilextutc	Aquifoliaceae	Merr.	0.93
<i>Ilex viridis</i>	Ilexviri	Aquifoliaceae	Champ. ex Benth.	3.26
<i>Itea chinensis</i>	Iteachin	Iteaceae	Hook. & Arn.	4.78
<i>Jasminum lanceolarium</i>	Jasmlanc	Oleaceae	Roxb.	0.24
<i>Lantana camara</i>	Lantcama	Verbenaceae	L.	0.12
<i>Lasianthus attenuatus</i>	Lasiatte	Rubiaceae	Jack	0.13
<i>Lasianthus chinensis</i>	Lasichin	Rubiaceae	(Champ.) Benth.	2.79
<i>Lasianthus fordii</i>	Lasiford	Rubiaceae	Hance	0.35
<i>Lasianthus verticillatus</i>	Lasivert	Rubiaceae	(Lour.) Merr.	0.16
<i>Lauraceae?</i>	Lauracea			0.22
<i>Ligustrum japonicum</i>	Ligujapo	Oleaceae	Thunb.	0.98
<i>Ligustrum liukiense</i>	Liguliuk	Oleaceae	Koidz.	0.25
<i>Liquidambar formosana</i>	Liquiform	Altingiaceae	Hance	1.53
<i>Lithocarpus corneus</i>	Lithcorn	Fagaceae	(Lour.) Rehder	0.68
<i>Lithocarpus glaber</i>	Lithglab	Fagaceae	(Thunb.) Nakai	0.12
<i>Lithocarpus haipinii</i>	Lithhaip	Fagaceae	Chun	0.12
<i>Lithocarpus iteaphyllus</i>	Lithitea	Fagaceae	(Hance) Rehder	0.13
<i>Litsea acutivena</i>	Litsacut	Lauraceae	Hayata	0.69

<i>Litsea glutinosa</i>	Litsglut	Lauraceae	(Lour.) C.B.Rob.	0.39
<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	Litsoblo	Lauraceae	(Nees) C.K. Allen	3.39
<i>Lophostemon confertus</i>	Lophconf	Myrtaceae	(R.Br.) Peter G.Wilson & J.T.Waterh.	6.29
<i>Macaranga Tanarius</i>	MacaTana	Euphorbiaceae	(L.) Müll.Arg.	0.14
<i>Machilus breviflora</i>	Machbrev	Lauraceae	(Benth.) Hemsl.	6.02
<i>Machilus chekiangensis</i>	Machchek	Lauraceae	S.K. Lee	18.9 4
<i>Machilus chinensis</i>	Machchin	Lauraceae	(Benth.) Hemsl.	1.11
<i>Machilus gamblei</i>	Machgamb	Lauraceae	King ex Hook. f.	9.61
<i>Machilus kwangtungensis</i>	Machkwan	Lauraceae	Yen C. Yang	2.43
<i>Machilus leptophylla</i>	Machlept	Lauraceae	Hand.-Mazz.	0.12
<i>Machilus oreophila</i>	Machoreo	Lauraceae	Hance	0.45
<i>Machilus pauhoi</i>	Machpauh	Lauraceae	Kaneh.	4.93
<i>Machilus</i> sp.	Machsp			0.20
<i>Machilus thunbergii</i>	Machthun	Lauraceae	Siebold & Zucc.	4.56
<i>Maclura cochinchinensis</i>	Maclcoch	Moraceae	(Lour.) Corner	0.24
<i>Maesa perlaria</i>	Maesperl	Primulaceae	(Lour.) Merr.	0.57
<i>Magnolia championii</i>	Magncham	Magnoliaceae	Benth.	0.17
<i>Mallotus paniculatus</i>	Mallpani	Euphorbiaceae	(Lam.) Müll.Arg.	0.43
<i>Melastoma malabathricum</i>	Melamala	Melastomataceae	L.	0.99
<i>Melastoma sanguineum</i>	Melasang	Melastomataceae	Sims	1.05
<i>Melicope pteleifolia</i>	Meliptel	Rutaceae	(Champ. ex Benth.) T.G. Hartley	2.72
<i>Meliosma fordii</i>	Meliford	Sabiaceae	Hemsl.	0.15
<i>Meliosma rigida</i>	Melirigi	Sabiaceae	Siebold & Zucc.	0.30
<i>Melodinus cochinchinensis</i>	Melococh	Apocynaceae	(Lour.) Merr.	0.13
<i>Memecylon ligustrifolium</i>	Memeligu	Melastomataceae	Champ. ex Benth.	1.43
<i>Microtropis obliquinervia</i>	Microbli	Celastraceae	Merr. & F.L. Freeman	0.13
<i>Microtropis reticulata</i>	Micrreti	Celastraceae	Dunn	0.12
<i>Mussaenda pubescens</i>	Musspube	Rubiaceae	Ait f.	0.12
<i>Myrica rubra</i>	Myrirubr	Myricaceae	(Lour.) Siebold & Zucc.	0.24
<i>Myrsine seguinii</i>	Myrssegu	Primulaceae	H. Lévl.	5.46
<i>Neolitsea cambodiana</i> var. <i>glabra</i>	Neolglab	Lauraceae	C.K. Allen	0.15
<i>Oldenlandia bodinieri</i>	Oldebodi	Rubiaceae	(H.Lévl.) Chun	0.16
<i>Osmanthus marginatus</i>	Osmamarg	Oleaceae	(Champ. ex Benth.) Hemsl.	0.12
<i>Osmanthus matsumuranus</i>	Osmamats	Oleaceae	Hayata	0.92
<i>Osmanthus matsumuranus</i>	Osmamats. 1	Vitaceae	Gagnep.	0.13
<i>Parthenocissus dalzielii</i>	Partdalz	Rubiaceae	Bremek.	0.17
<i>Pavetta hongkongensis</i>	Pavehong	Pentaphragaceae	Gardner & Champ.	0.61
<i>Pentaphragax euryoides</i>	Penteury	Rosaceae	Hance	0.13
<i>Photinia benthamiana</i>	Photbent	Rosaceae	Maxim.	0.35
<i>Photinia raupingensis</i>	Photraup	Rosaceae	K.C.Kuan	0.13
<i>Pinus elliottii</i>	Pinuelli	Pinaceae	Engelm.	1.40
<i>Prunus arborea</i> var. <i>montana</i>	Prunmont	Rosaceae	(Hook.f.) Kalkman	1.34
<i>Prunus phaeosticta</i>	Prunphae	Rosaceae	(Hance) Maxim.	0.83
<i>Prunus zippeliana</i>	Prunzipp	Rosaceae	Miq.	0.13
<i>Psychotria asiatica</i>	Psycasia	Rubiaceae	L.	34.0 9

