MODELLING AND COMMUNICATING THE ECOLOGICAL CHARACTERISTICS OF PEAT SWAMP FOREST COMMUNITIES IN BRUNEI

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ABSTRACT

An ecosystem approach to sustainable forest management aims to enhance ecological understanding at the level of the plant community. This thesis demonstrates a novel approach to the study of vegetation ecology in a tropical peat swamp forest (PSF) ecosystem which integrates ecology, visualisation and 3D visualisation in GIS (Geographic Information Systems).

The thesis presents some of the first detailed floristic information on the tree species diversity of the Badas PSF, Brunei. The study adds to the knowledge that intact PSF shows considerable variation even at the small, single site level. Three phasic communities (PC) were identified in a 2.25 ha study area namely PC 2, PC 4 Dipterocarpaceae, PC 4 Sapotaceae, in addition to a heath forest. Shannon-Weiner diversity index values of 1.70 to 2.99 are among the highest in Borneo.

Each community is unique in both species pool and ecological characteristics. The ecologically dominant species which are characterised by tree diameter of more than 80 cm dbh as well as the 11-20 cm tree diameter distribution class patterns in combination are both distinctive from other PSFs in Southeast Asia and lowland dipterocarp forest in Brunei.

Visualisation in 3D provided a novel exploration of floristic and structural data via photorealistic trees. Seamless integration of georeferenced data in a GIS environment replaced the traditional hand-sketch forest bisect through interactive query functions, manipulation of scale, orientations and perspectives, producing distinctive representations of PSF communities.

The approaches used can promote improved understanding of the conservation importance of Brunei’s PSFs, thereby enhancing knowledge of both species and community diversity. This is critical in light of the extreme rarity of this rich ecosystem.

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ABBREVIATIONS

APG	Angiosperm Phylogeny Group
ASEAN	Association of Southeast Asean Nation
BA	Basal Area
BRUN	Brunei Herbarium
BRAHM	Botanical Research And Herbarium Management System
CA	Correspondence Analysis
Dbh	Diameter at breast height
DCA	Detrended Correspondence Analysis (method)
DECORANA	Detrended Correspondence Analysis (program code)
DEM	Digital Elevation Model
DSM	Digital Surface Model
ESRI	Environmental Systems Research Institute
FRA	Forest Resource Assessment
GIS	Geographic Information Systems
GISc	Geographic Information Science
GPS	Global Positioning System
H’	Shannon-Weiner Diversity Index
IV	Importance Value Index
LDF	Lowland Dipterocarp Forest
LEDC	Less Economically Developing Country
MEDC	More Economically Developed Country
LiDAR	Light Detection And Ranging
MEA	Millennium Ecosystem Assessment
Mha	Million hectares
MSF	Mixed Swamp Forest
NMDS	Non-metric Multi Dimensional Scaling
NVC	National Vegetation Classification
PC	Phasic Community
PSF	Peat swamp forest
RA	Reciprocal Averaging
SFM	Sustainable Forest Management
TWINSPAN	Two Way Indicator Species Analysis
UNESCO	United Nations Education Scientific and Cultural Organization
UN	United Nations

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CHAPTER ONE

1 Introduction

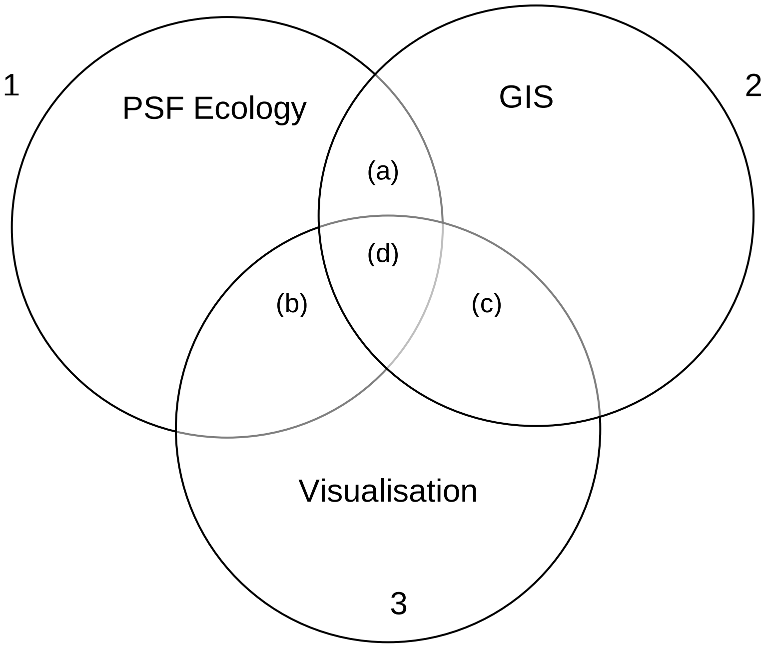
Forests are one of ‘the most biologically-rich terrestrial systems’ (Secretariat of the Convention on Biological Diversity, 2009; p.5). However, tropical forest loss has become a pressing issue at a global scale, in particular in areas where the population growth is rapid and accompanied by an increasing trend in the consumption of natural resources. Among other factors, this trend has been triggered by the aspiration of nations to increase their standard of living in the name of development, in order to keep pace with the global economic climate. The rate of loss of forest is alarming in some parts of the world, especially given the growing awareness of the contribution that deforestation makes to climate change. Hence there has been an increasing focus on sustainable management approaches to forests, including in the Southeast Asia region which is the geographical focus of this thesis (Jusoff *et al.*, 2007; Gunawan *et al.*, 2012).

A sustainable management approach takes into account the balance between socio-economic and environmental needs in development (Secretariat of the Convention on Biological Diversity, 2009). Within the context of forestry, sustainable forestry management requires knowledge of economic development and societal needs, alongside the forest ecology and assessment of the environmental impacts of resource utilisation. Thus to achieve the aim of development that can benefit many in the long run will inevitably require an understanding of the complex ecological processes at work. To this end, baseline information is crucial as a means to offer informed judgements on how best to utilise the forest resource. This thesis will focus on the peat swamp forest (PSF) ecosystem and offer various approaches to reach the objective of knowledge production and dissemination in support of the sustainable management of this forest type. In addition to presenting base line information on the phytosociology and physiognomy of PSF in northern Borneo, other types of information on PSF are also presented in this thesis, including visual representations of plant community types through the use of sketch profile diagrams of trees for each community type and photos of selected species with the aim of broadening the opportunities for knowledge transfer on this forest ecosystem. However while this information is important, it is static and requires regular updating. Potentially this baseline information could be further utilised in ways such as to create a vegetation diversity model through the possible integration of ecological knowledge/theory and Geographical Information Science (GISc). Thus new avenues for visualising forest features are investigated.

Ecology is broadly defined in this study as a branch of science which is concerned with the living and non-living matters as well as their interactions e.g. the link between PSF species distribution and climate factors. It is a wide ranging field which often necessitates information about the environment, chemistry, biology and statistics (Johnston, 2000). The ecological characteristics in this thesis refer to the elements of species diversity, plant composition structure and similarities of the communities (Wang *et al*., 2012).

Geographic Information Systems (GIS) refer to an information system, through which computer programs are harnessed to increase the capability and power of keeping data and executing tasks that deal with spatially referenced events and objects on earth (Longley *et al.,* 2011). Some authors (e.g. Kraak and Ormeling, 2010) have further defined the role of GIS as a decision support system based on the manipulation of GIS spatial and attribute data. GIS offers pattern analysis in vector or raster format, e.g. point and polygon pattern analysis (vector) and pixel (grid cell/raster) analysis. GIS originated in the mid-1960s as a tool for land inventory by the Canadian government, using an inventory tool called the Canada Geographic Information System (CGIS) (Longley *et al.,* 2011). Over time, the further development of GIS has led to widespread applications e.g. in forestry, utilities and cadastre (Kraak and Ormeling, 2010), out of interest from various stakeholders such as resource planners and management scientists (Longley *et al.,* 2011). Geographic Information Science (GISc) on the other hand refers to a discipline which is concerned with studying the methods and techniques of geographically referenced information (Kraak and Ormeling, 2010). One of the most important products of GIS are maps whereby scientific visualisation and cartography fields coincide, each with a varying degree of emphasis on the analysis (exploration) and communication (presentation) aspects of GIS data (Kraak and Ormeling, 2010). The applications of map or GIS data visualisation are varied, and examples of the four main areas are for exploration, analysis, synthesis and communication of new knowledge (Kraak and Ormeling, 2010).

Ecology and GIS visualisation both have spatial elements as a common feature. However, this feature is underutilized in the study of vegetation ecology that commonly uses independent approaches. Figure 1-1 illustrates the relationship between the three fields of study in which each field of study is represented by a circle, called a set, described using a Venn diagram. The mutually exclusive relationship between the two sets as denoted by intersections (a), (b) and (c) will be described first, which will be followed by the relationship of all sets combined at the core intersection (d). Set 1 is ecology; this consists of the phytosociologic and physiognomic details of the vegetation derived from field work. Set 2 is GIS; this applies to the use of both spatial and attribute data while set 3 is data visualisation, such as hand-sketch tree bisect (non-geographic) and point pattern analysis (geographic) containing feature classes or shapefile data.



Key:

a= attribute data of species phytosociologic/physiognomic details
b= non-geographic data
c= spatial pattern analysis
d= 3D tree model

Figure 1-1: Venn diagram showing the union of ecology, GIS and visualisation in the study of vegetation science, together with the interrelationships between them.

The intersection of ecology and GIS sets (a) describes the common features that are shared between them. This can include information on forest structure (physiognomy) or phytosociology in species space. For example, data on species diversity can be ordinated independently as illustrated by set 1 whereas in set 2 the species data could be arranged independently within GIS in either spatial or attribute format. The species attribute data can be separated into groups based on desired features of interest using the GIS query function as illustrated by intersect (a), without mapping the results, which explains the location of (a) outside set 3.

Secondly, there is a relationship between the ecology and data visualisation sets. Intersect (b) denotes the common datasets between set 1 and set 3 in non-geographic space, such as categorisation of tree species through indirect gradient analysis of PSF communities or clustering/dendrogram methods which can be visualised in species space. Further methods that fall into this intersect are the hand-sketch tree bisect, rank abundance plot, species-area curve and tree diameter class distribution. In geographic space, intersect (c) on the other hand describes visualisation of spatial data such as point pattern analysis. In this intersect, the capabilities for the analysis of certain non-geographic (species) data are extended, as the data could possibly be converted into geo-referenced data in GIS, and the spatial distribution pattern subsequently analysed.

Intersect (d) describes the PSF communities in species and geographic spaces. This section integrates the species attribute data, species spatial data and visualisation of such data i.e. hand-sketch tree bisect. An example is the use of photorealistic billboard on 3D tree model in GIS.

Modelling diversity is foreseen to help with identifying which species are confined to PSF based on knowledge of floral diversity, species distributions and environmental factors operating at various scales. This knowledge can then help to guide conservation efforts such as through preservation of biodiversity and improved ecological knowledge. There is also a need to identify the types of PSF community which might be most susceptible to either natural or human induced impacts. It is believed that sole reliance on knowledge of forest density e.g. via aerial photo interpretation, may hide the diversity/richness (alpha level), and evenness (dominance) within the forest community types. This knowledge is necessary to increase our understanding on the fundamental ecological processes operating within the PSF.

Furthermore, a previous study of tree stratification indicates that *Shorea albida* predominates in the upper canopy layer in PSF in northern Borneo, unlike the situation found in mixed dipterocarp forest on mineral soils in the same region where the dominant Dipterocarpaceae family can be found in all forest strata (Yamada, 1997). This distinct feature of PSF in relation to patterns of tree height implies the occurrence of a specific mechanism influencing the tree regeneration process.

The novel approach to the study of vegetation ecology presented in this thesis integrates PSF ecology, data visualisation and GIS, with the aim of advancing our knowledge on the PSF ecosystem, with the help of technology in order to instill an appreciation of nature, ecosystem services and the need for sustainable forest management. An additional aim is to provide an avenue for further research on forest diversity; a prerequisite through which the sustainable forestry management objective can be attained in the context of the local and global importance of the PSF ecosystem, with a focus on Brunei.

Based on previous preliminary work on the plant diversity of PSF by Page and Waldes (2005), this thesis attempts to fill the gap in the knowledge on PSF biodiversity by focusing on areas where the data are lacking or where an update is required. The purpose is to add value to existing knowledge through descriptions of the patterns exhibited by a number of floristic variables namely species diversity, species dominance and tree structure, all of which are foreseen to act as a framework to further understand the underlying processes determining these patterns. This information can then be used to assist with the prioritisation of conservation efforts for the remaining PSF within the Southeast Asian region and provide a framework for similar studies in other regions with tropical peatlands e.g. South America (Lähteenoja and Page, 2011).

1.1 Aims and Objectives

The overall purpose of this research is to investigate the relationship between tree species diversity and the distribution of peat swamp forest phasic community (PC) types, within the Badas PSF, Brunei. Phasic community was a term introduced by Anderson (1961; 1963) in his studies of PSF in northern Borneo. It is used to refer to a successional stage of peatland development both in space and in time. Despite the relatively small area of peatland in Brunei compared to other Southeast Asian countries, Anderson identified six PSF vegetation community types within this country's peatlands. The scientific findings will be used as a medium of communication to interested stakeholders through visualisation and to offer further understanding of the relationship between PSF and environmental gradients which has potential for further academic use, prioritisation of conservation areas, environmental impact assessment, ecological restoration and the sustainable management of PSF.

The research questions are divided into three themes namely peat swamp forest ecology, visualisation and GIS, described as follows:

1. Peat swamp forest ecology

- What are the plant communities within Badas from the perspective of plant species space?
- What is the relationship between species diversity and dominance in the PSF?

2. Visualisation and GIS

- How can an ecological understanding of PSF be visualised and communicated to a range of stakeholders for sustainable management of this ecosystem?

The following objectives were used to achieve these aims:

- to carry out a vegetation survey within the Badas PSF, Belait district where different PC types of PSF can be found
- to use the Shannon-Weiner Index to measure the present state of tree species diversity in this area
- to analyse patterns of tree abundance and diameter class distribution to understand species dominance and potential environmental gradients
- to use ordination and classification for identifying species types from the species pool and identify the potential environmental gradients. Also to identify characteristic and common species

- to use visualisation as a means of communication on forest ecology from multiple perspectives and to promote the need for sustainable approaches to forest management.

The focus of the work is on the structural and plant diversity variation in PSF phasic community (PC) types which are believed to be static within short (decades to centuries) ecological timescales. Moreover, these PC types are thought to have adapted to specific environmental conditions and are at an ecological climax stage for those specific environmental conditions. As there are no major external factors influencing their distribution, such as natural hazards, it is hypothesised that vegetation structure and distribution are influenced by a closed system inherent to their surroundings i.e. in terms of the spatial arrangement of dominant species.

A further assumption is that variations in patterns of floral diversity, whether at regional or local scales, can be explored and visualised through Geographic Information Systems (GIS) or modelling processes.

1.2 Thesis Outline

Chapter one introduces the thesis and covers issues related to biodiversity information such as the need for baseline information and integration of PSF ecology, visualisation and GIS in ecological/species modelling. This chapter also provides the aims and objectives of the thesis.

Chapter two is a literature review, which provides a critical overview of the knowledge gaps on peat swamp forest diversity and distribution and the factors affecting it. The ecosystem services as applied to the peat swamp forest ecosystem are also examined. An overview of the ecosystem approaches to the sustainable management of forest is given, with particular reference to peat swamp forest in the Southeast Asian region and Brunei in particular.

Chapter three provides the methodology and study site description. Methods for data acquisition on PSF species (including sampling) and visualisation of PSF communities are also described and explained in this chapter.