<i>Psydrax dicoccos</i>	Psyddico	Rubiaceae	Gaertn.	0.78
<i>Reevesia thyrsoides</i>	Reevthyr	Malvaceae	Lindl.	0.24
<i>Rhaphiolepis indica</i>	Rhapindi	Rosaceae	(L.) Lindl.	0.94
<i>Rhododendron simsii</i>	Rhodsims	Ericaceae	Planch.	0.25
<i>Rhodomyrtus tomentosa</i>	Rhodtome	Myrtaceae	(Aiton) Hassk.	2.19
<i>Rhus succedanea</i>	Rhussucc	Anacardiaceae	L.	0.18
<i>Rourea microphylla</i>	Rourmicr	Connaraceae	(Hook. & Arn.) Planch.	0.12
<i>Rubus leucanthus</i>	Rubuleuc	Rosaceae	Hance	0.12
<i>Rubus reflexus</i>	Ruburefl	Rosaceae	Ker Gawl.	0.12
<i>Sarcandra glabra</i>	Sarcglab	Chloranthaceae	(Thunb.) Nakai	1.70
<i>Sarcosperma laurinum</i>	Sarclaur	Sapotaceae	(Benth.) Hook.f.	3.03
<i>Saurauia tristyla</i>	Saurtris	Actinidiaceae	DC.	0.66
<i>Schefflera heptaphylla</i>	Schehept	Araliaceae	(L.) Frodin	5.24
<i>Schoepfia chinensis</i>	Schochin	Schoepfiaceae	Gardner & Champ.	0.12
<i>Sinopora hongkongensis</i>	Sinohong	Lauraceae	(N.H. Xia, Y.F. Deng & K.L. Yip) J. Li, N.H. Xia & H.W. Li	0.13
<i>Sloanea sinensis</i>	Sloasine	Elaeocarpaceae	(Hance) Hemsl.	0.18
<i>Smilax china</i>	Smilchin	Smilacaceae	L.	0.19
<i>Smilax hypoglauca</i>	Smilhypo	Smilacaceae	Benth.	0.12
<i>Smilax lanceifolia</i>	Smillanc	Smilacaceae	Roxb.	0.37
<i>Sterculia lanceolata</i>	Sterlanc	Malvaceae	Cav.	3.54
<i>Symplocos anomala</i>	Sympanom	Symplocaceae	Brand	2.07
<i>Symplocos cochinchinensis</i> var. <i>laurina</i>	Symlaur	Symplocaceae	(Retz.) Noot.	0.12
<i>Symplocos congesta</i>	Sympcong	Symplocaceae	Benth.	0.24
<i>Symplocos glauca</i>	Sympglau	Symplocaceae	(Thunb.) Koidz.	1.68
<i>Symplocos lancifolia</i>	Symlanc	Symplocaceae	Siebold & Zucc.	0.36
<i>Symplocos</i> sp.	Sympsp	Symplocaceae		0.14
<i>Symplocos sumuntia</i>	Sympsumu	Symplocaceae	Buch.-Ham. ex D. Don	1.88
<i>Symplocos wikstroemiifolia</i>	Sympwiks	Symplocaceae	Hayata	0.13
<i>Syzygium buxifolium</i>	Syzybuxi	Myrtaceae	Hook. & Arn.	0.28
<i>Syzygium hancei</i>	Syzyhanc	Myrtaceae	Merr. & L.M.Perry	5.42
<i>Syzygium jambos</i>	Syzyjamb	Myrtaceae	(L.) Alston	1.57
<i>Syzygium levinei</i>	Syzylevi	Myrtaceae	(Merr.) Merr.	1.30
<i>Syzygium nervosum</i>	Syzynerv	Myrtaceae	A.Cunn. ex DC.	0.21
<i>Syzygium rehderianum</i>	Syzyrehd	Myrtaceae	Merr. & L.M.Perry	0.13
<i>Ternstroemia gymnanthera</i>	Terngymn	Pentaphragaceae	(Wight & Arn.) Sprague	0.34
<i>Tetracera sarmentosa</i>	Tetrarm	Dilleniaceae	(L.) Vahl	0.24
<i>Tetradium glabrifolium</i>	Tetrglab	Rutaceae	(Champ. ex Benth.) T.G. Hartley	0.30
<i>Toxicodendron succedaneum</i>	Toxisucc	Anacardiaceae	(L.) Kuntze	0.92
<i>Triadica cochinchinensis</i>	Triacoch	Euphorbiaceae	Lour.	0.27
<i>Turpinia arguta</i>	Turpargu	Staphyleaceae	Seem.	0.12
<i>Turpinia montana</i>	Turpmont	Staphyleaceae	(Blume) Kurz	0.37
<i>Urceola rosea</i>	Urcerose	Apocynaceae	(Hook. & Arn.) D.J. Middleton	0.17
<i>Uvaria boniana</i>	Uvarboni	Annonaceae	Finet & Gagnep.	0.12
<i>Viburnum odoratissimum</i>	Vibuodor	Adoxaceae	Ker Gawl.	1.23
<i>Viburnum sempervirens</i>	Vibusemp	Adoxaceae	K. Koch	0.32
<i>Vitex quinata</i>	Vitequin	Lamiaceae	(Lour.) F.N. Williams	0.12