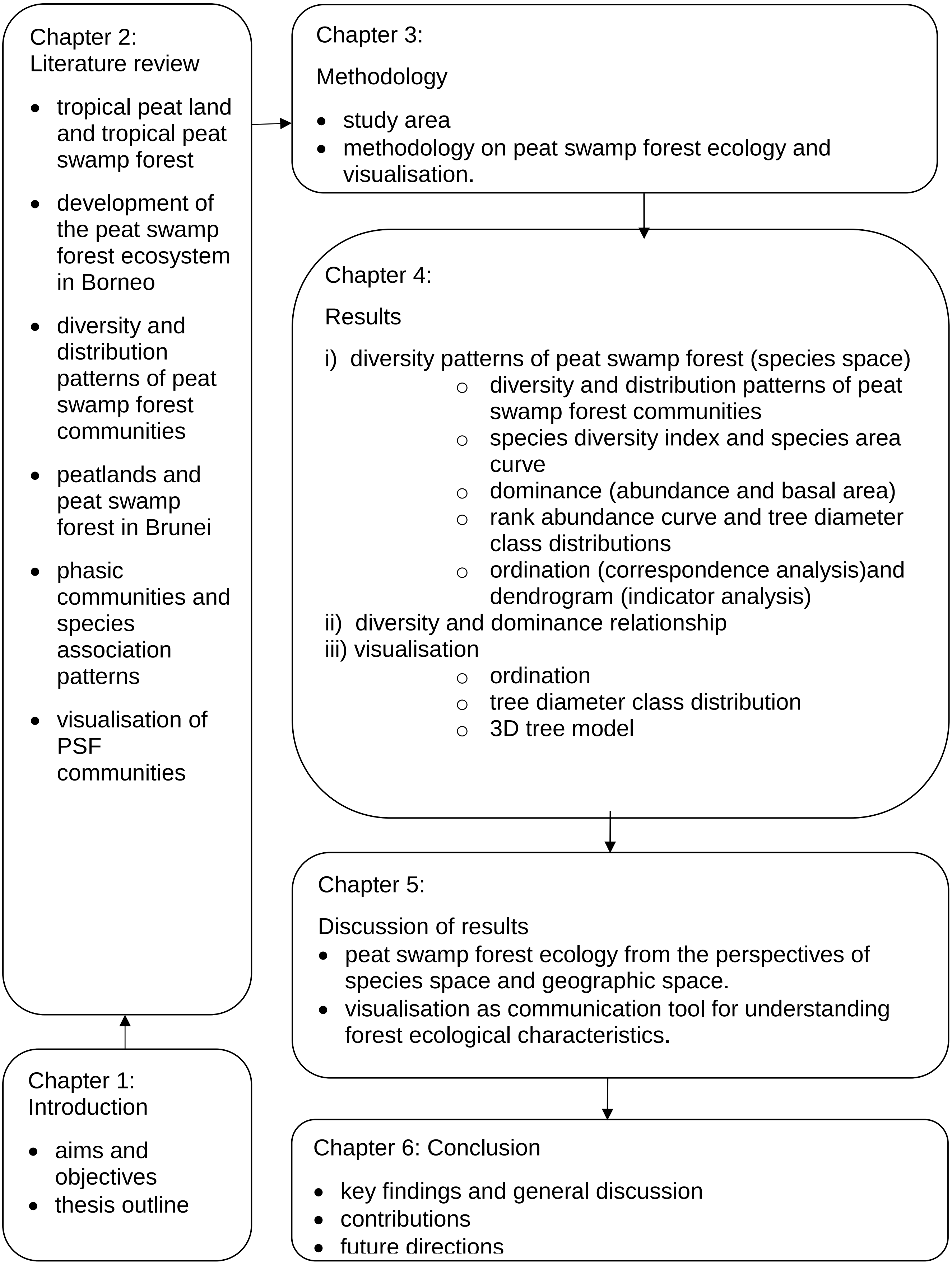
Chapter four is the results chapter which explores the species diversity-dominant relationships in addition to exploring various measures of species dominance. Furthermore it presents the results of ordination and classification processes of identifying plant community types on the basis of the species association concept, which includes determining the key species of the peat swamp forest.

Further results include the vegetation mapping i.e. 3D tree model as a visualisation and communication tool to increase the conceptual understanding of peat swamp forest diversity and ecology. This thereby indirectly provides knowledge for an ecosystem approach to the sustainable management of forests.

Chapter five is the discussion of the results chapter which provides a broader overview on the findings of PSF analysis of the study area compared against findings of previous analysis of PSF of other regions in SE Asia. For example, the chapter explores the diversity and dominance patterns of the PSF communities. Further discussion ensues on the advantages and limitations of the 3D tree modelling. This chapter also highlights some pertinent issues such as the diversity information crisis and data standardisation.

The final chapter, chapter six is the concluding chapter which synthesise the integrated applications of ecological paradigms and visualisation technology in vegetation science. Some contributions and limitations derived from this thesis are also provided in this chapter.

Figure 1-2 below provides a summary of the principal research pathways of this thesis, and the organisation of contents into appropriate research themes that comprise of the elements of ecology/ecological characteristics of the peat swamp forest, visualisation and GIS.



Chapter 2:
Literature review

- tropical peat land and tropical peat swamp forest
- development of the peat swamp forest ecosystem in Borneo
- diversity and distribution patterns of peat swamp forest communities
- peatlands and peat swamp forest in Brunei
- phasic communities and species association patterns
- visualisation of PSF communities

Chapter 3:

Methodology

- study area
- methodology on peat swamp forest ecology and visualisation.

Chapter 4:

Results

i) diversity patterns of peat swamp forest (species space)
  - diversity and distribution patterns of peat swamp forest communities
  - species diversity index and species area curve
  - dominance (abundance and basal area)
  - rank abundance curve and tree diameter class distributions
  - ordination (correspondence analysis)and dendrogram (indicator analysis)

ii) diversity and dominance relationship

iii) visualisation
  - ordination
  - tree diameter class distribution
  - 3D tree model

Chapter 5:

Discussion of results

- peat swamp forest ecology from the perspectives of species space and geographic space.
- visualisation as communication tool for understanding forest ecological characteristics.

Chapter 1:
Introduction

- aims and objectives
- thesis outline

Chapter 6: Conclusion

- key findings and general discussion
- contributions
- future directions

Figure 1-2: A schematic diagram to illustrate a summary of this research.

CHAPTER TWO

2 Literature review

Many of the Less Economically Developed Countries (LEDC) lie within the Tropics, where both forest cover and biodiversity are high. Increasing population pressure, especially in the Tropics, is associated with rapid land conversion, increased demand for food and, together with climate change, these tensions call for improved forest management practises that can benefit both people and the environment in the long run. In this context, there is potential for the application of spatial vegetation analysis and modelling, as a way to enhance our knowledge and understanding of forest ecosystems.

Land use and vegetation compositions/physiognomies within forests across climate types are among the many variables that are used to define forest or forest types and to describe variations from one region to another. In a global context, a standard definition of forest is based on the Forest Resource Assessment (FRA, 2010). This definition of forest implies that spatial extent, tree height and canopy coverage are the core metrics in forest characterisation. However, a global classification which accommodates the many diverse forest types is more difficult to accomplish, and the issue is further accentuated by the fact that forest-related information derived from field methods has not been able to keep pace with the rapid rate of forest change. Notwithstanding that information on forest mensuration is vital to forest management, it is equally important to understand the underlying ecological processes which contribute to the observed spatial patterns.

As well as ecological processes, species distribution/diversity patterns of forests and forest structure may also be influenced by disturbances such as logging or fire. In the PSF ecosystem, there are compounding problems from the repeat occurrences of and the susceptibility of these forests to fire. In addition, PSF that has been subject to multiple disturbances has been shown to undergo very slow regeneration (Page *et al.*, 2009). Hence, maintaining the stability of intact PSF can be regarded as not only important for regional biodiversity conservation but also as a last stronghold to maintain the huge pool of carbon stored in the peat beneath the PSF.

Furthermore, Levin (1992) stated that changes in biological diversity at both global and regional scales all have originated from and are the consequences of often small-scale events. Therefore this chapter will focus on the exploration and analysis of vegetation patterns at plot and landscape level, incorporating knowledge of PSF ecology, and the application of GIS and visualisation methods (chapter one), to infer the possible contributing processes forming such patterns. This knowledge will then be taken forward into an investigation of how this information can be visualised for improved understanding of the conservation importance of PSF.

2.1 Tropical Peatland and Tropical Peat Swamp Forest.

The dual nature of tropical peatland as both a carbon stock (both in aboveground biomass and, below ground, in the peat) and as a forest has ignited interest from various fields of study, and led to the recognition of accurate inventories as a facilitating tool for conservation of this important ecosystem. More than half of the global tropical peatland resource is located in Southeast Asia i.e. 247,778 km^2 out of a total estimated 441,025 km^2 (Page *et al.*, 2011). The eight countries of Southeast Asia with significant peatland are Brunei, Indonesia, Malaysia, Myanmar, Papua New Guinea, Philippines, Thailand and Vietnam (Page *et al.*, 2011), with the largest fraction contributed by Indonesia and Malaysia, while the least is in Vietnam. Figure 2-1 shows the main distribution of some of the Southeast Asia peatland, focusing on Malaysia, Indonesia and Brunei.

Figure 2-1: Map showing location of peatlands in insular Southeast Asia. Source: Page *et al.* (2004; 626).

2.2 Development of the Peat Swamp Forest Ecosystem in Borneo

The peatlands of Brunei and elsewhere in northern Borneo began their development some 5,500 years ago following the rapid rise and subsequent stabilisation of the sea level following the Last Glacial Maximum (Anderson, 1963). As alluvial deltas advanced seawards at that time, the new land was colonised first by mangroves, at the seaward edge, and in the interior of the delta, by peat swamp forest. The succession to peat-forming forest was likely facilitated by the low relief, favouring waterlogging, and the reducing conditions in the mangrove sediments, which limited the decomposition of organic material. The difference in time since the deposition of organic matter began has led to the formation of peat domes of varying thickness and also different patterns of different PSF vegetation communities, which exist from the edge to the centre of the peatland domes. Further inland, the accumulation of dead organic matter has created a raised bog type, which is dome shaped for mature peat swamp, such as the Baram dome in Sarawak and the Badas dome in Brunei. Due to the poor aeration and limited nutrient supplies, the vegetation at the centre of the peat dome will often appear to be stunted, and other features, such as thick, reduced leaves, may also increase resistance to stress through adaptation. The peat is oligotrophic with the only source of moisture and nutrients supplied by rainwater (i.e. these are ombrotrophic systems). Sabiham (1990) explained the smooth dome topography of peatlands at the present time as a reflection of the accumulation of peat and its ability to keep pace with the gradual rise in sea level. His study based on fossil-pollen analysis suggested that the vegetation composition in the peat indicates a catenary sequence of vegetation succession following the initial period of peat soil formation.

2.2.1 Ecosystem Services of Peat Swamp Forest

There are four main categories of ecosystem services summarised by the MEA report (Millennium Ecosystem Assessment, 2005b). These comprise the provisioning, cultural, supporting and regulating services. Provisioning services refer to tangible benefits such as timber, while intangible benefits are supporting, cultural and regulating services (Secretariat of the Convention on Biological Diversity, 2010). Figure 2-2 illustrates the broad range of services provided by forest ecosystems with some examples of the global dynamics which affect the resource functions, such as anthropogenic impacts on biogeochemical cycling operating both above and below ground, with subsequent effects on ecosystem services.

Page and Rieley (1998) categorised a number of natural resource values of PSF into functions performed, products generated and value attributes which corresponded to regulating, provisioning, and cultural services respectively (Millennium Ecosystem Assessment, 2005b). In addition, the forest ecosystem also provides supporting services, such as nutrient cycling and soil formation (Secretariat of the Convention on Biological Diversity, 2010). Carbon sequestration and water regulation are the two major regulatory ecosystem services provided by PSF, with disturbances of these functions having profound impacts at a local, to regional or even global level.

Figure 2-2: An illustration of the different types of global changes affecting ecosystem functions and delivery of ecosystem services (after Scherer-Lorenzen, 2014; 197, with modification).

Over the last two decades, various studies of PSF in Southeast Asia have underlined that this is a unique and complex ecosystem which is characterised by the interrelated components in the fields of hydrology, soil science, meteorology and forest ecology, and hence it provides a wide array of ecosystem services.

For instance, in terms of hydrology, this ecosystem harbours a rich aquatic life (Yule, 2010), with PSF fish providing an important source of protein for indigenous people living in or around peatlands in Malaysia (Yule, 2010). In the field of meteorology, peat, through the presence of a vegetation cover, provides a suitable microclimate (Ludang *et al.*, 2007) and hence refuge for a wide range of forest wildlife species (Yule, 2010). The PSF sequesters carbon from the atmosphere, with a proportion of the woody biomass being converted to peat in the waterlogged ground, and stored over millennial timescales (Page *et al.,* 2004). Disturbance of the peat carbon store, e.g. through drainage and fire, leads to the release of greenhouse gases and minute particles such as soot into the atmosphere. This not only has the potential to make a significant contribution to atmospheric greenhouse gas concentrations and hence to climatic change but, during fire events, can also lead to acute health problems. For example, the *El Niño* related fire event in 1997 (Page *et al.*, 2002), which resulted in widespread forest fires across Southeast Asia, affected for example in Malaysia, in excess of 20 million people, through the dispersion of micro inhalant particles in smoke, which caused a sudden sharp increase in the incidence of respiratory-related illnesses (Brown, 1998). Since 1997, there have also been extensive, severe fires during subsequent *El Niño events* such as in 2002 (Yulianti and Hayasaka, 2013); in 2006 (Worden *et al*., 2013; Yulianti and Hayasaka, 2013) and in 2009 (Yulianti and Hayasaka (2013). PSF ecosystem services may also be related to the productivity and diversity of species. Many of the PSF types in Southeast Asia are known to support tree species that have significant commercial value, e.g. *Gonystylus bancanus* (Ramin), or provide a source of food, e.g. *Durio carinatus* (Durian) and *Tetrameristra glabra* (Punah) for mammals and avian species, or a suitable niche for breeding e.g. *Alstonia angustiloba* is a preferential nesting spot for storks (Jusoff *et al.*, 2007). Moreover, the animal and insect communities supported by PSF play an important role as agents of pollination and seed dispersal (e.g. Poesie *et al.,* 2011). The multi-component characteristics of the PSF ecosystem therefore support a wide spectrum of ecosystem services, all of which are susceptible to loss under intensive human utilisation of the forest environment.

In Brunei as elsewhere in the region, the ecosystem services rendered by intact PSF include its role as a natural flood protection control by regulating the overland flow, absorbing the excess water for groundwater recharge during the peak flood period, and maintaining sub-surface flows i.e. throughflow and base flow during dry periods. During peak flood periods, the sheer presence of a peat surface in the landscape results in a reduced chance of flooding by allowing the excess water to spread across a wide peat surface. By so doing, the dead and live organic mass e.g. the low wing and spreading buttresses of the peat swamp trees increases friction and hence allows water to be held in large quantities in the hollows and surface depressions on the peatland (Dommain *et al.,* 2010). The surface roughness slows down the speed of the overland flow and as a result, there will be ample time for the excess water to infiltrate the sub-surface layer leading to groundwater recharge. Being a natural water reservoir, intact PSF also offers other hydrological services.

There is a range of different vegetation communities in PSF, which vary with varying peat thickness and distance from the peat dome and hence the ecosystem service may equally vary on a local scale i.e. PSF located at the top of the peat dome may have a higher water table than that located on the dome slope, while the peat adjacent to the coastal margin or freshwater swamp may be subject to riverine or even occasional marine flooding (Figure 2-3). In this respect, the role of PSF in regulating flood water may vary between the different phasic community types of PSF, in influencing the evapotranspiration rate and hydrological balance at the sub-surface level, all of which depend upon other factors such as peat bulk density, porosity, infiltration capacity and the underlying geology underneath the peat soil. In a study comparing the different soil types, peat was found to increase soil infiltration capacity through reduction in the bulk density in soil, and hence it reduces overland flow and soil erosion (Ekwue and Harrilal, 2010). On the other hand, peat compaction due to disturbance will reduce infiltration and increase the chances of overland flow taking place (Ekwue and Harrilal, 2010).

2.3 Diversity and Distribution Patterns of Peat Swamp Forest Communities

Across the Southeast Asian region, PSF plant community types differ greatly in their plant community and floral species composition and forest structure (Table 2-1). The earliest comprehensive work on the PSF floristic composition by Anderson (1961) focused on Brunei and Sarawak in northern Borneo. He noted that despite other studies on PSF having been carried out in the region at that time, such as in East Borneo, South and Central Sumatra, Malaysia and southern New Guinea, there had been a lack of detailed study of the ecology or floristic composition of PSF (Anderson, 1963). Thus knowledge on the floral distribution and diversity patterns was limited. Further, more recent field surveys in the Southeast Asian region have revealed distinctive patterns of PSF communities in terms of their species composition, operating at various scales from sub-regional to regional. Within Borneo, the PSF of the northern part of the island (i.e. Sarawak and Brunei) comprises of up to six phasic community types (Anderson, 1961) whereas in the southern part of the island (i.e. in the Indonesian portion, Kalimantan) five community types have been described (Shepherd *et al.*, 1997; Waldes and Page, 2001). Although there may be superficial similarities in terms of the physiognomy and structure of these communities, with tall marginal forest communities on shallow peat usually being replaced by lower canopy, much denser pole forests on deeper peat towards the centre of the peat dome, the communities themselves are often quite different in terms of their floristics.

PSFs are also widely distributed on the large Indonesian island of Sumatra. The four forest types which have been reviewed from various studies by Gunawan *et al.* (2012) in Sumatra are Mixed PSF, *Meranti paya* forest, *Padang Suntai (Palaquium)* and *Bintangur (Calophyllum)* forest. In some locations, the number of communities is reduced, e.g. in Gunawan's study area in Giam Siak Kecil-Bukit Batu he only identified Mixed PSF and *Bintangur* forest types. Beyond Sumatra and Kalimantan, there is almost no floristic information available on the peat swamps of the other areas of Indonesia with extensive peatland, i.e. southern New Guinea (West Papua province). Beyond Indonesia, the plant species composition of PSF again differs greatly, with two different studies of PSF in Thailand describing five and three tree communities respectively (Suzuki and Niyomdham, 1992; Bunyavejchewin, 1995). The number of PSF community types in Thailand is not only fewer than is found in Borneo, but the forest is also dominated by different species, such as *Macaranga pruinosa*, which may be indicative of forest disturbance (Graham, 2009). Although the overall number of communities in Thailand was about four times higher, the non-tree communities were also included. In addition, on the Malaysian peninsula, Jusoff *et al.* (2007) identified five PSF sub–habitat types - all within one Mixed PSF community, indicating a higher level of floristic differentiation at the sub-community level. The floristic composition of the Mixed PSF in Malaysia is different from that of Mixed PSF in Borneo. For instance, while five different sub-types in MSF have been described on the basis of species assemblages (Jusoff *et al.*, 2007) in Brunei (Borneo) only two main MSF sub-types have been described based on different dominant species (Yamada, 1997) (Table 2-1).

Table 2-1: Summary of PSF community types described from Southeast Asia (in chronological order).

Location	Plant community types	Number of plant communities	Reference source
Brunei Darussalam and Sarawak	PC 1 Mixed PSF (*Gonystylus-Dactylocladus-Neoscortechinia assoc.)* PC 2 *Shorea albida-Gonystylus-Stemonurus* association PC 3 *Shorea albida* consociation PC 4 *Shorea albida-Litsea-Parastemon* PC 5 Padang mixed species (*Tristania-Parastemon-Palaquium* association) PC 6 *Combretocarpus–Dactylocladus* association	6	Anderson (1961)
Sabah	*Dactylocladus stenostachys / Gonystylus bancanus* *Dacrydium elatum / Gymnostoma nobile* *Lophopetalum multinervium*	3	Fox (1972) cited in CAIMS (2005)
Thailand (Narathiwat)	Mixed swamp forest (*Baccauria bracteata-Endiandra macrophylla*) *Macaranga pruinosa* community *Schima wallichii-Fagraea fragrans* community *Lygodium microphyllum- Melaleuca cajiputi* community *Evodia roxburghiana-Melaleuca cajiputi* community	5	Suzuki and Niyomdham (1992)
Thailand (Narathiwat)	Mixed peat swamp Mixed peat swamp with *Macaranga pruinosa* community *Macaranga pruinosa* community	3	Bunyavejchewin (1995)
Brunei Darussalam	Mixed peat swamp; MSF (1) and MSF (2) forest type Alan forest (PC 2) and Alan batu forest (ageing PC 2) Alan bunga forest (PC 3) Padang Alan forest (PC4 Sapotaceae dominant) Alan Padang forest (PC4 Dipterocarpaceae dominant)	5	Yamada (1997)
C. Kalimantan	Riverine forest Transition forest Mixed swamp forest Low pole forest Tall interior forest	5	Shepherd *et al.* (1997); Waldes and Page (2001).
East and South Sumatra (Padang Sugihan, Sugihan East and Padang Island)	Chablis forest Mixed forest Tall pole forest (*Calophyllum*) Low pole forest	4	Brady (1997)
Sumatra	Mixed peat swamp Meranti paya (*Shorea*) forest Padang Suntai (*Palaquium*) forest	3	Momose and Shimamura (2002)
Peninsular Malaysia (Pahang state)	Mixed PSF (with 5 different sub-habitat types within)	1	Jusoff *et al.* (2007)
East Sumatra (Giam Siak Kecil-Bukit Batu)	Mixed PSF Bintangur (*Calophyllum*) forest	2	Gunawan *et al.* (2012)

Published vegetation classifications for tropical PSF in Southeast Asia have applied various approaches, often using a combination of phytosociology and physiognomy. An example is the contrasting use of approaches in different PSF sites within Narathiwat province, Thailand whereby the Braun-Blanquet system was used by Suzuki and Niyomdham (1992). On the other hand, a relative Importance Value (IV) index, based on tree density and basal area relation, was used by Bunyavejchewin (1995). Species relative basal area dominance, relative frequency and relative abundance, which make up the IV index, have also been used in several other PSF classification studies e.g. Gunawan *et al.* (2012), with the resultant distinction between different forest types, e.g. Mixed peat swamp forest and the Calophyllum forest. The sole use of a phytosociological approach was deemed inadequate for describing other aspects of PSF diversity. In the PSF of Southeast Asia forest structure has become the prime interest in inventories due to the presence of multiple forest stratification (Bunyavejchewin, 1995), with relevance in both ecological studies (Graham, 2009) and raising conservation awareness (Posa *et al.*, 2011). The number of PSF communities in Southeast Asia ranges from one to six (Anderson, 1963; Fox, 1972 cited in CAIMS, 2005; Suzuki and Niyomdham, 1992; Bunyavejchewin, 1995; Yamada, 1997; Shepherd *et al.*, 1997; Brady, 1997; Waldes and Page, 2001; Momose and Shimamura, 2002; Jusoff *et al.*, 2007 and Gunawan *et al.*, 2012), while the first detailed account of PSF in Thailand, which has also included secondary plant communities, revealed a combined total of 22 forest and non-forest communities i.e. including shrub and grassland vegetation (Suzuki and Niyomdham, 1992).

One of the issues confronting any study of forest biodiversity is that there is no single international standard which can be used to classify vegetation and, specifically, forest and peatland vegetation. In 1973, an attempt was made by UNESCO to provide a classification based on vegetation physiognomic-structural features along with some ecological data (UNESCO, 1973). Specific to peatland vegetation classification, some finer level classifications for peatlands do exist. For example (beyond the tropics), a comprehensive classification systems of wetland vegetation in Canada were proposed (Harris *et al.,* 1996 cited in Rydin and Jeglum, 2013) with 36 different types of wetland vegetation encompassing all wetland types such as marsh and fen (Rydin and Jeglum, 2013).

In the UK, phytosociology formed the foundations of the British National Vegetation Classification (NVC), based on species frequency and abundance with the use of frequency class and the Domin scale respectively (Rodwell, 1991). Within the British NVC, 38 mire (peatland) communities were described based on floristic variations only (Rodwell, 1991; Elkington *et al.,* 2002) and some ecological data such as peat depth, peat pH and nutrient content, altitude and climate were also given (Rodwell, 1991). The application of the NVC has been widespread in the UK, including advice on the selection of Sites of Special Scientific Interest, and scientific research of plant-environment relations affecting the distribution and composition of plant communities (Rodwell, 2006).

Forest biodiversity information is thus one of the core elements of sustainable forest management (FAO Corporate Documentary Repository, 2011), since it provides essential prerequisite knowledge for the development of appropriate conservation strategies for protecting species diversity at various levels. It can also contribute to an improved understanding of the relationship between floral diversity and other natural resource functions, e.g. carbon and water dynamics (Simbolon and Mirmanto, 1999).

2.3.1 Inventory of Peat Swamp Forest diversity/ecology

In 2003, a survey within the Southeast Asian region had identified fires and loss of biodiversity as major problems (ASEAN Peatland Management Initiatives, 2003). A crisis in biodiversity knowledge/inventory, ambiguity in the delimitation of species, their distributions and potential uses were also highlighted as obstacles in a more recent study by Webb *et al.* (2010). The substantial provision of commercial products from forested lands has made Southeast Asia highly reliant economically on forestry and natural resource exploitation; in addition, forested areas are identified as particularly susceptible to climate change (Asian

Development Bank, 2009). Thus there is considerable concern about, and interest in, promoting better understanding and conservation of forest biodiversity within the Southeast Asian region.

The PSFs of the region require an approach to management that not only protects their biodiversity but also provides a range of other long-term ecosystem services and benefits. This thesis will primarily deal with the plant diversity of PSF, its distribution and factors affecting it at one study location in Brunei, discussed within the wider context of the current state of limited knowledge and understanding of the complexity of the ecology of the PSF ecosystem across the Southeast Asian region. Hence, information on both the forest species composition and forest structure is needed to provide the foundation on which further long-term assessment of biodiversity and factors affecting it can be based, and forest resources can be conserved. As discussed above, the tropical peat ecosystems of Southeast Asia are recognised as having important natural resource values (Page and Rieley, 1998).

Moreover, Phillips (1998) stated that the lowland PSF ecosystems were rare outside the Southeast Asian region, further adding that there was an urgent need for more ecological information on the natural PSF ecosystem. Recent research has improved our knowledge of the extent of tropical peatlands on a global scale through meticulous assessment of peatland inventory across the tropics (Page *et al.*, 2011), but there has been no such systematic inventory for the peat swamp forests. Page and Waldes (2005) noted that there was a need for more detailed description of PSF plant communities amid high rates of disturbance of PSFs in recent times, while, more recently, Posa *et al.* (2011) highlighted the urgent need for research on the biodiversity and ecology of the remaining PSFs of Southeast Asia.

It is generally agreed that the two most important problems facing the management of PSF in ASEAN countries in recent years have been fire and biodiversity loss (ASEAN Peatland Management Initiatives, 2003).

Arguments in support of the conservation of this ecosystem have revolved around the prioritisation of forest types (Paoli *et al.*, 2010). While it is widely acknowledged that the plant diversity associated with PSF can be lower than that of some other forest types found on mineral soils within the Southeast Asian region (Yamada, 1997; Page and Waldes, 2005; Posa *et al.*, 2011), this ecosystem does however still have a high conservation importance. Some other authors have even gone further and argued that undue emphasis has been placed on the conservation of PSF as opposed to other forest types in Southeast Asia (Paoli *et al.*, 2010). One reason for this has been that the carbon stocks in PSF in the aboveground biomass, but more particularly belowground in the peat, are much higher than in other forest types. While no marked distinction in aboveground carbon stocks was found for forests on two different soil types, i.e. mineral and organic (peat) soils, the belowground carbon stock of lowland forest on peat was eight times higher than forests on mineral soil (Paoli *et al.*, 2010). This study concluded by highlighting the need for a regulatory framework as a way to achieve a balance between management to maintain forest carbon along with the preservation of biodiversity, particularly in areas that are species rich and which are focal areas for threatened species. In spite of this, other authors have stressed the biodiversity value of PSF, which, although not as species diverse as some mineral soil forests, nevertheless supports a number of species of restricted distributional range, some of which are endemic to the PSF ecosystem, e.g. the tree species *Shorea albida*, which is restricted to peat soils in northern Borneo, and a number of blackwater fish species (Giam *et al.,* 2012).

2.3.2 Factors Affecting Diversity and Distribution of Peat Swamp Forest

A large number of studies have attempted to explain the various biotic and abiotic factors influencing the diversity, distribution and dominance of PSF species, including Anderson (1963), Brady (1997), Ibrahim (1997), Shepherd *et al.* (1997), Stoneman (1997), Yamada (1997) and Shimamura and Momose (2005). Table 2-2 provides a summary of the main factors identified in these studies. Abiotic factors relevant to the PSF environment include microclimatic factors such as the amount and seasonality of precipitation, levels of solar radiation, air and peat temperature, along with nutrient supply and degree and duration of waterlogging. Biotic factors refer to processes such as species interactions at different trophic levels, invasion and competition. The importance of these factors will be influenced by the scale of observation of the field study. At a regional level, for example, abiotic factors influence the distribution of species in relation to general climatic patterns, while biotic factors are important in influencing the local-scale distribution and variation of species due to local processes such as competition and seed dispersal, which can affect smaller-scale population dynamics. There have been very few studies which have investigated the biotic factors operating in PSF, with most studies focusing on abiotic influences.

Table 2-2: Summary of some physical and human factors affecting the species distribution of PSF in Southeast Asia based on previous studies.

Physical factors	**Reference source**
History	Anderson (1963)
Wind	Anderson (1963)
Lightning	Anderson (1963)
Insect infestation (caterpillar)	Anderson (1963)
Peat depth	Anderson (1963)
Alan double root system	Yamada (1997)
Leaf-litter, organic matter	Brady (1997)
Water table and peat depth	Shepherd *et al.* (1997), Stoneman (1997)
Regeneration	Kobayashi (1999)
Microtopography	Stoneman (1997), Shimamura & Momose (2005)
Microclimate; temperature & soil moisture	Ludang *et al.* (2007)

Human factors	**Reference source**
Logging	Ibrahim (1997)
Agriculture	Suzuki and Niyomdham (1992), Ludang *et al.* (2007)

Historical events also play a role in PSF species distribution; these operate at a regional level. Anderson (1963), for instance, suggested that sea level changes and associated coastal erosion and sediment deposition during the period immediately after the postglacial period were a significant contributory factors to the current distribution of PSF in northern Borneo. At a local scale, a study by Brady (1997) on organic matter (biomass and litter) and peat depth relationships in Sumatra demonstrated that the four main PSF forest types in his study location showed a direct correlation with peat depth although he failed to establish a direct link between the vegetation type and water table level (average depth and amplitude). A further study by Shepherd *et al.* (1997) on the distribution of plant communities in a PSF in Central Kalimantan focused on peat depth and surface elevation, as well as on peat hydrology and chemistry. They observed that average tree heights were not related to peat depth and suggested instead that peat chemical analysis and hydrological data provided a stronger relationship with floral diversity, with hydrology the prime factor. Stoneman (1997) came to a similar conclusion on the relationship between hydrology and PSF community distribution in his study of the Badas swamp in Brunei, while also establishing that there was no significant correlation between microtopographic variations i.e. between the vegetation on large peat surface hummocks and that of the intervening hollows (Stoneman, 1997). A similar study on forest microtopography was conducted by Shimamura and Momose (2005), who explored the relationship between organic matter accumulation and tree species, with reference to dominant and co-existing species. Their results showed that the distribution of dominant trees to some extent had an influence on, and were influenced by the organic matter dynamics surrounding them. They determined the presence of coexisting regenerating species based on the species tolerance to flooding which was reflected in species' preferences for particular microtopographic and microclimatic conditions i.e. mounds, hollows and canopy gaps.

In Central Kalimantan, Ludang *et al.* (2007) investigated the role of land use changes in the PSF forest microclimate through investigations on sites with agriculture, forest and forest regrowth and cleared forest. Daily and diurnal temperature fluctuations for different land use types were recorded. The findings showed that the vegetation cover exerted a strong influence on the aboveground temperature of the surface peat layer, which subsequently affected the soil moisture content of the peat. There was significant correlation between the vegetation cover, the temperature of the top peat layer and the air temperature. The increase in both peat surface and air temperatures for areas with reduced vegetation cover compared with forest ranged from 1.09 to 2.97 °C, while fluctuations in daily and diurnal temperatures ranged from 2.25 to 5.55 °C, leading to a significant loss of soil moisture content of 11.65% in the upper 20 cm of the peat layer.

An extreme example of how conversion to agricultural use can affect the PSF ecosystem is the failed 1.5 Mha Mega Rice Project in Central Kalimantan which was implemented between 1996 and 1999 (Ludang *et al.*, 2007), with disastrous consequences for the PSF habitats. This project not only led to the widespread clearance of PSF and extensive peatland drainage, with associated loss of forest biodiversity, it also greatly increased the risk and frequency of peat fires, leading to the loss of forest regenerative capacity and the replacement of tall forest by shrub and fern-dominated vegetation (Hoscilo *et al.,* 2011), thereby greatly reducing the chances of forest recovery. On a less dramatic scale, other human factors have been noted to affect PSF plant species distribution and diversity, as illustrated in a study of PSF in Malaysia (Ibrahim, 1997). This author found that the diversity of small trees within the PSF was higher for the virgin forest in Pekan, Pahang than in Kuala Langat, where excessive drainage has led to high tree mortality especially of the smaller trees.

The PSF of Thailand provides an example of human-induced effects on this ecosystem. In this country, some 90% of the population are involved in some form of agricultural activities, which include burning, draining and reclamation of the soil (Suzuki and Niyomdham, 1992). One of the most profound effects of the opening up of PSF for agriculture has included an increase in the extent of acid sulphate soils, since peatland drainage often exposes the underlying potential acid sulphate materials, thereby impeding subsequent cultivation (Suzuki and Niyomdham, 1992). In this case, the forest cover provided an important service in terms of preventing the exposure of underlying toxic substrates. But once the acid sulphate soils were exposed, regeneration of the original forest vegetation was hindered. In Narathiwat, only 6,000 ha out of the former 26,600 ha of primary PSF in that province remained intact (Bunyavejchewin, 1995). The Klias Peninsula, Sabah, on the other hand, provided an example of a natural event affecting the PSF vegetation whereby an estimated loss of 100 ha of the PSF was recorded as a result of droughts and wildfire during the 1997-98 *El Niño* event (Nilus *et al.*, 2011). The initial estimated PSF cover in Sabah was 100,000 ha (Nilus *et al.*, 2011), but now only a small fraction of Sabah PSF remains, as some 80% has been affected by the process of urbanization, logging and wildfires (Nilus *et al.*, 2011).