<i>Wikstroemia nutans</i>	Wiksnuta	Thymelaeaceae	Champ. ex Benth.	1.84
<i>Zanthoxylum avicennae</i>	Zantavic	Rutaceae	(Lam.) DC.	1.91
<i>Zanthoxylum scandens</i>	Zantscan	Rutaceae	Blume	0.12

---

**Appendix 2** Species occurrence in plots with age category of GT70 (greater than 70 years old), sorted in descending order according to IVI (Important Value Index)

Species	P01	P13	P22	P23	Total	IVI
<i>Cryptocarya chinensis</i>	34	60	144	140	378	50.71
<i>Bridelia balansae</i>	15		2	1	18	21.22
<i>Choerospondias axillaris</i>	1		2	3	6	15.68
<i>Lasianthus chinensis</i>	151				151	15.56
<i>Elaeocarpus dubius</i>	2	5	6	2	15	15.55
<i>Elaeocarpus chinensis</i>		22		3	25	13.04
<i>Machilus gamblei</i>		8	3	5	16	12.35
<i>Psychotria asiatica</i>	47	22	2	2	73	11.30
<i>Memecylon ligustrifolium</i>	104				104	10.78
<i>Sarcosperma laurinum</i>	38		1	1	40	9.43
<i>Machilus pauhoi</i>	2		4		6	7.55
<i>Bischofia javanica</i>		1	2	1	4	5.59
<i>Aporosa octandra</i>	7	7		2	16	5.42
<i>Schefflera heptaphylla</i>	1	8		1	10	4.98
<i>Machilus chinensis</i>	1		2	2	5	4.97
<i>Machilus breviflora</i>	1	11	1		13	4.89
<i>Garcinia oblongifolia</i>	12	2	9		23	4.88
<i>Sterculia lanceolate</i>	8		6		14	4.59
<i>Ardisia quinquegona</i>	19		10		29	4.54
<i>Machilus chekiangensis</i>		7			7	4.22
<i>Elaeagnus loureiroi</i>		2	3	1	6	3.28
<i>Prunus arborea</i> var. <i>montana</i>	2	2			4	3.16
<i>Desmos chinensis</i>	1	2	1		4	3.08
<i>Acronychia pedunculata</i>	1	3			4	3.07
<i>Psydrax dicoccos</i>	4				4	2.83
<i>Lasianthus fordii</i>	19				19	2.71
<i>Chrysophyllum roxburghii</i>	14				14	2.68
<i>Cinnamomum porrectum</i>		1			1	2.64
<i>Syzygium hancei</i>	1	4			5	2.30
<i>Beilschmiedia glandulosa</i>	1				1	2.03
<i>Turpinia montana</i>			1	1	2	2.02
<i>Ardisia hanceana</i>		1	1		2	1.99
<i>Symplocos glauca</i>	1	1			2	1.99
<i>Cornus hongkongensis</i>		1			1	1.58
<i>Lauraceae?</i>			1		1	1.41
<i>Euonymus tsoi</i>	5				5	1.37
<i>Photinia benthamiana</i>		2			2	1.35
<i>Lasianthus verticillatus</i>			4		4	1.28
<i>Sarcandra glabra</i>		4			4	1.28
<i>Sloanea sinensis</i>			2		2	1.27
<i>Ficus fistulosa</i>		3			3	1.22
<i>Syzygium jambos</i>	3				3	1.20
<i>Diospyros eriantha</i>		3			3	1.20

<i>Dysoxylum hongkongense</i>	1		1	1.18
<i>Syzygium rehderianum</i>		2	2	1.09
<i>Lasianthus attenuatus</i>		2	2	1.09
<i>Meliosma rigida</i>	2		2	1.09
<i>Canarium pimela</i>	2		2	1.09
<i>Homalium cochinchinense</i>		1	1	1.09
<i>Aidia canthioides</i>	2		2	1.09
<i>Castanopsis lamontii</i>			1	1.08
<i>Microtropis obliquinervia</i>	1		1	1.04
<i>Alangium chinense</i>		1	1	1.01
<i>Diospyros tutcheri</i>	1		1	1.01
<i>Antidesma fordii</i>	1		1	1.00
<i>Aidia pycnantha</i>	1		1	1.00
<i>Syzygium levinei</i>	1		1	1.00
<i>Helicia cochinchinensis</i>	1		1	1.00
<i>Castanopsis faberi</i>		1	1	1.00
<i>Celtis timorensis</i>		1	1	1.00
<i>Ilex pubescens</i>		1	1	1.00
<i>Pavetta hongkongensis</i>	1		1	1.00
<i>Symplocos anomala</i>		1	1	1.00
<i>Diospyros morrisiana</i>		1	1	0.99
<i>Glochidion eriocarpum</i>		1	1	0.99
<i>Ilex asprella</i>		1	1	0.99
<i>Vitex quinata</i>	1		1	0.99
<i>Citrus japonica</i>	1		1	0.99

---

**Appendix 3** Species occurrence in plots with age category of LT70 (less than 70 years old), sorted in descending order according to IVI (Important Value Index)

Species	P04	P05	P09	P11	P21	Total	IVI
<i>Psychotria asiatica</i>	126	178		193		497	36.35
<i>Machilus gamblei</i>		32		11		43	16.17
<i>Machilus chekiangensis</i>	2	1	20	14	2	39	13.41
<i>Myrsine seguinii</i>			43		43	86	10.63
<i>Aporosa octandra</i>	27	28		50		105	10.57
<i>Diospyros morrisiana</i>	3	15	3	9	1	31	10.10
<i>Machilus breviflora</i>	1		5	10	16	32	9.87
<i>Ilex viridis</i>			44		4	48	9.47
<i>Machilus thunbergii</i>			33		1	34	8.88
<i>Liquidambar formosana</i>				6		6	6.25
<i>Cunninghamia lanceolata</i>	2	6				8	6.21
<i>Schefflera heptaphylla</i>	3	2		6		11	4.84
<i>Camellia caudata</i>			24		3	27	4.74
<i>Machilus pauhoi</i>	1	3		4		8	4.69
<i>Acronychia pedunculata</i>	22			1		23	4.60
<i>Desmos chinensis</i>	34	2		2		38	4.54
<i>Sterculia lanceolata</i>	31		1			32	4.33
<i>Syzygium hancei</i>		26		15		41	4.27
<i>Symplocos sumuntia</i>			13		10	23	4.25
<i>Prunus arborea var. montana</i>	2			2		4	3.80
<i>Osmanthus matsumuranus</i>	4				1	5	3.79
<i>Viburnum odoratissimum</i>	1			8		9	3.60
<i>Syzygium jambos</i>		34				34	3.58
<i>Daphniphyllum calycinum</i>	2	4		15	1	22	3.57
<i>Ilex rotunda</i>	1			2		3	3.19
<i>Litsea acutivena</i>					23	23	3.08
<i>Sarcandra glabra</i>			10	7	9	26	3.07
<i>Machilus kwangtungensis</i>		4				4	2.97
<i>Ilex asprella</i>	1	3		7		11	2.95
<i>Canarium pimela</i>	21					21	2.84
<i>Prunus phaeosticta</i>					29	29	2.82
<i>Garcinia oblongifolia</i>	4	4		3		11	2.81
<i>Maesa perlaria</i>	2	2	5			9	2.73
<i>Archidendron lucidum</i>	3		1	5		9	2.69
<i>Zanthoxylum avicennae</i>		2	2	2		6	2.51
<i>Glochidion eriocarpum</i>	2	2		2		6	2.48
<i>Eurya macartneyi</i>					24	24	2.45
<i>Elaeocarpus japonicus</i>			1		5	6	2.44
<i>Itea chinensis</i>	2	1	2			5	2.41
<i>Litsea rotundifolia var. oblongifolia</i>	2			6		8	1.96
<i>Melicope pteleifolia</i>		1		6	1	8	1.93
<i>Ardisia quinqueгона</i>		5		1		6	1.79
<i>Ligustrum japonicum</i>			8		1	9	1.76

<i>Rhaphiolepis indica</i>			1	2	3	1.72
<i>Wikstroemia nutans</i>		1	1		3	1.70
<i>Ficus formosana</i>	3			1		1.69
<i>Saurauia tristyla</i>	3		1			1.69
<i>Syzygium levinei</i>	1			2	1	1.64
<i>Elaeagnus loureiroi</i>	2		2			1.64
<i>Ficus fistulosa</i>		1		1		1.54
<i>Bridelia balansae</i>				1	2	1.53
<i>Gardenia jasminoides</i>			1	1		1.51
<i>Eurya groffi</i>			12			1.51
<i>Camellia oleifera</i>			9			1.46
<i>Alangium chinense</i>	2					1.42
<i>Symplocos anomala</i>			1		8	1.37
<i>Elaeocarpus sylvestris</i>			1			1.36
<i>Ilex pubescens</i>			5		2	1.29
<i>Ternstroemia gymnanthera</i>			3			1.28
<i>Eurya nitida</i>			3		1	1.14
<i>Rhus succedanea</i>	1					1.09
<i>Parthenocissus dalzielii</i>	1					1.04
<i>Aquilaria sinensis</i>	4					0.96
<i>Castanopsis faberi</i>			1			0.96
<i>Machilus oreophila</i>		2				0.95
<i>Ficus variolosa</i>				3		0.93
<i>Camellia sinensis</i>				1	2	0.91
<i>Syzygium buxifolium</i>					2	0.90
<i>Canarium album</i>	3					0.89
<i>Diospyros tutcheri</i>			3			0.88
<i>Eriobotrya fragrans</i>			1			0.87
<i>Sarcosperma laurinum</i>				2		0.86
<i>Breynia fruticosa</i>				2		0.83
<i>Lasianthus chinensis</i>	2					0.83
<i>Lithocarpus iteaphyllus</i>			2			0.82
<i>Symplocos wikstroemiiifolia</i>			2			0.82
<i>Osmanthus matsumuranus</i>		1				0.79
<i>Ficus variegata</i>	1					0.78
<i>Ligustrum liukuense</i>			1			0.78
<i>Carallia brachiata</i>	1					0.78
<i>Dimocarpus Longan</i>	1					0.77
<i>Elaeocarpus dubius</i>				1		0.77
<i>Triadica cochinchinensis</i>		1				0.77
<i>Ilex tutcheri</i>					6	0.76
<i>Rhodomyrtus tomentosa</i>				1		0.76
<i>Ardisia hanceana</i>	1					0.76
<i>Ficus nervosa</i>	1					0.76
<i>Symplocos congesta</i>		1				0.75
<i>Daphniphyllum macropodum</i>				1		0.75