Across the whole Southeast Asian region, the degradation and loss of forests and specifically PSF, is continuing at a rapid rate. Miettinen *et al.* (2011) reported a decline in PSF from 13.97 Mha in 2000 to 11.21 Mha in 2010, a loss of 19.7%, the highest loss by far of any forest type in this region (losses for mangroves and lowland evergreen forest in the same period were 12.5% and 11.1% respectively). This would lead to the loss of a range of unique biodiversity and forest communities (Posa *et al.*, 2011). Hence, there is a need for increased awareness not only of the plant species but also their contribution to forest ecology. For instance, the awareness of the mutual interdependence of PSF, peat and water, due to the fact that disturbance in any of these three ecosystem components will have detrimental impacts on other components of the ecosystem, for example through the interrelated processes of plant adaptation to suitable environmental conditions, hydrological dynamics and nutrient cycling (Dommain *et al.,* 2010). These authors further stress that high conservation prioritisation should be given to any surviving areas of PSF, for example due to the extreme rarity of intact or almost intact peat domes in Southeast Asia at the present time (Miettinen & Liew 2010a, b, cited in Dommain *et al.,* 2010).

Issues of species loss in the tropics have recently been addressed by joint scientific endeavour through the Millennium Ecosystem Assessment (MEA), which raised concerns about the threats to and loss of forest ecosystems, species and populations on a significant and rising scale across the world. The main cause has been identified as concurrent forest habitat loss and degradation, but the consequences of loss of forest diversity will likely be made more severe as a result of increasing climate change effects over the coming decades (Millennium Ecosystem Assessment, 2005a cited in Secretariat of the Convention on Biological Diversity, 2009).

2.4 Peatlands and Peat Swamp Forest in Brunei

The FRA country report for Brunei Darussalam (FRA, 2010) defined forest as land of more than 0.5 ha with trees more than 5 m tall and a canopy cover greater than 10 percent, or with trees which can reach such thresholds in its original site (FRA, 2010). The FRA categories distinguish forest from other types of wooded land by the percentage canopy cover; despite the instances where the land cover and tree heights for wooded land may have similar characteristics to forests. Brunei had some 75% forest cover in 2010, including wooded land (FRA, 2010).

According to the study by Anderson (1963), PSF in Brunei covers an area of about 380 sq. miles i.e. 98,419 ha; Anderson described these areas as ‘coastal and deltaic peat swamps’ (Anderson, 1963; p.131). Based on other reference sources, Rieley (2005) has stated that the area of peatland is 110,000 ha. The more recent FRA (2005) country report indicates, based on 1996 data, that the area of PSF is 103,705 ha, of which, 87,267 ha are defined as intact PSF. In terms of peatland extent, Page *et al*., (2011) reviewed data on the extent of peatland derived from Anderson (1963) and Anderson & Marsden (1984) and provided minimum and maximum values for peatland extent in Brunei of 909 to 984 km^2 i.e. 90,900 to 98,400 ha. The maximum range of 98,400 ha is more conservative than the value of 110,000 ha stated by an earlier study (Rieley, 2005). There are slight variations in terms of the definitions used and extent of PSF or peatland since the original study by Anderson in 1963. The more recent, somewhat lower value for peatland given by Page *et al.* (2011) implies a gradual decrease in peatland area (over which PSF may be found), owing to various factors.

Table 2-3 provides an excerpt from the FRA (2005) data for PSF, based on the 1996 values. This is the reference value which was used in this thesis because it refers specifically to PSF (instead of peatland), in addition to the exclusion of other swamp forest types such as freshwater swamp forest.

Table 2-3: The nine types of forest in 1979 and 1996, Brunei Darussalam. Source FRA (2005).

In Brunei, forests have been categorised into nine different National Classes (FRA, 2005; FRA, 2010) based on the previous work by Anderson & Marsden in 1984 (FRA, 2010). The nine categories are Mangrove, Freshwater Swamp Forest, PSF, Kerangas, Mixed Dipterocarp, Montane, Mixtures, Plantations and Secondary/Others (Table 2-3). It is estimated that these forests support around 3,955 plant species, with the last inventory being carried out in 1996 with assistance from the Royal Botanic Gardens, UK (The Brunei Times/Asia News Network Asia One, 2011).

Within Brunei, PSF covers about 17.9% of the total land area, but its vegetation has not been described in much detail. On a large scale, detailed studies by Anderson in the 1960s provide the earliest descriptions of the PSF of northern Borneo and its floral diversity (Anderson 1961; 1963). These works provided a cornerstone for subsequent floristic studies of PSF in the region and thus form the basis of our current understanding of the PSF tree species composition in Brunei.

Since Anderson’s work some 50 years ago (Anderson, 1963), further contributions to information on the vegetation of Brunei’s PSF have been provided by Yamada (1997), Stoneman (1997) and Van der Meer & Verwer (2011). The paucity of studies highlights the compelling need for further knowledge about the PSF communities in Brunei, especially given the importance of PSF as the second major forest type in the country, after the Mixed Dipterocarp forest (Table 2-3). The most recent study of Brunei’s PSF involved the estimation of aboveground carbon (Van der Meer & Verwer, 2011) but this was based on historical plot data by Anderson from the 1960s, rather than contemporary field data collection. Thus there has been almost no recent research involving primary data collection, other than that carried out in the 1990s by Stoneman (1997) and by Page and Waldes (unpublished data) which contributed to a review (Page and Waldes, 2005) on the phytogeography of the PSF flora at regional and sub-regional levels. None of these previous studies are sufficient to enable exploration and visualisation of diversity patterns of PSF communities within or even beyond Brunei.

2.5 Phasic Communities and Species Association Patterns

A plant community is defined as a group of plants that inhabit a particular area and which are adapted to the surrounding environmental conditions in which they interact with one another (Park, 2008). A plant community therefore consists of two or more species at a given location.

A plant association can be perceived as a continuum concept for partitioning groups of plants based on environmental space i.e. how plant species are distributed along an environmental gradient with groupings distinguished by constant and differential species (Austin, 2005). The plant association concept was illustrated by Austin (2013) (Figure 2-3). Here constant species A and B form a discrete pattern with some overlaps in Association 2, which could be interpreted as a transitory stage. The differential/characteristic species are shown as lines found at lower amplitude below each constant species (which have a much higher amplitude); these also show some degree of overlap.

Figure 2-3: Plant association concept of species-environment relationship. Source: Austin (2013; 91-123).

In terms of range, constant species have a wider distribution in environmental space than differential species (Figure 2-3). Although two associations can share constant species, the characteristic species will be unique to one particular plant association. In Figure 2-3 for instance, Associations 1 and 2 share the same constant species A, but different characteristic species, namely Species C and D for Association 1, while species E and F for Association 2. Certain species are more common and widespread under differing environmental conditions and can be regarded as existing in a true continuum state, as illustrated by the lateral solid line i.e. species I is found in all three associations.

To date, there has been no consensus on whether the concepts of either discrete vegetation community units, i.e. associations, or the continuum concept should be applied in vegetation classification. It is therefore important to use actual field survey data to explore these hypothetical patterns since the actual patterns may vary across regions/environments, species types and scale of study.

The following section briefly describes each of the PSF phasic community types previously described from northern Borneo by Anderson (1963), using the association concept. This concept originated from the International Botanical Congress in 1910, whereby the floristic composition is considered to be a fairly consistent trait (Barbour *et al.*, 1980). The communities are distinguished by both floristic and physiognomic differences (i.e. differences in tree height, canopy type and principal dominant species). The terms *constant* and *differential* species were used by Anderson (1963) to refer to dominant species and characteristic species, respectively. The phasic communities are summarised in Table 2-4.

Table 2-4: Summary of forest metrics of PSF phasic community types from northern Borneo, with metric unit modification; after Anderson (1963).

PC 1 is a Mixed Swamp Forest community which is characterised by an uneven forest canopy; the height of the dominant trees ranges from 130 to 150 feet (40 to 46 m). It is characterised by a *Gonystylus-Dactylocladus-Neoscortechinia* association. There is a mixed floristic composition in all storeys of the canopy, which closely resembles the situation in lowland dry land forest. Four *Shorea* species can be found here (but excluding *Shorea albida* which is absent) and these form the principal dominants, i.e. *S. platycarpa*, *S. scabrida, S. teysmanniana* and *S. uliginosa.* Other principal dominant species are *Gonystylus bancanus* and *Dactylocladus stenostachys.* The peat water table is high for most of the year. In the understorey a species of the Arecaceae, *Eleidoxa conferta* (syn. *Zalacca conferta)*, is often in abundance, especially where the peat is shallow.

PC 2 is a transitional forest zone between the PC 1 and PC 3 communities. Referred to as Alan forest, it is comprised of a *Shorea albida-Gonystylus-Stemonurus* association. It is characterised by an uneven canopy and the dominance of large *Shorea albida* species, with most specimens of this species exceeding 127 cm (dbh). PC 1 species types can be found in a moderately dense amount in the mid and low storeys. A characteristic species of this forest community type is *Stemonurus umbellatus.*

PC 3 is also known as Alan bunga forest, a *Shorea albida* consociation. Consociation refers to domination by a single species. Tree heights of the upper canopy layer of *Shorea albida* range between 160 and 190 feet (49 to 58 m) and are different from the other community types in having tree crowns that are even or almost flat. The average density of *Shorea albida* trees is in the range of 86 to 124 trees/ha, while a midstorey is almost entirely absent. Single species frequently dominate the moderately dense understorey including *Tetractomia holttumii, Cephalomappa paludicola* and *Ganua curtisii.* Most of the time herbaceous vegetation is absent, and the shrub layer comprises a dense vegetation of *Pandanus andersonii.*

PC 4 (Padang Alan or Padang medang forest) is characterised by a *Shorea albida-Litsea-Parastemon* association. Tree heights range between 100 and 120 feet (30 to 37 m) and the tree canopies are tightly spaced and even. Most of the trees are small and have a pole-like appearance. Both *Shorea albida* (Alan) (with a density of about 445 stem/ha) and *Litsea palustris* (medang) are the principal dominants of this community type, while other species such as *Parastemon spicatum, Combretocarpus rotundatus* and *Callophyllum obliquinervum* are examples of characteristic species.

PC 5 is referred to as Padang mixed species. It is characterized by a *Tristania-Parastemon-Palaquium* association which occupies a narrow zone separating PC 4 and 6. This community type has a thick and uniform canopy layer, with the presence of some emergent trees, and average tree heights of between 50 and 70 feet (15 to 21 m). The tree density for species with a 12 inch girth (10 cm dbh) and over is about 988 to 1236 stems/ha. The trees are small throughout this community, with the most abundant comprising species such as *Tristania obovata* and *affmaingayi, Parastemon spicatum, Palaquium cochleariifolium* and *Dactylocladus stenostachys*. Herbaceous plants are mostly absent.

The last PC type is PC 6 (Padang keruntum) characterized by a *Combretocarpus-Dactylocladus* association. Being an open forest type, it is mostly comprised of stunted trees and shrubs of a xerophytic nature. Only *Combretocarpus rotundatus* trees have a girth of more than 3 feet (29 cm dbh), and seldom do they exceed a height of 40 feet (12 m). Also abundant are *Dactylocladus stenostachys, Litsea palustris* and *Garcinia rostrata,* although their sizes are mostly small. Species such as the insectivorous pitcher plant *Nepenthes* spp. can be found in particularly large numbers as well as other species such as the sedge *Thorachostachyum bancanum* and *Pandanus Ridleyi*; Sphagnum moss (*Sphagnum junghuhnianum*) can also be found on the peat surface.

Vegetation cover in PC 1-4 is generally of a more complex forest type in comparison to PC 5-6 (Figure 2-4) due to the multiple stratification of the forest. The upper canopy layers form much of the cover due to their large canopy size in PC 1-4. For less complex/simple forest type, the forest cover in PC 5 is thicker than in PC 6. The figure below shows the description of phasic communities to illustrate, according to whether the communities are made of complex or simple forest types, and whether the canopy is open or closed.

Figure 2-4: Bisect diagrams showing the variation in forest structure found at different phasic community types in relation to the depth of peat. The canopies are described by using symbols representing the complexity of forest and the spacing of the upper canopy layer. Image source: Anderson (1961) summarised by Tie (1990), as cited in Paramananthan (2008; 7), with modification.

2.5.1 Dominant Species

PSF tree species composition and dominance in northern Borneo (Brunei and Sarawak) differs from that in southern Borneo (Kalimantan). In particular, the Brunei PSFs more closely resemble Sarawak PSF than those found in Kalimantan in terms of the dominant tree species. For example, in Central Kalimantan, Alan (*Shorea albida*) which is the dominant species in some northern Borneo PSF communities does not occur (Shepherd *et al.*, 1997) and there are also differences in the dominant species of the phasic communities. The distribution of *Shorea albida* is restricted to an area from the Sadong river in Sarawak to the Badas swamps in Brunei (Anderson, 1963). Anderson also identified another PSF species, *Ganua curtisii*, which also has a restricted distribution in Brunei. This tree is exclusively found only in the Badas PSF where it can be found in association with *Shorea albida*. A subsequent study in the Badas swamps by Stoneman (1997) also found the same species types. The presence of PSF tree species with such a narrow distributional range is noteworthy and could imply that competitive and/or synergistic relationships exist between certain species sharing the same micro-habitat with consequent influences on diversity patterns. To understand such relationships at a greater level, small-scale habitat studies are recommended as a fundamental foundation to improve understanding of diversity patterns and the potential presence of a species-area relationship, while at a larger scale, Anderson (1963) argued that an improved understanding of the peat swamp flora should be set within the context of knowledge of the distribution of tree species across Borneo as a whole.

2.5.2 Constant Species

In British NVC classification method, *constant* (dominant) species are especially important. These are defined as those species known to be present in more than 60% of the samples, equivalent to frequency classes IV and V (Rodwell, 1991; Elkington *et al.,* 2002), from a particular survey site.

Using the species association concept, constant species are defined in this thesis as the most frequent species found in a particular study site, which exhibit dominance in terms of both floristic distribution range and tree physiognomy. An example of a common constant species in Brunei PSF is *Shorea albida*.

2.5.3 Species Response Curves Along Environmental Gradients

In 2003, Gaston highlighted the complexity of spatial variation in the environment, and cited previous work by Austin *et al*. (1984) who distinguished three different types of environmental gradients namely indirect, direct and resource gradients. Indirect gradients operate at large scale where the influence of the gradient on plant growth is secondary, such as the altitude factor. This factor co-exists with the direct gradient, which has a prime influence on plant growth such as temperature. On the other hand resource gradients are factors that species directly use as a resource, such as soil nitrogen content. Further to the environmental gradient types is the specific pattern of change in abundance values of species across such a gradient, namely the response curve. Gaston further explained the presumption for this curve: where peak abundance exists this is related to the species’ fitness to life, which progressively declines with increasing distance away from the peak at the centre.

There can be various conceptual patterns used to illustrate the species response along the same environmental gradient. A large sample across the environmental gradient is foreseen to reveal distinctive patterns from which inferences can be made on species assemblages within a community group, with awareness that the data sampled are not usually normally distributed, and hence the traditional Gaussian approach may not be suitable (Lehmann *et al*., 2002).

Figure 2-7 shows various response curves along a shared environmental gradient (Austin, 2013). The range or tolerance for each species to the environment is indicated by variations in the width and amplitude within and between the models of the mostly Gaussian curve, while some skewed curves are also present in 2-7 (e). Some species respond to the environmental gradient in a consistent way such that the environmental range is fixed, thereby forming a discrete model such as depicted in Figure 2-7 (a). In this respect such vegetation types are said to form a community, i.e. a discontinuous pattern. However at the other extreme, the patterns show that some species may respond to the environmental gradient in an individualistic manner. In this sense, the species distributions can be found in continuum, showing independent patterns in relation to other species, such as in Figure 2-7 (f).

Figure 2-5: Figure (a) to (f) showing different conceptual models of species-environment relationships. Source: Austin (2013; 91-123).