<i>Tetracera sarmentosa</i>		1	1	0.75
<i>Ardisia crenata</i>	1		1	0.75
<i>Maclura cochinchinensis</i>	1		1	0.75
<i>Melastoma malabathricum</i>		1	1	0.75
<i>Symplocos glauca</i>	1		1	0.75
<i>Rubus leucanthus</i>	1		1	0.75
<i>Smilax lanceifolia</i>		1	1	0.75
<i>Embelia vestita</i>		1	1	0.75
<i>Symplocos lancifolia</i>			10	0.67
<i>Meliosma rigida</i>			3	0.30
<i>Oldenlandia bodinieri</i>			4	0.25
<i>Neolitsea cambodiana var. glabra</i>			3	0.22
<i>Ilex lohfaensis</i>			3	0.21
<i>Eurya loquaiana</i>			2	0.17
<i>Symplocos sp.</i>			2	0.15
<i>Pentaphylax euryoides</i>			1	0.14
<i>Prunus zippeliana</i>			1	0.11
<i>Enkianthus quinqueflorus</i>			1	0.08
<i>Dendropanax proteus</i>			1	0.08
<i>Alyxia sinensis</i>			1	0.06
<i>Euonymus laxiflorus</i>			1	0.06
<i>Osmanthus marginatus</i>			1	0.06

---

**Appendix 4** Species occurrence in plots with age category of LT52 (less than 52 years old), sorted in descending order according to IVI (Important Value Index)

Species	P03	P08	P12	P15	P19	P20	P24	P27	Total	IVI
<i>Psychotria asiatica</i>	146	222	235	224		154	117	76	1174	53.40
<i>Lophostemon confertus</i>	7			35			6		48	21.93
<i>Aporosa octandra</i>	17	45	24	10		26	5	4	131	10.54
<i>Eurya macartneyi</i>		1		18	21			71	111	8.62
<i>Machilus chekiangensis</i>		5	7	2	2	3	1	13	33	8.38
<i>Castanopsis fissa</i>	1		2			1			4	7.68
<i>Syzygium hancei</i>		13	12	2		67	10	7	111	7.33
<i>Myrsine seguinii</i>					31		1	23	55	6.86
<i>Machilus gamblei</i>			5			8	1		14	6.24
<i>Machilus kwangtungensis</i>			1		4	3			8	6.05
<i>Garcinia oblongifolia</i>	1	18	1	25	3	6	1	8	63	5.80
<i>Machilus pauhoi</i>	1	1	2			1	2		7	5.23
<i>Itea chinensis</i>				11	11		10	11	43	5.23
<i>Cryptocarya chinensis</i>				1			85	4	90	4.98
<i>Diospyros morrisiana</i>	2	5	4	4	2	1	1	8	27	4.79
<i>Eurya nitida</i>			1	20	37		1		59	4.26
<i>Sterculia lanceolate</i>		7	16	2			8	1	34	4.24
<i>Schefflera heptaphylla</i>	3	4		6			8	1	22	3.99
<i>Sarcosperma laurinum</i>		33	2						35	3.97
<i>Acronychia pedunculata</i>		9	1	7		3	2	10	32	3.66
<i>Desmos chinensis</i>	15	5	3	8		3	1		35	3.51
<i>Endospermum chinense</i>	2								2	3.29
<i>Machilus thunbergii</i>			1		7				8	3.14
<i>Machilus breviflora</i>		1	2	2	3	1	3	3	15	3.05
<i>Pinus elliotii</i>	3								3	2.69
<i>Symplocos anomala</i>			1			1		19	21	2.60
<i>Melicope pteleifolia</i>	6	1		2		3	1	2	15	2.56
<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>			1	5		2	4	2	14	2.54
<i>Syzygium jambos</i>	9	13		1				1	24	2.33
<i>Ilex viridis</i>				3	10				13	2.26
<i>Grewia nervosa</i>	5	2		3					10	2.24
<i>Archidendron lucidum</i>	3		1		2	3			9	2.12
<i>Ardisia quinquegona</i>		13	2				2	1	18	2.03
<i>Cinnamomum porrectum</i>							3	1	4	2.02
<i>Sarcandra glabra</i>		1		2		2	1	3	9	1.98
<i>Camellia caudata</i>				4	14			3	21	1.95
<i>Ilex pubescens</i>				13			2	2	17	1.84
<i>Ilex asprella</i>	12	1	2						15	1.82
<i>Elaeocarpus dubius</i>			1	1			10		12	1.79
<i>Daphniphyllum calycinum</i>	1	3				4	2		10	1.74
<i>Wikstroemia nutans</i>		1		2	4		2		9	1.67
<i>Rhodomyrtus tomentosa</i>		2	1	2				2	7	1.63
<i>Symplocos sumuntia</i>					7				7	1.61