While there have been a few other floristic studies of Brunei following Anderson's work in the 1960s, these studies have neither addressed PSF communities, nor their diversity in particular. As an example to illustrate the level of plant species diversity of PSF in northern Borneo, an extensive floristic survey conducted by Anderson during the 1950s and 1960s (Anderson, 1963), revealed that 1,706 species had been found in the PSFs of Sarawak and Brunei (this number is not limited to tree species only but includes other plant types as well). In a different approach to species data collection, based on secondary data source compilation, Posa *et al.* (2011) estimated the number of plant species from the PSFs of Southeast Asia to be 1,524 species, out of which a small fraction, i.e. 172 plant species, were habitat endemics restricted to PSF. Posa *et al.* (2011) however, noted that that these numbers should be treated with care, and be subject to further addition and correction due to the incomplete knowledge of the distribution of many species and habitats which still remain undersurveyed. By comparison, the recorded plant diversity in the PSFs of Thailand is much lower than in northern Borneo, amounting to 88 families and 298 species of flowering plants, based on a study of the largest extent of PSF in Narathiwat natural PSF (Suzuki and Niyomdham, 1992). A subsequent study in the same province in Toh-Daeng PSF, did however, record a somewhat higher number of species i.e. 109 families and 437 flowering plant species (Bunyavejchewin, 1995). The PSFs of northern Borneo and Brunei, in particular, do therefore appear to be relatively species diverse.

A study by Page and Waldes (2005) noted that PSF vegetation in Southeast Asia exhibits considerable heterogeneity at both regional and sub-regional levels. The deduction of sub-regional scale variations was based on phytosociologic studies while inferences on regional scale patterns were derived from a comparative study of PSF in northern Borneo and various other locations within Kalimantan. In addition, these authors identified one characteristic PSF species, namely *Dactylocladus stenostachys*, as being of particular interest since it was one of only three widespread PSF species in Borneo, and one of only a very few specialist tree species of PSF. Thus despite its widespread distribution within the Southeast Asian region, this species is almost exclusive to a unique habitat i.e. PSF, and any disturbance to the PSF ecosystem could greatly affect its conservation status owing to its restricted habitat range. In support of the heterogeneous nature of PSF floristics, a study by Posa *et al.* (2011) on dominant dipterocarp (e.g. *Shorea* spp.) species in PSF, revealed a heterogeneous pattern at a large regional scale, implying that conservation efforts for this tree family would require protection of various peatland sites across the region in order to cover the full range of diversity. For example, the dominant endemic species

Shorea albida is found in the northern part of Borneo but is absent in Kalimantan, except for the northwest region (Posa *et al.*, 2011), while a different dominant species of riverine forest namely *Shorea balangeran* (Shepherd *et al.*, 1997), is mostly found in the southern part of Borneo. This study emphasises the need for more detailed vegetation studies of PSF at the regional to local levels.

Furthermore, applying a much larger scale comparison of PSF floristics, Posa *et al.* (2011) concluded that floral diversity was the highest for the tropical PSF in comparison to other peatland types across the globe. Interestingly, reference to the study by Page *et al*., (2011), which provides best estimates for the mean peat thickness of tropical peatland, indicates that the two highest values came from Brunei with 7.7 m followed by Indonesia with 5.5 m, in comparison to the rest of the tropics. Therefore, it could even be generalised that there is potentially a linear relationship pattern between the floristic variations with peat depths occurring in a large-scale study, e.g. following phasic community theory and the interdependence on peat depth variation, at least in Borneo (Anderson, 1961; Tie, 1990).

Apart from peat depth, there are other factors that influence PSF plant community structure and diversity on a smaller scale, including variations in the organic matter composition of the peat surface layer (Brady, 1997) as well as peat and water nutrient contents (Lähteenoja and Page, 2011). Hence, other environmental gradients may dominate on a smaller scale but contribute to overall high plant species composition. With a growing body of literature on PSF plant diversity and associated ecology, it should become increasingly possible to draw general inferences based on spatial patterns and distribution ranges of plant species at various levels. This improved knowledge will hopefully allow better understanding of the conservation priorities for tropical PSFs, for example based on differences in local to regional diversity, species distribution patterns and species endemism.

2.5.4 Pattern Analysis and Spatio-Ecological Research

The patches concept of vegetation pattern was first described by Watt (1947), a concept which has now become a standard (Van der Maarel, 2005). Watt's work described a plant community from contrasting perspectives, namely as an attribute for identification and plant classification, and as a process, with a particular focus on this latter aspect (Watt, 1947). Classification of vegetation into potential plant communities and habitat types is important not only in order to understand the distribution of plant communities and factors controlling their distribution but it can also contribute to conservation planning. Pattern analysis on vegetation can be performed in many different ways and at different scales. Discerning the characteristic patterns derived from multivariate analysis of patterns and statistical modelling has been considered to be a core element that can also make a contribution to the sustainable management of vegetation including forests (Austin, 2005).

Legendre and Fortin (1989) argued against the assumption of the uniform distribution of living organisms that was found in most studies on quantitative ecology during the 19th century, by asserting on the presence of spatial structure in the environment. Further they stated that the source of such structure was a multitude of energy inputs, which led to the presence of environmental gradients or a patchy appearance. A patch is defined as an area which is spatially uniform, within which at least one variable is similar, of either a land cover category (e.g. a shrub) or a quantitative measure (e.g. soil moisture level) (Dale and Fortin, 2014). Recent research on vegetation structure has been carried out by Van der Maarel (2005) who described the general notion of many plant communities, whereby many species of plant exist in patches. A mosaic is created from these patches, within which these patches are dynamically inter-linked and form a community (Watt, 1947).

The patch mosaic is one approach to identifying species plant units through an analysis of the spatial distribution of the patterns of vegetation i.e. their clustered pattern. The other two distribution patterns are regular or random dispersion, random pattern being exhibited by all plant species of a truly homogeneous community (Van der Maarel, 2005). This implies that plant species of the same community share somewhat similar environmental conditions while the environmental gradients can be identified from patches. For example an open canopy of cropland and closed canopy forest receive different amounts of light energy, with subsequent implications for the different soil moisture, soil surface temperature and relative humidity levels present in the areas. However, the relationship between species and environment may not be straightforward, and in addition, can be contributed to by other factors, such as biotic processes. Thus the presence of different types of patches within vegetation, i.e. vegetation patterns, implies different areas and methods by which such patterns could be analysed.

Methods for spatial pattern analysis were elaborated by Legendre and Fortin (1989) who organised the methods depending on the types of ecological questions being investigated and the study objectives. For instance, ordination is used to identify patterns. Further development of the pattern analysis methods has occurred over the last two decades, including direct and indirect ordination, and classification methods.

Direct or indirect ordination methods for vegetation pattern analysis are defined based on the inclusion or exclusion of environmental variables in the analysis. Species distribution patterns (e.g. abundance data) and their community properties (e.g. species richness) can be explored through comparisons with the associated environment variables. In this case, the ordination method is known as direct ordination, due to the inclusion of the environmental variable, which had its origin in Whittaker's (1956) direct gradient analysis. Indirect ordination, on the other hand, refers to the use of species composition data alone (which excludes the environmental variable) in the vegetation analysis, in order to detect the main axis of variation based on the similarity of the plant species composition at one site relative to another (Austin, 2005). Examples of indirect ordination methods are Non-Metric Multi-Dimensional Scaling (NMDS) (Austin, 2005) and Detrended

Correspondence Analysis (DCA) (Hill & Gauch Jr., 1980, ter Braak, 1986). These methods of arranging species is based on plant species and habitat sample data. The results can reveal structural patterns and indicate the presence of distinct vegetation communities, thereby indirectly assuming the presence of environmental gradients along the ordination axes, which may warrant further investigation.

While the main axes of variation are illustrated by ordination, plant classification works by the detection of clusters and outliers (Austin, 2005) i.e. similarities and differences of a site. An example of a classification method is a Two Way Indicator Species Analysis (TWINSPAN) devised by Hill *et al.* (1975) which involves the use of intricate divisive procedures of clustering of species samples (Pisces Conservation Ltd., 2013). An important output from the hierarchical approach in TWINSPAN is the identification of the characteristic species, which are also known as the indicator species, of a site. The identification of indicator species is especially useful to determine and infer species associations in a phytosociologic approach that can then be used to partition a plant community.

Although ordination has been commonly used to describe spatial structure in separating different vegetation types in two or three dimensional spaces e.g. Simonson *et al.* (2012) for woodlands and Mediterranean forests in Portugal and Shearer and Clarkson (1998) for wetlands in New Zealand, there has been a limited number of studies in the use of ordination with respect to describing the vegetation types of tropical forests. The limited studies in the Southeast Asian region include ordination using Principal Components Analysis of heath forests in Sarawak and Brunei (Newbery, 1991) and NMDS ordination of lowland mixed dipterocarp forest in Brunei (Sukri *et al.*, 2012). Therefore further application of ordination is extended to the PSF types.

Vegetation maps of the PSF community types were first illustrated by Anderson in his study of the PSF of Brunei and Sarawak (Anderson, 1961). Apart from the accompanying field survey records and an estimation of PSF community extent which were based on textural analysis via aerial photo interpretations and expert knowledge in plant taxonomy, there has been little further development beyond this early study. Further information on the structure of the different forest types is needed to increase our understanding of the processes operating within the forest for various inter-related uses in the fields of socio-economics and environment/ecology. Theory on the presence of different phasic communities (section 2.6) has suggested that within a major forest type i.e. PSF, structural variations exist within the different forest sub-types (Figure 2-4).

Forest structural patterns have traditionally been examined through a field survey approach. This is a labour intensive and time consuming process in addition to having small areal coverage, usually at a plot level. Moreover, changes in forest conditions over time will necessitate repeat field survey in order to get up-to-date information for the area concerned.

The viability of spatial analysis in vegetation science is manifested in the published literature addressing the different forest types, the state of the art in data collection methods, data analysis and presentation, which have slowly pushed forward our ecological knowledge. Examples of recent work include those of Bässler *et al.* (2011) on discriminant analyses and Simonson *et al.* (2012) on clustering and ordination of forest data. The analysis of vegetation patterns was commonly conducted at a plot level and the advent of GIS has played a role in bridging between the vegetation pattern analysis at plot and landscape level. Spatial statistical approaches have further advantages by being a method of vegetation classification which is less subjective than those performed through human visual interpretation, offering data manipulation and visualisation capabilities, handling large amounts of data and offering fast computing speeds. The potential for use in further spatio-ecological research on the tropical PSF is clear.

2.5.5 GIS and Forest Ecology

Aerial photographs and field sampling methods have complemented each other and been used in the past (e.g. Anderson, 1961) for PSF classification (hand-drawn interpolated map) and ecological inferences. There is a trade-off between resolution and areal extent of a study area e.g. resulting in masking the potential presence of sub-community types, and the associated factors of plant species distributions operating at the plot level. The distribution of plant diversity using GIS application was not explored by Anderson (1963), as the GIS applications have only proliferated in the mid-1960s especially in the More Economically Developed Countries (MEDC), with geostatistics (e.g. spatial interpolation) further offering increased capabilities for hypothesis testing, hence reducing conjecture in manually inferred species-environment relation.

An example of the use of GIS for exploring variation in wetland forests is a study by Horssen *et al.* (1999) of wetlands in the Netherlands which used 78 plant species and a number of variables including soil type, land use as well as hydrology, infiltration, position of groundwater table and other groundwater quality variables. Multiple stepwise Gaussian logistic regression was used to select the key variables that explained most of the variation in the data which resulted in a unique regression equation for each species, which were then used to predict the presence or absence of species (Horssen *et al.*, 1999). Input variables of groundwater quality e.g. pH value were based on secondary data from various sources, which were used in a Kriging spatial interpolation method, while other variables were digitised from existing maps. The resulting model's accuracy varied considerably across space, especially with the use of a confidence model to assess the accuracy of the prediction of plant species (Horssen *et al.*, 1999). The authors further noted that while Kriging products were used as input into the regression, the model could be improved further with the use of a spatially varying regression coefficient.

Furthermore, GIS offers multivariate analysis in forest mapping/modelling, which can be operationalised at both landscape and plot levels, in addition to a replacement for hand drawn vegetation profiles (bisects) through improved visualisation.

2.6 Visualisation of Peatswamp Forest Communities

Chapter one described the application of scientific visualisation for synthesis and communication (Kraak and Ormeling, 2010). An example of this would be the application of visualisation using a forest bisect as a way to offer an improved understanding of the species-environment relationship in the Badas PSF.

A forest bisect is a manual depiction of vegetation which is scaled (Barbour *et al*., 1980), in which the x-axis represents the distance along a line while the y-axis represents tree height in feet/metres. It was originally applied to tropical forests in 1933 (Barbour *et al*., 1980), and for the PSF of Borneo, in particular, some thirty years later by Anderson (1961). A recent example of its use is the study of evergreen swamp forest in Cambodia (Theilade *et al*., 2011) (Figure 2-6). A characteristic feature of a forest bisect is that the vegetation projects from a single perspective/vertical plane, in addition to the provision of a numerical reference for individual trees at a species level. Alternatively, the vegetation may also be represented at a plant community level, e.g. as illustrated by Suzuki and Niyomdham (1992) for PSF in Narathiwat, Thailand.

Figure 2-6: Illustrations of forest bisects of Borneo PSF (60 X 36 m in this excerpt) (Anderson, 1961) and evergreen swamp forest of Cambodia (35 X 50 m) (Theilade *et al*., 2011).

The information obtained on Badas PSF was used to illustrate the change in plant species composition and structural differences to enhance the understanding of how the PSF tree species are organised into communities with different characteristics when viewed from multiple perspectives. Hence, 3D visualisation was employed to increase conceptual understanding and serve as a communication tool for the purpose of educational use to improve knowledge of PSF ecology in Brunei. The conceptual approach to improved knowledge on forest ecosystems is in support of the MEA in which education is one of the ecosystem services (cultural services) derived from wetlands (Millennium Ecosystem Assessment, 2005b).

2.7 Summary

This chapter has reviewed the ecosystem services of the peat swamp forest ecosystem, which provides both tangible and intangible benefits, according to the four areas identified by the MEA (Millennium Ecosystem Assessment, 2005b). This review emphasises the two main threats to PSF forest biodiversity identified in Brunei Darussalam, namely threats to ecosystems and threats to species (Forestry Department, 2010), while the effects of climate change are considered as an emerging threat (Forestry Department, 2010).

This chapter has also reviewed some case studies of disturbed PSF in other regions in Southeast Asia, to illustrate the extent of unfavorable impacts on biodiversity (from natural and human induced causes) and consequently, the loss of ecosystem services. The review also highlights the need to better understand the floristics of PSF in Southeast Asia, which is in part driven by the rapid degradation and loss of PSF over recent decades.

With issues such as knowledge gaps on the biodiversity of the remaining PSF, a lack of available appropriate data sets, i.e. up-to-date floristic data on an appropriate scale, along with other previously acknowledged issues such as vegetation classification issues, it is clear that there is a need not only for more detailed studies but also approaches that lend themselves to improved understanding of the value of PSFs amongst different stakeholders' interests. It is also clear that information on floristic diversity on the large scale could potentially hide information, e.g. species variations on a small scale, and the related processes affecting it.

It is generally understood that the plant species diversity of PSF in Southeast Asia is relatively low in comparison to some other forest types on mineral soils (e.g. Posa *et al.*, 2011) but that the PSFs of northern Borneo and Brunei in particular, house a high diversity of this forest type within the region.

This chapter has provided the definition of peat related terminology for the PSFs in Brunei and Southeast Asia, and highlighted the critical gaps in knowledge on the study of their biodiversity and ecology. Several physical and human factors affecting the PSFs of Southeast Asia have been raised, including the need for the sustainable management of this particular forest type. The role that Brunei plays as a custodian of the rainforest, including the PSF, is emphasised. This is underscored by the rarity of undisturbed PSF ecosystems outside of Brunei, which now houses some of the last remaining pristine wetland forests in the region. Nevertheless these forests remain vulnerable to various human and physical factors previously mentioned and thus there is a need for improved awareness of the need for continued forest protection.

Species dominance was described in this thesis on the basis of basal area (ecological dominance) and abundance. Such description is needed in order to subsequently infer the relation between diversity and dominance.

This chapter had reviewed the ordination and classification methods in the analysis of vegetation pattern/ identification of PSF communities from the perspectives of species space.

The visualisation section in this chapter has illustrated the ways by which the ecological understanding of PSF could be visualised and communicated to a range of stakeholders for sustainable management of this ecosystem, including education which is key goal of the Millennium Ecosystem Assessment.

The subsequent chapter concerns itself with the methodology, which details the field survey method employed in forestry inventory as a way to increase the knowledge of the PSF ecosystem in Brunei and provide the basis for improved ecosystem conservation, based on enhanced awareness and understanding of this forest’s unique characteristics.

CHAPTER THREE

3 Methodology

3.1 Introduction

This chapter provides an overview of the steps taken throughout the thesis in order to answer the respective research questions which cover the elements of diversity and dominance, classification of peat swamp forest community and visualisation. Each element will be individually dealt with under separate section headings in this chapter.

The research question on relationships between diversity and dominance in chapter one necessitates a thorough description on both elements of diversity and dominance of PSF species. Diversity will be described from the perspectives of species space, whereas dominance will be described through the ecological characteristics of PSF species in the environmental space. Hence, the focus of this chapter is to describe and explain the sequence of operations undertaken to answer the research question on diversity and dominance as well as other subsequently related research questions in this thesis. The focus of this thesis on modelling and communicating the ecological characteristics of the PSF communities has triggered several important questions within this methodological chapter as follows:

- How will the peat swamp forest community be viewed from both species space and environmental space?
- How do ecological characteristics shape our inferences on patterns and processes, and ecological understanding i.e. in the geographic space?

The methodological pathways taken which act as a blueprint to answer these generic questions are illustrated in the data model and communication elements respectively in Figure 3-1.

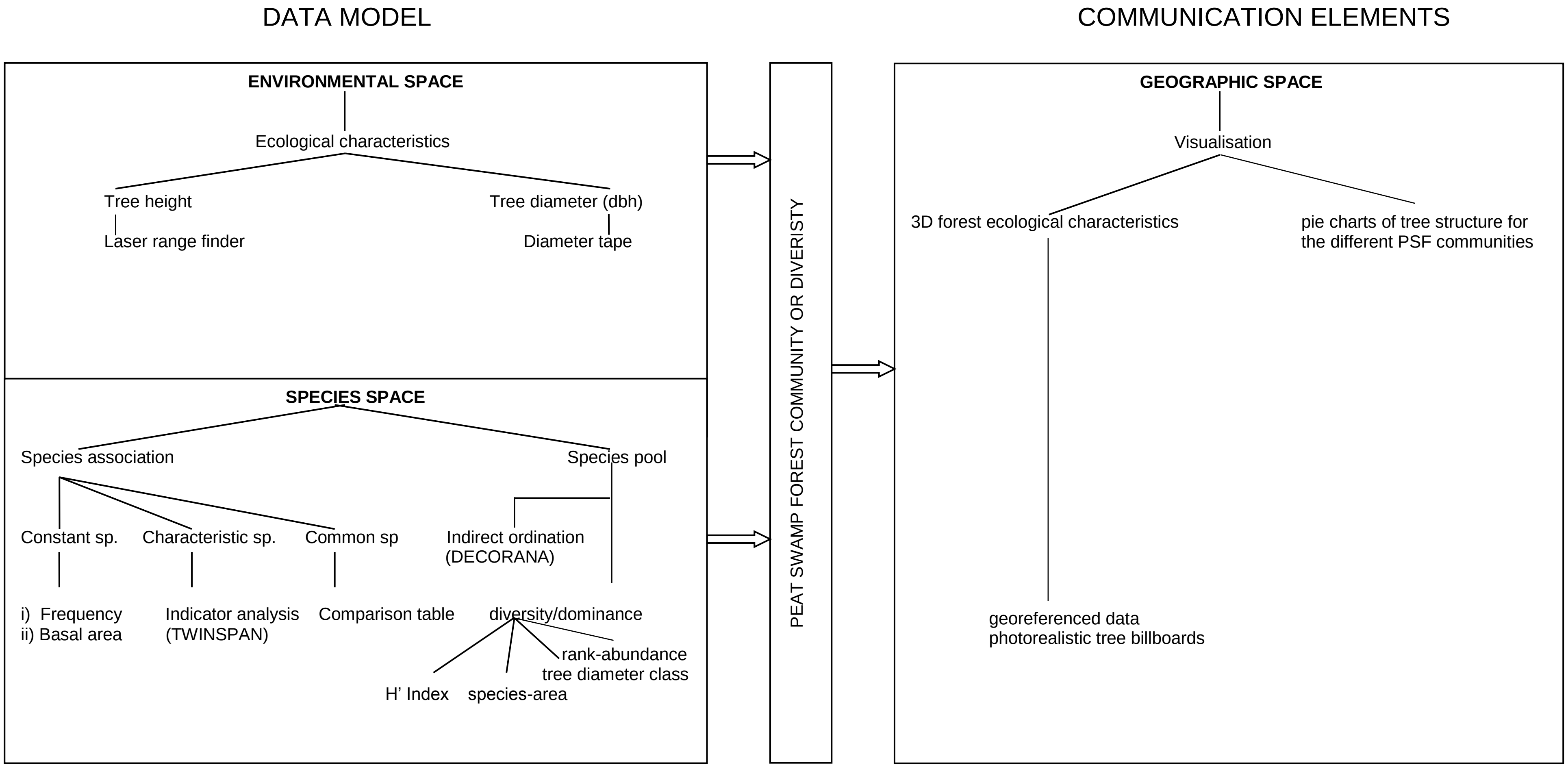


Figure 3-1: The vegetation (pattern) analyses are divided into three themes, on the basis of environmental, species and geographic spaces. TWINSPAN=Two Way Indicator Analysis, DECORANA=Detrended Correspondence Analysis, H'=Shannon-Weiner Diversity Index.

The species pool and species association are grouped into the species space. The species space is concerned with the phytosociological approach to describing the PSF communities which will be covered in sections 3.2 and 3.3.

The ecological characteristics of the forest are related to a tree physiognomy approach, in order to provide details on forest structure. These characteristics are related to the environmental gradient as identified in the literature review. This thesis uses surrogates namely the tree diameter class distribution and tree heights (i.e. the ecological characteristics) to describe the environmental variables. The tree diameter class distribution is used with the aim of classifying the PSF communities through the perspective of environmental space. On the other hand, the environmental variable of tree height is used to visualise the structural differences of PSF communities. Both of these environmental variable surrogates will be covered in section 3.2.4.

The 3D forest models and pie charts of structural diversity are grouped into the visualisation theme, which expresses the properties (plant species/structural diversity or ecological characteristics) of the PSF in geographic space. The model and chart will be covered in section 3.4 of this chapter. In addition to this, the visualisation of ordination, tree diameter class distribution in species space is compared against the PSF structural diversity in geographic space, as a way to enhance understanding on the forest ecological characteristics of each community type of the PSF.

3.1.1 Study Area

Brunei (4°53.417‘N; 114°56.533’ E) has an estimated total land area of 5765 km^2 (FRA, 2010) with PSF covering about 1000 km^2 (chapter two). Located in the Belait district, the Badas peat dome is the largest in Brunei. The sediments, comprised of both marine clay and mangrove deposits, which underlie the Badas peat are thought to indicate a longer peat formation process than elsewhere in this region and thus the Badas dome is one of the oldest peat domes in Brunei and older than domes in the western region in Belait (Sabiham, 1990). The site is typical of other coastal, lowland peatlands of Southeast Asia. The peat depth ranges from 6 to 8 m deep (Sabiham, 1990) while a recent study identified the mean peat thickness of some 7.7 m (Page *et al*., 2011). Peat formation commencing around 5,500 years ago (Anderson, 1963), but with occasional sand ridges on which the peat is much shallower (Stoneman, 1997). Most of this peatland remains in a pristine condition, but there have also been small, partial impacts such as by fire. The natural vegetation on the Badas dome is PSF, comprising a sequence of forest communities which replace each other according to the sequence first described by Anderson (1961). The PSF is very biodiverse and of high conservation interest. Several of the forest communities either support or are dominated by the dipterocarp tree *Shorea albida.* This species is confined to peat soils in northern Borneo with the greatest contiguous extent of *Shorea albida* forest found on the Badas dome. In choosing the Badas PSF as a study location, the information gathered would not only be providing the data for this thesis but would also add to knowledge on forest types that are of high conservation value.

3.2 Plant Diversity and Dominance

The following sections describe and explain the approach taken to obtain measures of plant diversity and dominance in order to analyse the data for patterns across a range of scales. Prior to this, the field sampling technique will be described and explained, followed by tree species identification.

3.2.1 Field Sampling Technique

The Badas PSF is enclosed by the coast to the north and the Sungai (river) Belait to the south. Figure 3-2 below shows the systematically located Sites A and B, which are about 2 km apart, while sites B and Site C are about 1.5 km apart as measured on a straight line distance. Site C is furthest inland and the closest to the river with a distance of about 800 metres from this site to the river.

Figure 3-2: A conceptual diagram illustrating the location of study site A, B and C in the Badas peat swamp forest. Insert: Map showing the location of Brunei. Map source (above): Map data © 2016 Google (with modification) and (below): Mortadelo (2005).

Plant species data were collected based on purposive systematic techniques, which is a non-probability type of sampling (Schreuder *et al*., 2001). Simple random and stratified sampling could have been used with perceived improved and less biased results, but impeded access is the major obstacle to the application of such methods in the permanently inundated PSF forest (including a barrier in the form of thick thorny undergrowth species of about 1m tall), which have generally seen the much favoured purposive sampling as the practical solution. Purposive sampling is the most commonly used approach in the study of PSF diversity (Istomo *et al.,* 2009; Mirmanto, 2010 and Gunawan *et al.,* 2012). For example, Istomo *et al.* (2009) used a research sample plot of 0.2 ha in primary, slightly degraded and heavily degraded PSF. Mirmanto (2010) on the other hand used eight plots of 0.25 ha, in relatively intact forest on peat with variable thickness, and with distances of some 500 m to 1 km separating each plot. Moreover, Gunawan *et al.* (2012) used six plots with a size of 0.5 ha in a three hectare total study area of intact and disturbed forests. The limited literature on the assessment of PSF diversity index also identified the use of systematic sampling design in ten plots of 50 X 20 m in burnt and unburnt areas of PSF (Ainuddin and Goh, 2010) in which, differing from the previous examples, is the fact that the area covered was very large indeed i.e. 416 ha. In addition to the impediments in Badas PSF are cost, time and safety factors. Despite these constraints, the data sampled in a non-probabilistic manner are nevertheless useful and crucial, on condition that the limitations are acknowledged (Schreuder *et al*., 2001).

In Badas, three study locations were chosen in intact forest that were believed to be representative of the range of PSF plant community types identified in this area based on the previous work of Anderson (1961) and Stoneman (1997) with additional local knowledge gained from staff of the Forestry Department, Brunei. The criteria for selection of each site was on the basis of homogeneous physiognomy such as crown size and general tree heights of the peat swamp forest identified through visual perceptions. If no apparent pattern exists, the result will be one group of quite similar plant species as an indicator that they belong to the same forest type (Figure 3-3).

Figure 3-3: A view of Badas peat swamp forest (left to right) of Site A, B and C. From the outside of site A and B, the forest types are quite similar, comprising of homogeneous stand but with the exception of a few emergent in site A (a few trees on the left hand side). Site C has many trees of relatively low height and small crown canopy size, with apparent gap spaces in between the trees.

The field campaigns were divided into two stages, the first in November 2011-January 2012 and the second in March 2012. A total of seven plots were established during the first phase and a further two (Sites B and C) during the second stage. A team of four to five local staff from the National Herbarium centre in Brunei were involved in setting up the tree diversity survey plots. Each site was established in intact forest and comprised of three plots starting with the first plot closest to the track and then moving towards the forest interior (Figure 3-4).

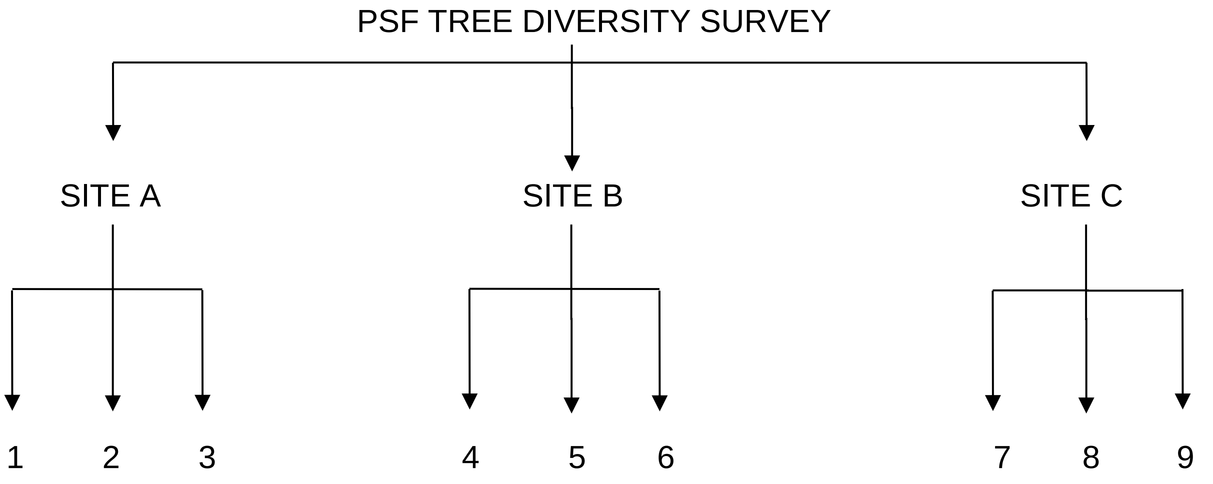


Figure 3-4: Description of sites and plots of study area in Badas PSF, Brunei.

In an earlier study of 3.25 ha of PSF in the Badas and Rasau districts of Brunei, Yamada (1997) used multiple plot sizes i.e. 50 X 50 m, 100 X 50 m and 100 X100 m, in which 50 X 50 m (0.25 ha) was used as the basic size and then the size was increased based on a combination of tallest tree heights and the tree species diversity. In contrast, Stoneman (1997), in a study in the Badas region, used smaller 30 X 30 m (0.09 ha) plots. Plot-based studies of PSF floristics elsewhere in the region have also employed randomly arranged 30 X 30 m (0.09 ha) plots (for a study in Sumatra by Brady, 1997), while Shepherd *et al.* (1997), in Central Kalimantan, used 50 X 30 m (0.15 ha) plots set up along two, parallel transects from the forest riverine edge towards the forest interior.

The sampling size used in this study was comparable with these previous studies in that a plot size of 50 x 50 m (0.25 ha) was employed, systematically separated at 50 metre intervals, with a total plot area of 2.25 ha from the nine plots. The choice of a relatively large plot size was made with the objective of providing maximum information on species diversity as well as using a plot size that would be representative of the different plant communities. Moreover, the choice of plot size was made in order to realistically achieve the objectives within the time frame among which included the collection of x, y co-ordinates from plots located in different phasic community types which could be employed in subsequent analyses.

The type of primary data collected were forest metrics of plant physiognomy (maximum tree height, diameter and location), species type and vernacular reference which have served as an input into the classification of the PSF based on species data.

3.2.2 Tree Species Identification

Information on the species pool for each plot was collected. In order to ensure the correct use of plant taxonomy, assistance with plant identification was sought from local botanists of the Brunei Forestry Department.

Plant species identification was carried out on site, whereby some of the more common species were identified directly in the field through the use of bark textures, sap, fruits, leaf samples' shape and size and smell. In cases where reasonable doubt occurred (on the identity of individual species), voucher specimens were collected and compared against the keys for species classification and the specimen record in the National Herbarium Centre collection (BRAHM database). The nomenclature used was based on the commonly accepted Angiosperm Phylogeny Group (APG) plant classification standard. Previous classification of the peat swamp forest plant species had used the Bentham and Hooker system e.g. Anderson (1963).

3.2.3 The Different Measures of Peat Swamp Forest Diversity

Diversity measures vary in relation to scale such that different types of diversity exist in accordance to cumulative changes in the size of the area being considered. Whittaker (1972), and Gaston and Spicer (2004) distinguished between three different types of diversity: alpha diversity refers to the species number that exists within a habitat or community; beta diversity is a measure of the rate of change of species along a gradient from one habitat or community to another; lastly, gamma diversity refers to the species number that can be found throughout a range of habitats or communities within a specific region.

There are various different measures of representing the level of diversity and the types of dominant species with respect to PSF. Anderson (1963) described the total number of species per hectare. This has been a common method used also in other studies describing the floral diversity of PSF e.g. the study by Yamada (1997) which used species number per plot. However, the heterogeneous nature of the tree species composition of PSF at a landscape level indicates that this approach could hide the actual variation in species composition at a plot level which may be attributed to local variations in biotic and abiotic factors.

The use of species richness alone can hide the contribution of individual species to a particular community type, as the total number of species is aggregated in a plot. Therefore, for the purpose of this research, the Shannon-Weiner index (Equation 3-1, Qinghong, 1995) is the preferred approach as it provides more opportunity for exploring the contribution of individual species towards plot diversity, as well as being useful for providing a cumulative diversity value as a single reference value for each plot. A further advantage of this method is that it enables comparisons to be made between this study and those of other researchers.

The Shannon-Weiner Index formula is:

$$H' = -\Sigma p_i \times \log (p_i)$$

(Equation 3-1)

Key:

H' = Shannon-Weiner Diversity Index
$\sum p_i$ = the sum of species *i*

where;
$p_i = n_i / \Sigma n_i$,
n_i = abundance of *i*th.species
i = species number

The Shannon-Weiner (SW) Index is calculated by knowing the number of species in an area, i.e. the species richness. The proportion of each species within the area is then calculated, which is then multiplied by the logarithmic function. The range for SW Index values is usually about 1.5 to 3.5 and seldom exceeds 4.5 (*Species Diversity & Richness*, 2007).