<i>Choerospondias axillaris</i>				1		1		2	1.56
<i>Garcinia multiflora</i>					17		1	18	1.55
<i>Ficus fistulosa</i>	1	2			1			4	1.54
<i>Viburnum odoratissimum</i>				2	4		1	7	1.49
<i>Glochidion wrightii</i>				6		1	1	8	1.38
<i>Diospyros tutcheri</i>		1						9	1.37
<i>Lithocarpus corneus</i>					12			12	1.37
<i>Ardisia hanceana</i>		1	2	6				9	1.35
<i>Toxicodendron succedaneum</i>			1	1			1	3	1.31
<i>Homalium cochinchinense</i>				19				19	1.31
<i>Zanthoxylum avicennae</i>	1			13				14	1.31
<i>Syzygium levinei</i>	1					2	3	6	1.27
<i>Eucalyptus exserta</i>	1							1	1.21
<i>Ilex tutcheri</i>					13			13	1.20
<i>Ficus variolosa</i>				1			6	7	1.06
<i>Camellia kissii</i>					6			6	1.02
<i>Aphananthe cuspidata</i>					2			2	0.99
<i>Artocarpus tonkinensis</i>				2				2	0.95
<i>Dimocarpus Longan</i>	6	1						7	0.94
<i>Castanopsis concinna</i>			1	4				5	0.94
<i>Machilus chinensis</i>	1						1	2	0.93
<i>Eurya chinensis</i>				3	1			4	0.92
<i>Ilex triflora</i>					1			1	0.91
<i>Ilex rotunda</i>						2	1	3	0.90
<i>Diospyros eriantha</i>			1				5	6	0.89
<i>Cratoxylum cochinchinense</i>		1	1					2	0.82
<i>Gardenia jasminoides</i>						2	1	3	0.78
<i>Bridelia balansae</i>	1						1	2	0.78
<i>Diospyros vaccinioides</i>				1			1	2	0.78
<i>Diplospora dubia</i>							11	11	0.76
<i>Castanopsis fabri</i>					1			1	0.75
<i>Euonymus tsoi</i>				1		1		2	0.74
<i>Lasianthus chinensis</i>				1		1		2	0.74
<i>Gnetum luofuense</i>				1			1	2	0.74
<i>Calophyllum membranaceum</i>						1	1	2	0.73
<i>Reevesia thyrsoides</i>						10		10	0.73
<i>Syzygium nervosum</i>	1							1	0.70
<i>Huodendron biaristatum var. parviflorum</i>							1	1	0.64
<i>Callicarpa nudiflora</i>				5				5	0.61
<i>Duranta erecta</i>	2							2	0.60
<i>Elaeocarpus japonicus</i>							4	4	0.58
<i>Prunus phaeosticta</i>					1			1	0.57
<i>Magnolia championii</i>							2	2	0.55
<i>Prunus arborea var. montana</i>				4				4	0.55
<i>Mallotus paniculatus</i>	4							4	0.55
<i>Machilus oreophila</i>				2				2	0.55

<i>Symplocos glauca</i>			4		4	0.54
<i>Citrus japonica</i>				4	4	0.54
<i>Elaeocarpus sylvestris</i>		1			1	0.50
<i>Glochidion lanceolarium</i>				2	2	0.50
<i>Photinia benthamiana</i>				2	2	0.50
<i>Bridelia tomentosa</i>		4			4	0.48
<i>Canarium pimela</i>	1				1	0.44
<i>Pavetta hongkongensis</i>				2	2	0.44
<i>Saurauia tristyla</i>		2			2	0.44
<i>Macaranga Tanarius</i>	1				1	0.43
<i>Dysoxylum hongkongense</i>	2				2	0.41
<i>Melodinus cochinchinensis</i>				1	1	0.41
<i>Ficus hirta</i>		2			2	0.41
<i>Callicarpa rubella</i>		2			2	0.41
<i>Eriobotrya fragrans</i>				1	1	0.40
<i>Diospyros tsangii</i>		2			2	0.40
<i>Eurya loquaiana</i>				2	2	0.40
<i>Antidesma bunius</i>	1				1	0.40
<i>Litsea glutinosa</i>				1	1	0.40
<i>Daphniphyllum macropodum</i>	1				1	0.40
<i>Dendrotrophe varians</i>		1			1	0.40
<i>Photinia raupingensis</i>				1	1	0.40
<i>Ficus formosana</i>		1			1	0.39
<i>Osmanthus matsumuranus</i>	1				1	0.38
<i>Mussaenda pubescens</i>				1	1	0.38
<i>Microtropis reticulata</i>		1			1	0.38
<i>Lithocarpus haipinii</i>		1			1	0.38
<i>Rhododendron simsii</i>				1	1	0.38
<i>Machilus leptophylla</i>				1	1	0.38
<i>Lantana camara</i>		1			1	0.38
<i>Ficus variegata</i>	1				1	0.38
<i>Myrica rubra</i>				1	1	0.38
<i>Schoepfia chinensis</i>		1			1	0.38
<i>Zanthoxylum scandens</i>		1			1	0.38
<i>Elaeagnus loureiroi</i>	1				1	0.38
<i>Lithocarpus glaber</i>	1				1	0.37
<i>Dichroa febrifuga</i>		1			1	0.37
<i>Gordonia axillaris</i>		1			1	0.37
<i>Casearia velutina</i>	1				1	0.37
<i>Antidesma montanum var. microphyllum</i>		1			1	0.37
<i>Maclura cochinchinensis</i>		1			1	0.37
<i>Rourea microphylla</i>				1	1	0.37
<i>Smilax hypoglauca</i>				1	1	0.37
<i>Symplocos lancifolia</i>				1	1	0.37
<i>Breynia fruticosa</i>		1			1	0.37
<i>Dalbergia benthamii</i>		1			1	0.37

<i>Ficus nervosa</i>	1		1	0.37
<i>Melastoma sanguineum</i>	1		1	0.37
<i>Rubus reflexus</i>	1		1	0.37
<i>Turpinia arguta</i>	1		1	0.37
<i>Helicia cochinchinensis</i>		1	1	0.37

---

**Appendix 5** Species occurrence in plots with age category of LT26 (less than 26 years old), sorted in descending order according to IVI (Important Value Index)