The diversity index values obtained for the Badas forest plots were calculated by using MS Excel, which were then used to measure and compare against values derived from other studies of PSF diversity across Southeast Asia, in order to pursue a discussion based on the analysis of patterns at a regional scale.

3.2.3.1 Species-Area Curve

A species-area curve is a method commonly used to illustrate the increment of species number in relation to areal accretion within a habitat (Lepš, 2005), with a steep slope of the curve indicating rapid change in species number and vice-versa. The rate of increase in the number of species varies across different communities (Lepš, 2005) and the number of plant species may increase or decrease with area depending on various factors such as disturbance and regeneration. All plots chosen for the field study were located in intact forest and hence plant species were expected to increase with increase in area surveyed. In order to visualise the changes in species number with area, aggregated plots were used instead of constructing species-area curves for individual plots, due to the small number of plots involved. This analysis used the Species Accumulation Curve programme (Species Diversity and Richness, v.4.1.2., 2007).

3.2.4 Species Dominance

Dominance can be measured using a number of approaches, such as the frequency of tree counts (constant species) or density/abundance i.e. the number of trees per ha, ecological dominance based on the tallest tree that receives direct insolation, and crown cover. Dominance may be applied in different ways depending on the purpose of the study. For instance, studies focusing on the habitat of undergrowth species or on merchantable timber species may perceive dominance in different ways. Dominance for non-tree species may refer to ground cover abundance which is usually recorded subjectively using a percentage scale e.g. the Domin scale. For tree species, however, dominance may refer to dominance in terms of the basal area of trees measured in the field.

3.2.4.1 Rank abundance Curve

In this study, the species rank abundance curve (Verberk, 2012) was used to identify patterns of dominance based on abundance i.e. tree stem count per plot. This approach was selected because abundance as a measure of dominance was previously used in studies of PSF by Anderson (1963), thus enabling comparable comparisons to be made with plant community types. Importantly, the rank abundance curve was a preferred approach in this study due to its good visualisation capabilities enabling ease of interpretation of the relative abundance of dominant species across the different community types. The total numbers of individual species were recorded and then organised into the most to least abundant, with the x-axis representing the ranking of species based on abundance value while the y-axis is the abundance value of each species.

3.2.4.2 Tree Diameter Class

In addition to species abundance as a basis of determining species dominance within a plot, dominance based on basal area was also calculated in order to make comparisons across plots. For this purpose, the basal area values for each plot were divided into tree diameter classes at 10 cm intervals. The x-axis represents the tree diameter class distribution for each plot while the y-axis is the abundance value. Similar to rank abundance curve, the analysis for tree diameter class distribution was performed using MSExcel.

The diameter of all trees was measured according to the diameter at breast height (dbh) for trees ≥ 10 cm in diameter. A diameter tape was used to measure the tree diameter at 1.3 m above breast height (Figure 3-5). However, the inclusion of stems of less than 10 cm dbh including the non-tree species would potentially increase species diversity. For this reason, a target population i.e. 10 cm dbh must be set in order to get comparable results should a species diversity comparison be made.

Figure 3-5: Tree diameter being measured at diameter breast height.

As a general protocol, only living trees were included in the sample; dead and uprooted trees were excluded. Accuracy control was also imposed whereby all enumerated trees were tagged using small, numbered aluminium plates attached to the trees to prevent missing or double counting. In order to prevent double counting, all nine 50X50 m plots were divided into 10X10 m sub-plots and recording of tree variables was conducted in these smaller plots in a zig-zag pattern (row by row). However, the designation of small size was not intended for further analysis in this study. Tree locations were recorded using handheld GPS and some digital photos were also taken. The analysis of tree structural data was performed in MSExcel.

3.2.4.3 Tree Structural Dominance/Diversity

In relation to the research question on the link between diversity and dominance, this thesis will further explore the spatial distribution of forest structure/height as a proxy for the distribution of light availability and the relationship with the diversity index. A handheld laser instrument i.e. Nikon ProStaff 500 Range Finder was used to measure the total tree height from the ground. Some of the tall trees have a very large canopy diameter. The canopy tree diameter was not measured from the ground, but through field observation. Through general observation, the distance between two dominant trees is about 10 metres, and the sizes of an upper canopy tree diameter were estimated to be within this range distance. Across the study sites, the change in distribution patterns of forest structure including the dominant species was assumed to be followed by a change in the canopy cover density, which influences the amount of light energy penetrating through to the forest floor.

The vegetation was structurally diverse and comprised of multiple strata. Thus, at each site, the tree species were divided into different strata using a stratification appropriate for tropical PSF i.e. upper canopy >30 m, mid canopy 15-29 m and lower canopy of 5-14 m based on Anderson (1963) but with slight modifications (See Appendix Two for species list at each forest layer). These data were also used to construct pie charts showing the proportion of the upper, mid and lower canopy layers for each community type, which were subsequently used as input in the visualisation section of this thesis.

3.3 Classification of Peat Swamp Forest Community

The analysis of plant species data was executed using Community Analysis Package 4, v.4.1.3 (2007) software, for Detrended Correspondence Analysis (DECORANA) and Two-Way Indicator Species Analysis (TWINSPAN) were used to identify plant community and characteristic species, respectively.

Species score and sample score, and indicator value for 89 plant species recorded in 9 plots were used in indirect ordination (DECORANA) to examine potential environmental gradients.

The results from the indirect ordination allowed groupings of forest plots (as clusters), identified based on the axes of variations. Plots within the same cluster were regarded as one community. Species association patterns were used to verify that the plots within each ordination cluster belonged to the same forest community in terms of the presence of constant and characteristic species.

3.3.1 Detrended Correspondence Analysis (DCA)

Detrended Correspondence Analysis, also known as DCA (Hill and Gauch, 1980) is an ordination method use to analyse the vegetation patterns of an area. Hill (1979) created an ordination tool or programme code called DECORANA which was based on the DCA method. DCA is a modification from the Reciprocal Averaging (RA) method, alternatively called the Correspondence Analysis (CA) method (Pisces Conservation Ltd., 2013). Furthermore, RA is a way of illustrating, in a reduced space, the relationship between species and samples through the use of distance values using a chi-square method. The detrending process in DECORANA involves the removal of the unfavourable effects of arch-like point distributions when the points are plotted in RA, which results from the quadratic association among axes, instead of being caused by a relationship that exists among the samples. The other effect of RA is a compression of end points, which are removed by axis segmentation and terminal segments expansion so that the points are compressed towards the centre rather than at the ends of the first axis (Pisces Conservation Ltd., 2013).

The inputs are the names of plant species and their respective abundance values.

3.3.2 Species Association Pattern; Constant and Characteristic Species

In the absence of a standard used to define constant species, the disproportionate distribution of structurally dominant species within a plot made the identification of constant species in the field fairly straightforward. Nevertheless, posterior analysis was run to identify constant species and co-dominant species from species lists using MSExcel. Previous literatures were checked against the results for verification of the constant species (Anderson 1963; Yamada 1997). In this study, a co-dominant species is described as a fairly dominant species in the PSF. The selection of co-dominant species was made in a similar way to constant species, taking into account firstly, the tree heights and then followed by abundance and distribution range i.e. frequency across a site.

Characteristic species were identified using the divisive procedure in the TWINSPAN programme, defined as species found in abundance within a plot, distinctive to other plots. In other words, these species showed strong locational preferences for a particular plot, in comparison to all other plots. MSExcel was also used to identify the characteristic species for further separation of plant community type where necessary, based on the absence or presence of characteristic species compared to other plots.

3.3.2.1 Two Way Indicator Species Analysis (TWINSPAN)

TWINSPAN is a type of vegetation pattern analysis that uses a classification approach since it involves identification of similarities and differences of plant species data. The data are used to assemble and group plant communities on the basis of the presence of an indicator (characteristic) species through an iterative divisive procedure.

The concept of TWINSPAN is based on pseudospecies; i.e. different variables according to the species abundance level. It first involves some ordination via the RA method and the creation of dichotomous groups, i.e. positive or negative groups of samples (Pisces Conservation Ltd., 2013). The negative side of the split contains samples that have a value less than the mean value from the original ordination, while the opposite is true for samples on the positive side (Hill *et al.*, 1975). Furthermore indicator values for species are assigned as 1 if the species occurs at all sample sites, on either side of the dichotomy. In contrast, the indicator value is 0 for species with no definitive preferences. In other words, they have a similar tendency to be located on either side of the split (Hill *et al.*, 1975). The equation (Hill *et al.*, 1975, Equation 3-2) for calculating the indicator value for a species is:

$$I_j = | m_1 / M1 - m_2 / M2 |$$

(Equation 3-2)

where;
I_j = indicator value for species j
$m_{1, 2}$ = species abundance on either side (negative or positive) of the dichotomy
M1, 2 = total number of abundance on either side (negative or positive) of the dichotomy

The negative or positive signs of the indicator species are assigned depending on their tendency to one or other side of the dichotomy i.e. on the positive or negative sides (Hill *et al.,* 1975). The process is carried out in a repetitive manner, with similar sample clusters being arranged in close proximity. Further sub-divisions result in a dendrogram until the smallest group size pre-defined by the user is reached, and then sample classifications are used to classify the species (Pisces Conservation Ltd., 2013).

The input data for this analysis were the species and their abundance values for each plot. A custom value was used in the analysis whereby the cut value was set to 5 at each interval to reflect the number of species used as pseudospecies in the TWINSPAN analysis.

Common species were analysed using a compare tool in Community Analysis Package 4 v.4.1.3 (2007) software in order to identify common species between two samples. Plant species in Site A were compared against those at Site B and Site C. In addition Site B was also compared against Site C in order to find the shared species, indicating common species between plots and possible patterns of these common species throughout Badas. The presence of common species may indicate species individualistic behaviour, whereby the species can be found across a wide environmental range.

Hence, methods on how the PSF communities are viewed from the species space have been described in this section.

3.4 Forest Visualisation

Methods for forest visualisation are divided into the 3D tree model of PSF communities, visualisation of forest ordination results and the pie chart of forest structural diversity. The aim is to enhance the ecological understanding, through visualisation of PSF diversity when viewed from the species and geographic spaces.

3.4.1 3D tree model

ESRI delivered the 3D Vegetation library in its ESRI product in 2014 (ESRI, 2014) as a result of integration with plant factory software by E-on, but the capability of its suitability in the study of vegetation ecology has not been previously explored. While there are other leading 3D immersive nature technologies e.g. by E-on software for animation and rendering purposes (ESRI, 2014), ESRI ArcMap was preferred in this study due to its ease of use, in addition to the spatial and analytical capabilities that it offers which are necessary in the study of vegetation ecology. For example, the 3D thematic maps (ESRI, 2014) can provide structural analysis of a plant ecosystem as an individual GIS layer. Another added advantage of using the ESRI 3D tree library (billboard) is the seamless integration with the geodatabase in ArcMap compatible format for the purpose of performing interactive queries.

As the 3D tree model by ESRI was only developed recently, for the purpose of the analysis presented in this thesis, certain species types in the 3D tree library were used to represent the tropical species of PSF. The selection of species was based on physiognomy such as colour e.g. red coloured species are inappropriate for tropical species, crown shape e.g. pine and needle shapes were avoided, and tree trunk height e.g. not too short is preferred. The stag headed *Shorea* species was represented by *Acacia*, a type which is also commonly found in heath forest in Brunei as an invasive species (Osunkoya and Damit, 2005).

In a plot, the upper, mid and lower canopy species were separated, e.g. trees with height of 5-15 m are the lower canopy species, 15–29 m are the mid canopy species while trees ≥ 30 m are the upper canopy species. The analysis was performed in ESRI ArcMap v.10.1 (ESRI, 2012) for selection by height attributes for specified tree heights. Further divisions into 5 m height intervals for each species were carried out for enhanced visualisation of forest stratification/structural diversity, rather than emphasis on species diversity per se. For lower canopy species the classes (representing the GIS layers) used were 5-10.5 m and 10.6-15.5 m. The mid canopy species were 15.6-20.5 m, 20.6-25.5 m and 25.6-29.5 m. The upper canopy species were >29.5 m (Table 3-1). If the tree stratification was too coarse, too many canopy gaps would appear and thus defeat the purpose of a fair representation of the PSF community type. A balance in good visual impression was found through the use of 5 m height intervals, since if the height division was too fine, there was a considerable amount of noise in the data with subsequent poor visual effect. The selected tree height attribute function was subsequently used to create an individual GIS vector layer representing the tree heights accordingly e.g. a PSF community may have about six GIS tree height layers.

Only 8 plant species were used out of the original 89 species (Table 3-1) for the purpose of simplicity and directive focus on tree structural diversity, assuming the plant species at each tree height layer were constant. The selected tree height GIS layers were explored using Arc Scene v.10.1 (ESRI).

Table 3-1: A list of 3D tree models used to represent tropical PSF. Source: ESRI 3D vegetation library (ESRI, 2014).

Height (m)	**Species**	**Local equivalent**
>29.5	*Umbrella acacia*	Upper canopy species; *Shorea albida*
≥25.6-≤29.5	*White oak*	Mid-canopy species; *Palaquium cochlearifolium*
≥20.6-≤25.5	*Southern magnolia*	Mid-canopy species; *Dactylocladus stenostachys*
≥15.6-≤20.5	*California walnut*	Mid-canopy species; *Polyalthia glauca*
≥10.6-≤15.5	*Black locust*	Lower canopy species; *Cotylelobium burckii*
≥5≤10.5	*Red hickory*	Lower canopy species; *Syzygium tawahense*
<5	*Common hawthorn*	Undergrowth species; *Elaeocarpus mastersii*
1-2	*Hedgehog agave*	Undergrowth; spiky *Pandanus* species

The undergrowth *Pandanus* layer was placed randomly and its distribution was illustrated by using one plot. The square plot used either 3D texture fill effect of wood mulch or picture fill of leaves from the ESRI 3D ground cover library. The picture fills were especially time consuming to run.

The symbol size used the lowest value for each height class. For example, for a mid-canopy species represented by tree billboard *White oak* species (Table 3-1), the symbol size for all trees which fall within this particular GIS layer was set to be one only i.e. 25.6 m.

The 3D placement in y-axis offset value for species input was set to be between -0.018 to -0.08 m depending on the species type, in order to prevent certain tree species appearing to be floating in a mid-air location.

For the purpose of simplicity and ease of interpretation, only one plot was used to represent each of the community types, due to the structural similarities among plots within a plant community. Interactive selection of a forest GIS layer (previously created based on tree heights) was performed in ArcMap v.10.1 and ArcScene v.10.1, to visualise the individual components of the upper, mid and lower forest canopy layers, both in profile and perspective views.

3.4.2 Forest ordination and structural diversity in species space

Each cluster in the ordination result/ tree diameter class distribution was compared against the 3D tree model to visualise the different PSF communities on the basis of species-geographic space relation. In a similar manner, the 3D tree model of each PSF community was compared against pie charts prepared in MSExcel (see structural diversity data section 3.2) describing the forest structural compositions expressed in percentage terms, for each site based on the field study data.

3.5 Summary

The introduction section in this thesis provides an account of the principle methods used to undertake the vegetation analysis of the PSF in Badas, which are approached from the species, environmental and geographic realms. Furthermore, this chapter provides an overview of the study area and the methodology.

An account of field sampling technique was given, including the criteria for the selection of sites, followed by identification of tree species and sampling of forest structure.

Methods on classification of PSF from species space were described and explained in sections 3.2 and 3.3. The elements of diversity and dominance covered in these sections are the Shannon-Weiner Diversity Index, species area curve, rank abundance curve and ecological dominance. On the other hand, groupings into communities are approached through ordination (DCA) and classification (TWINSPAN) for identification of characteristic species.

The visualisation element of the PSF was covered in section 3.4 where PSF communities were viewed from the perspectives of species and geographic spaces. These included the detailed operation of the creation of a 3D tree model and the utilisation of ordination, tree diameter class distribution and tree structural diversity results compared against the 3D tree model. The following chapter will give the results of each of the methods previously outlined in this chapter.

CHAPTER FOUR

4 Results

4.1 Introduction

The ecological characteristics of the PSF (chapter one) are explored and explained in this results chapter. The results will be outlined in separate sections with the aim of addressing the various research questions one by one; firstly the PSF ecology (i.e. on plant diversity and dominance), secondly the PSF communities which is subsequently followed by the visualisation results. The visualisation results are used to communicate the ecological characteristics of the peat swamp forest.

4.2 Results on Plant Diversity and Dominance

This section will describe and explain the results of species diversity index and species dominance patterns.

4.2.1 Species Diversity Index

Patterns in species-diversity were explored using values for species richness and the Shannon-Weiner diversity Index (H’). The floral diversity survey revealed a total of 33 families comprising 60 genera and 89 species. See Appendix two for the full species list.