Species	P02	P06	P14	P25	P26	P28	Total	IVI
<i>Psychotria asiatica</i>	186		19	112	110	22	449	30.47
<i>Machilus chekiangensis</i>	6	12	1	17	12	41	89	26.35
<i>Itea chinensis</i>		2	43		1	8	54	12.76
<i>Ilex asprella</i>	8		2	62	19	19	110	10.76
<i>Acronychia pedunculata</i>			80	20	2		102	10.51
<i>Syzygium hancei</i>	13			22	3	9	47	9.89
<i>Machilus breviflora</i>			4	3	3	37	47	9.63
<i>Castanopsis fissa</i>	4						4	9.05
<i>Diplospora dubia</i>			23	2	1	89	115	8.70
<i>Diospyros morrisiana</i>	2			36	14	3	55	8.68
<i>Castanopsis concinna</i>			1	5			6	8.41
<i>Aporosa octandra</i>	42			30	19		91	8.03
<i>Machilus thunbergii</i>		19				2	21	6.81
<i>Myrsine seguinii</i>		5	1	18	5	12	41	5.36
<i>Cinnamomum porrectum</i>	3				1		4	5.25
<i>Schefflera heptaphylla</i>	1		1	9	2	7	20	5.22
<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>	2		10	6	6	8	32	4.72
<i>Rhodomyrtus tomentosa</i>			4	20	6	10	40	4.43
<i>Daphniphyllum calycinum</i>	4			17	13	5	39	4.36
<i>Garcinia oblongifolia</i>			19	5	1		25	4.09
<i>Symplocos glauca</i>				37	2		39	3.95
<i>Wikstroemia nutans</i>		4	2	6	2	3	17	3.59
<i>Pinus elliottii</i>					3		3	3.20
<i>Ilex pubescens</i>		1	12	2	2		17	3.15
<i>Machilus gamblei</i>		1			3		4	2.97
<i>Melastoma sanguineum</i>			12	9		3	24	2.92
<i>Desmos chinensis</i>	4		3	5	1		13	2.81
<i>Ilex viridis</i>		10	3				13	2.77
<i>Ficus variolosa</i>			4	1	3	2	10	2.69
<i>Ardisia quinquegona</i>	1			8	9		18	2.68
<i>Ligustrum japonicum</i>		28					28	2.63
<i>Castanopsis faberi</i>		1					1	2.61
<i>Eurya nitida</i>		8	2	5			15	2.59
<i>Symplocos sumuntia</i>		6					6	2.57
<i>Archidendron lucidum</i>	1	3			1	2	7	2.56
<i>Glochidion wrightii</i>			7	6	4		17	2.51
<i>Camellia caudata</i>		24					24	2.45
<i>Symplocos anomala</i>		3			1	1	5	1.98
<i>Zanthoxylum avicennae</i>			2	2		2	6	1.95
<i>Sterculia lanceolate</i>	3		1	1			5	1.83
<i>Eurya macartneyi</i>			10			1	11	1.76
<i>Homalium cochinchinense</i>			13				13	1.72
<i>Machilus pauhoi</i>						8	8	1.66

<i>Pavetta hongkongensis</i>			2	7		9	1.63	
<i>Viburnum sempervirens</i>		1		7		8	1.46	
<i>Lasianthus chinensis</i>		5		1		6	1.39	
<i>Rhaphiolepis indica</i>				5		1	6	1.34
<i>Toxicodendron succedaneum</i>		4				1	5	1.33
<i>Syzygium levinei</i>				1		1	2	1.28
<i>Melicope pteleifolia</i>				1	3		4	1.22
<i>Euonymus tsoi</i>			2			2	4	1.22
<i>Lithocarpus corneus</i>		1			1		2	1.21
<i>Eurya groffii</i>			5				5	1.19
<i>Psydrax dicoccos</i>	1				2		3	1.17
<i>Smilax lanceifolia</i>		2	1				3	1.16
<i>Jasminum lanceolarium</i>			2				2	1.15
<i>Antirhea chinensis</i>			8				8	1.13
<i>Breynia fruticosa</i>			1			1	2	1.11
<i>Enkianthus quinqueflorus</i>			3				3	1.10
<i>Dendrotrophe varians</i>			5				5	1.05
<i>Elaeocarpus dubius</i>		2					2	0.99
<i>Casearia glomerata</i>			1				1	0.99
<i>Adina pilulifera</i>						4	4	0.98
<i>Machilus sp.</i>				1			1	0.95
<i>Euonymus laxiflorus</i>			4				4	0.86
<i>Carallia brachiata</i>				1			1	0.78
<i>Gordonia axillaris</i>			5				5	0.78
<i>Ardisia lindleyana</i>			5				5	0.78
<i>Ilex tutcheri</i>		2					2	0.76
<i>Diospyros vaccinioides</i>			4				4	0.75
<i>Sarcosperma laurinum</i>	1						1	0.70
<i>Cratoxylum cochinchinense</i>			1				1	0.69
<i>Alyxia sinensis</i>						3	3	0.68
<i>Eurya chinensis</i>						3	3	0.67
<i>Antidesma japonicum</i>			3				3	0.66
<i>Mallotus paniculatus</i>					2		2	0.63
<i>Callicarpa nudiflora</i>					2		2	0.62
<i>Diospyros eriantha</i>					2		2	0.62
<i>Cryptocarya chinensis</i>			2				2	0.62
<i>Ardisia crenata</i>			2				2	0.61
<i>Turpinia montana</i>			1				1	0.58
<i>Ligustrum liukuense</i>		1					1	0.58
<i>Ilex rotunda</i>		1					1	0.57
<i>Ternstroemia gymnanthera</i>		1					1	0.57
<i>Tetracera sarmentosa</i>	1						1	0.57
<i>Croton tiglium</i>					1		1	0.57
<i>Ardisia hanceana</i>					1		1	0.57
<i>Viburnum odoratissimum</i>				1			1	0.56
<i>Camellia sinensis var. waldenae</i>		1					1	0.56

<i>Glochidion eriocarpum</i>		1	1	0.56
<i>Gnetum luofuense</i>	1		1	0.56
<i>Calophyllum membranaceum</i>	1		1	0.56
<i>Embelia laeta</i>			1	0.56
<i>Symplocos congesta</i>		1	1	0.56
<i>Albizia corniculata</i>	1		1	0.56
<i>Uvaria boniana</i>	1		1	0.56
<i>Callicarpa dichotoma</i>	1		1	0.55
<i>Sarcandra glabra</i>	1		1	0.55
<i>Ilex memecylifolia</i>	1		1	0.55

---

**Appendix 6** Species occurrence in plots with age category of LT14 (less than 14 years old), sorted in descending order according to IVI (Important Value Index)

Species	P07	P10	P16	P17	P18	Total	IVI
<i>Machilus chekiangensis</i>	83	115	8	5	14	225	69.81
<i>Machilus gamblei</i>	1		7	3	12	23	15.21
<i>Aporosa octandra</i>				7	89	96	14.04
<i>Psychotria asiatica</i>			10	47	43	100	13.52
<i>Diospyros morrisiana</i>				32	9	41	13.20
<i>Schefflera heptaphylla</i>	4	8	4	5	9	30	10.70
<i>Litsea rotundifolia</i> var. <i>oblongifolia</i>				5	48	53	10.48
<i>Melicope pteleifolia</i>	1		32	6	9	48	9.72
<i>Gordonia axillaris</i>	22					22	7.25
<i>Melastoma malabathricum</i>	28	3	1		2	34	6.90
<i>Ilex asprella</i>	6	3			15	24	5.57
<i>Machilus pauhoi</i>	4	7	1		1	13	5.40
<i>Zanthoxylum avicennae</i>	4		1		15	20	5.32
<i>Acronychia pedunculata</i>					17	17	5.14
<i>Ilex pubescens</i>			1	1	18	20	4.92
<i>Daphniphyllum calycinum</i>	2		1	2	6	11	4.43
<i>Rhodomyrtus tomentosa</i>	1		1	2	7	11	4.33
<i>Machilus thunbergii</i>	2	5	1			8	4.17
<i>Eurya chinensis</i>	22					22	3.92
<i>Machilus breviflora</i>		9			3	12	3.71
<i>Ficus subpisocarpa</i>			1			1	3.48
<i>Glochidion wrightii</i>			2		4	6	3.20
<i>Liquidambar formosana</i>	1				2	3	3.16
<i>Ficus fistulosa</i>		3	9			12	3.01
<i>Symplocos anomala</i>	1				1	2	2.95
<i>Cratoxylum cochinchinense</i>				4	1	5	2.71
<i>Archidendron lucidum</i>			3	6		9	2.67
<i>Breynia fruticosa</i>	5		2			7	2.43
<i>Ficus hispida</i>			3			3	2.39
<i>Symplocos glauca</i>				1	4	5	2.32
<i>Tetradium glabrifolium</i>	2		1			3	2.29
<i>Melastoma sanguineum</i>				2	4	6	2.23
<i>Sterculia lanceolate</i>				1	4	5	2.18
<i>Garcinia oblongifolia</i>				1	3	4	2.07
<i>Litsea glutinosa</i>			1		1	2	2.00
<i>Ficus hirta</i>	3		1			4	1.98
<i>Saurauia tristyla</i>			6			6	1.97
<i>Rhaphiolepis indica</i>			1		1	2	1.79
<i>Toxicodendron succedaneum</i>				1		1	1.78
<i>Cinnamomum porrectum</i>				1		1	1.78
<i>Itea chinensis</i>		7				7	1.76
<i>Smilax china</i>	2					2	1.55
<i>Acacia confusa</i>	4					4	1.51

<i>Urceola rosea</i>	1		1	1.39
<i>Glochidion lanceolarium</i>			3	1.14
<i>Triadica cochinchinensis</i>	1		1	1.14
<i>Meliosma fordii</i>		3	3	1.13
<i>Ilex tutcheri</i>		3	3	1.10
<i>Machilus kwangtungensis</i>	2		2	1.02
<i>Embelia laeta</i>			1	1.00
<i>Sinopora hongkongensis</i>		1	1	1.00
<i>Dendrotrophe varians</i>			2	1.00
<i>Ardisia quinqueгона</i>		2	2	0.99
<i>Callicarpa cathayana</i>		2	2	0.99
<i>Wikstroemia nutans</i>	2		2	0.99
<i>Eurya nitida</i>			2	0.99
<i>Ficus variolosa</i>			1	0.90
<i>Myrica rubra</i>		1	1	0.90
<i>Myrsine seguinii</i>	1		1	0.90
<i>Mallotus paniculatus</i>	1		1	0.90
<i>Rhododendron simsii</i>	1		1	0.90
<i>Maesa perlaria</i>			1	0.90
<i>Diplospora dubia</i>		1	1	0.89
<i>Machilus oreophila</i>		1	1	0.89
<i>Albizia corniculata</i>			1	0.89
<i>Syzygium levinei</i>			1	0.89
<i>Ardisia hanceana</i>			1	0.89
<i>Ilex viridis</i>		1	1	0.89
<i>Sarcandra glabra</i>		1	1	0.89
<i>Elaeagnus loureiroi</i>		1	1	0.89
<i>Casearia velutina</i>		1	1	0.89
<i>Boehmeria nivea</i>		1	1	0.89
<i>Symplocos cochinchinensis var. laurina</i>	1		1	0.88