An illustration of species richness, the plant species diversity index and tree stem counts are provided in Table 4-1. In terms of species richness, species count per ha and H’, there are quite subtle differences between plots 1 to 6. Species richness ranges from 13 to 19; species count per ha from 52 to 76 and the H’ value from 1.7 to 2.19. For these plots, the tree stem count values per plot are also similar, with a range of 94 to 106. Plots 7, 8 and 9, however, are distinctive from plots 1 to 6, both in terms of species richness and tree species count per ha. In these plots, the species richness and species count per ha are higher, with a range of 21 to 34 and 84 to 136, respectively, while the tree stem count per plot is lower, ranging from 55 to 80 and H’ value from 2.11 to 2.99.

Table 4-1: Species richness, diversity index and species and tree stem counts for the nine Badas plots (50X50 m).

Plot	**Species richness**	**Species count per ha**	**H'**	**Tree stem count (per plot)**	**Tree stem count per ha**
1	18	72	2.02	106	424
2	17	68	2.05	101	404
3	15	60	1.90	94	376
4	19	76	2.19	99	396
5	19	76	2.08	101	404
6	13	52	1.70	103	412
7	34	136	2.96	80	320
8	21	84	2.11	74	296
9	26	104	2.99	55	220

The general pattern exhibited by these results is that low species richness is related to high tree stem count per ha and vice-versa. For plots 1 to 6 the species richness values are all below 20 species per plot while the tree stem count per ha values are quite high (376 to 424 trees/ha). On the other hand, for plots 7, 8 and 9 where the species richness is high at more than 20 per plot, the tree density is lowest, and lies within the range of 220 to 320 trees/ha (Table 4-1).

4.2.1.1 *Species Accumulation Curve*

The total number of tree species recorded was 89 species across the whole plot survey area of 2.25 ha. The species-area pattern is illustrated by a species accumulation curve for constant areal extent of 50 x 50 m (Figure 4-1).

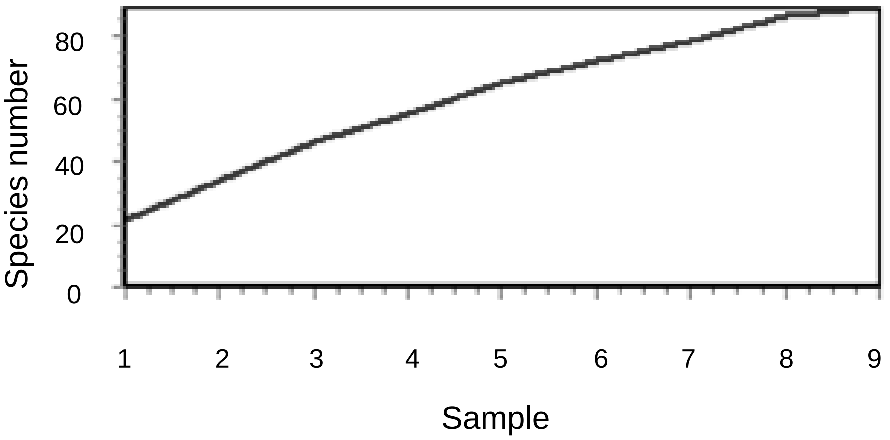


Figure 4-1: Species accumulation curve for Badas plots showing a steady increase in species encountered with the increase in plot area sampled (i.e. plots 1 to 9).

On Figure 4-1 (from left to right), the x-axis refers to the cumulative increase in area sampled. At a landscape level, these results show that the number of species increases with increasing area but that the rising curve begins to level off as indicated by plot 8, indicating that most of the species were collected and represented in this type of forest within a total study area of around 2.0 ha. The gently inclined (almost linear) shape of the species accumulation curve suggests a less rapid or gradual change in the species composition with increasing area. This may be an indicator of low tree species number which is a characteristic feature of PSF.

4.2.2 Species Dominance Patterns

The term dominant species as used in this study refers to both the tree stem count/abundance of the numbers of an individual tree species as well as the species basal area per plot. Dominance based on tree stem count is described first.

4.2.2.1 Dominant Species Based on Tree Abundance at Plot, Site and Landscape Level within Badas

For dominance based on the number of tree stem count (abundance), the species with the first three or four highest counts were arranged in hierarchical order (species rank) in order to focus on the broad patterns of dominance.

Dominance based on tree abundance has not been able to distinguish between the upper and lower canopy species. The data presented in Tables 4-2, 4-3 and 4-4 show changes in the most dominant species, when observation was made at a different study level.

Table 4-2: Dominant tree species at plot level (based on tree stem count).

Plot	Dominant 1	Dominant 2	Dominant 3
1	*Lithocarpus dasystachyus*	*Diospyros evena*	*Palaquium sp*
2	*Madhuca curtisii*	*Palaquium ridley*	*Shorea albida, Diospyros evena*
3	*Madhuca curtisii*	*Diospyros evena*	*Shorea albida, Lithocarpus dasystachyus.*
4	*Shorea albida*	*Syzygium acuminatissima*	*Xanthophyllum amoenum*
5	*Syzygium acuminatissima*	*Shorea albida*	*Garcinia sp.*
6	*Shorea albida*	*Austroboxus nitidus*	*Garcinia sp.*
7	*Madhuca curtisii*	*Dyera costulata*	*Blumeodendron tokbrii, Polyalthia glauca*
8	*Madhuca curtisii*	*Dyera costulata*	*Shorea albida*
9	*Dryobalanops rappa*	*Naphelium lappaceum*	*Syzygium tawahense*

Table 4-3: Dominant species at site level, comprising groups of plots (based on tree stem count).

Site	Dominant species
A	*Madhuca curtisii*, *Lithocarpus dasystachyus*, *Diospyros evena*
B	*Shorea albida, Syzygium acuminatissima, Garcinia sp.*
C	*Madhuca curtisii*, *Dyera costulata*, *Dryobalanops rappa*, *Shorea albida*

Table 4-4: Dominant species at the landscape level (based on tree stem count) indicating the top six dominant species arranged in hierarchical order for the entire surveyed area.

Item	Dominant species	Tree count
1.	*Madhuca curtisii*	146
2.	*Shorea albida*	138
3.	*Diospyros evena, Lithocarpus dasystachyus*	58
4.	*Syzygium acuminatissima*	53
5.	*Garcinia sp*.	35

Changes in the most dominant species occur from plot to site, and up to landscape level. For example, the dominant species of plot 1 is *Lithocarpus dasystachyus* but at the site level, it is replaced by *Madhuca curtisii* (Site A). *Madhuca curtisii* also dominates at the landscape level.

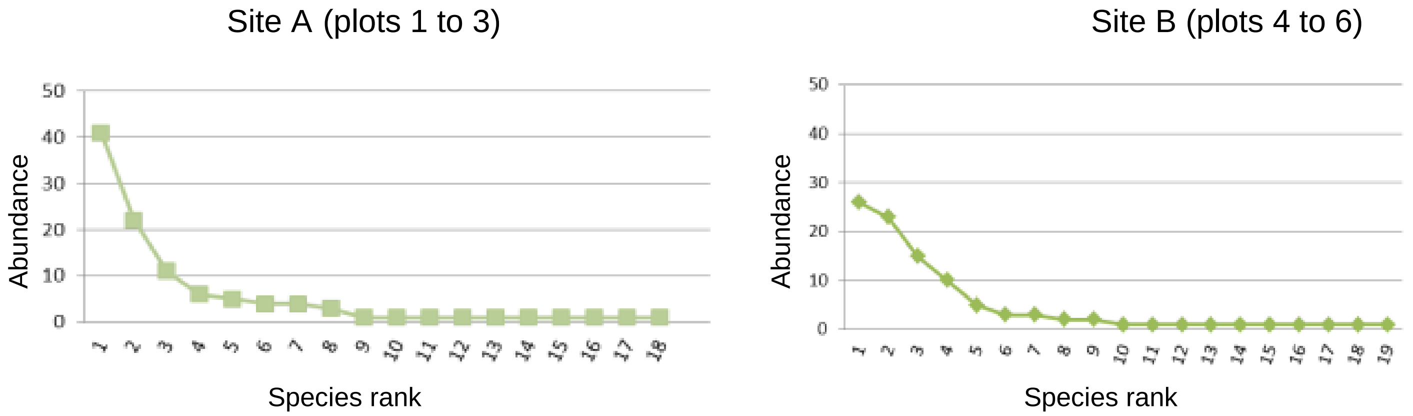
But this is not true for plots 2 and 3 (Site A) and plots 7 and 8 (Site C) whereby *Madhuca curtisii* consistently dominates at all level of observations. As for the case of plots 4 and 6, *Shorea albida* becomes the most dominant species, and this species also dominates at the site level (site B). But the effect of dominance for *Shorea albida* is not readily apparent at the landscape level, since at this level, *Madhuca curtisii* is the most dominant species, although *Shorea albida* became the second dominant (Table 4-4). Interestingly, the dominant feature of *Syzygium acuminatissima* for plot 5, did not match against the most dominant species at plots 4 and 6 (of site B) or at the landscape level. The same also holds true for *Dryobalanops rappa* for plot 9 when compared against plots 7 and 8 (of Site C), and at a landscape level i.e. the species did not match against the most dominant species at different levels of observation, which may suggest that plot 9 belongs to a different plant community.

At landscape level, *Madhuca* and *Shorea* can be separated due to their distinctive abundance values, i.e. tree stem count which is more than twice larger than the rest of the species (Table 4-4). Hence, at a family level of these species, a general pattern of *Sapotaceae-Dipterocarpaceae* dominant family can therefore be derived from the abundance values of the *Madhuca* and *Shorea* species respectively, which can be used as a basis of dominance at a landscape/ family level for the Badas PSF.

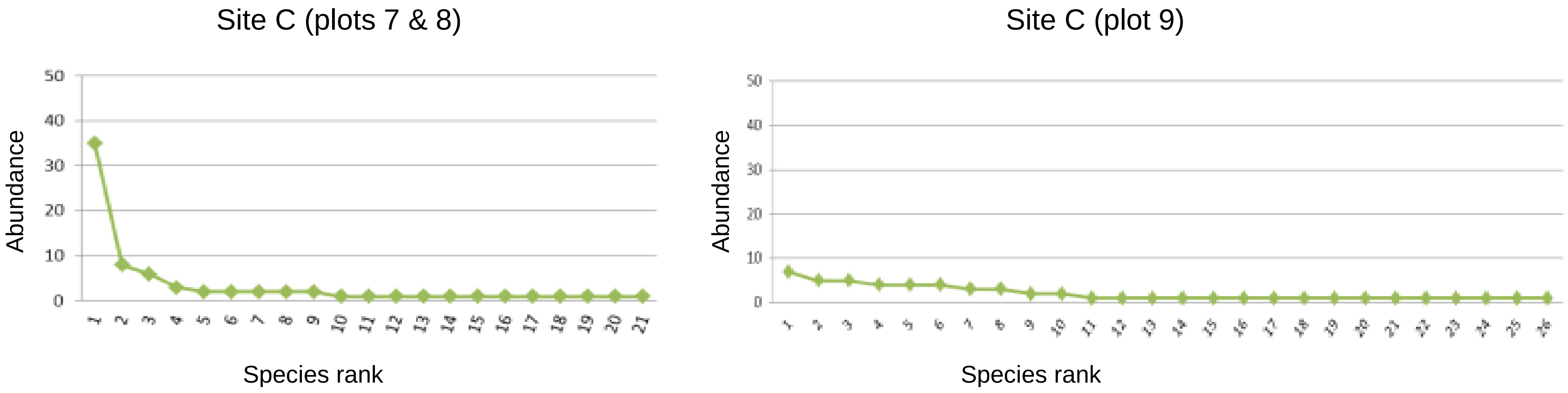
4.2.2.2 Rank-Abundance Curve of Badas Peat Swamp Forest

In order to explore species richness and evenness, species rank abundance curves are used (Figure 4-2). These are plotted by arranging the plots into four different groupings (prior to the application of the ordination method). Site A refers to plots 1-3, Site B to plots 4-6, Site C is represented by plots 7-8 and also an individually assigned plot 9. These groups were defined based on visual judgement of the site characteristics, reference to previous literature and proximity between plots. In particular, site C was divided into two i.e. plots 7 and 8 as one group, with plot 9 as another group on the basis of species composition (Table 4-2). None of the first three dominant species in plot 9 is in common with any of the species in plots 7 and 8 of the same site. For this reason, it is independently assigned as a separate group in this analysis. No other grouping was attempted here, as these sites are disconnected spatially and are relatively far from one another. Only one of the plots was used to represent each site, since the rank abundance patterns were fairly similar (with exception to site C) between plots of the same site (Figure 4-2).

The species rank abundance curve at different sites for selected Badas plots is shown in Figure 4-2. The x- axis represents the rank abundance of each species in a plot, which are organised from highest to smallest abundance values while the y-axis represents the actual abundance values of each species. The four groups shown below have variable lengths of the x-axis and heights at the y-axis. The longest x-axis belongs to plot 9. At a small 50 x 50 m plot level, individual plots show both primacy and binary patterns. Primacy pattern refers to where the species with the highest number of counts greatly exceeds the total number of counts for the second dominant species within the same plot. The binary pattern refers to a dominant species that is accompanied by co-dominant species within the plot. Sites A and C show a primacy pattern. The primacy pattern was more pronounced for Site C compared to site A. Site B shows a binary pattern. The variation in patterns of arrangement of species based on abundance value potentially implies habitat diversity within the study location, with each site belonging to a different plant community. In site C (plot 9) no single species dominates.


Site A (plots 1 to 3)

Site B (plots 4 to 6)


Site C (plots 7 & 8)

Site C (plot 9)

Figure 4-2: Species rank abundance curves for four different study sites with tree species ranked from most to least abundant.

4.2.2.3 Basal Area and Tree Diameter Class Distribution

The second measure of dominance is basal area, which is described in this sub section. Basal area (BA) refers to the diameter of a cross-section of a tree, where the diameter is measured at breast height (dbh). Table 4-5 presents the total basal area for each of the nine plots. The values range from 7.45 m^2/ha (plot 9) to 40.13 m^2/ha (plot 6). While other plots have a BA value that is more or less similar, plot 9 is distinctive from the other plots. The BA of this plot is 7.45 m^2/ha, which is roughly 5 times less than the highest BA value recorded for plot 6. As commented earlier, this again indicates the possibility of this plot being located in a different transitional community between heath forest and PSF (See Appendix Three for further information on basal area per family of the Badas PSF).

Table 4-5: Summary of basal area (BA) data for the nine Badas plots.

Plot	**Maximum diameter (cm)**	**Mean diameter (cm)**	**Basal area (total BA/0.25ha)**	**Basal area in m^2/ha (total BA/ha)**
1	98.7	19.8	5.55	22.18
2	106.0	26.5	9.65	38.61
3	96.8	24.1	7.71	30.83
4	87.3	26.2	8.20	32.64
5	75.9	25.2	7.46	29.83
6	71.5	30.3	10.01	40.13
7	135.0	25.6	7.42	29.68
8	100.4	29.2	7.56	30.22
9	70.0	17.4	1.86	7.45

In terms of tree diameter class, the most common tree diameter class across all plots is 11-20 cm dbh which comprises of more than half of the total tree count (Table 4-6). To illustrate, plot 8 (Figure 4-3, coloured green) shows a slightly different distribution in that the 11-20 cm dbh class only slightly exceeds other dbh classes, whereas in all other plots this is by far the dominant class. Furthermore, the upper canopy species of >80 cm dbh (light purple and red) were used as a threshold value for comparing the potential community types based on the abundance patterns of both the upper and the lower canopy layers.

Table 4-6: Distribution of tree diameter dbh (cm) across the plots.

Plot	**0-10**	**11-20**	**21-30**	**31-40**	**41-50**	**51-60**	**61-70**	**71-80**	**81-90**	**91-100**	**101-110**	**111-120**	**121-130**	**131-140**	**Total trees**
1	7	75	14	4	0	1	0	2	1	2	0	0	0	0	106
2	6	55	22	4	0	2	3	1	4	3	1	0	0	0	101
3	5	56	17	4	0	2	3	2	3	2	0	0	0	0	94
4	2	54	16	7	3	5	9	2	1	0	0	0	0	0	99
5	3	61	11	2	7	14	1	2	0	0	0	0	0	0	101
6	1	51	5	8	19	13	5	1	0	0	0	0	0	0	103
7	4	39	18	11	3	0	0	1	1	0	1	1	0	1	80
8	6	21	20	17	3	0	1	2	1	3	0	0	0	0	74
9	2	43	7	1	0	0	2	0	0	0	0	0	0	0	55
Total	**36**	**455**	**130**	**58**	**35**	**37**	**24**	**13**	**11**	**10**	**2**	**1**	**0**	**1**	**813**

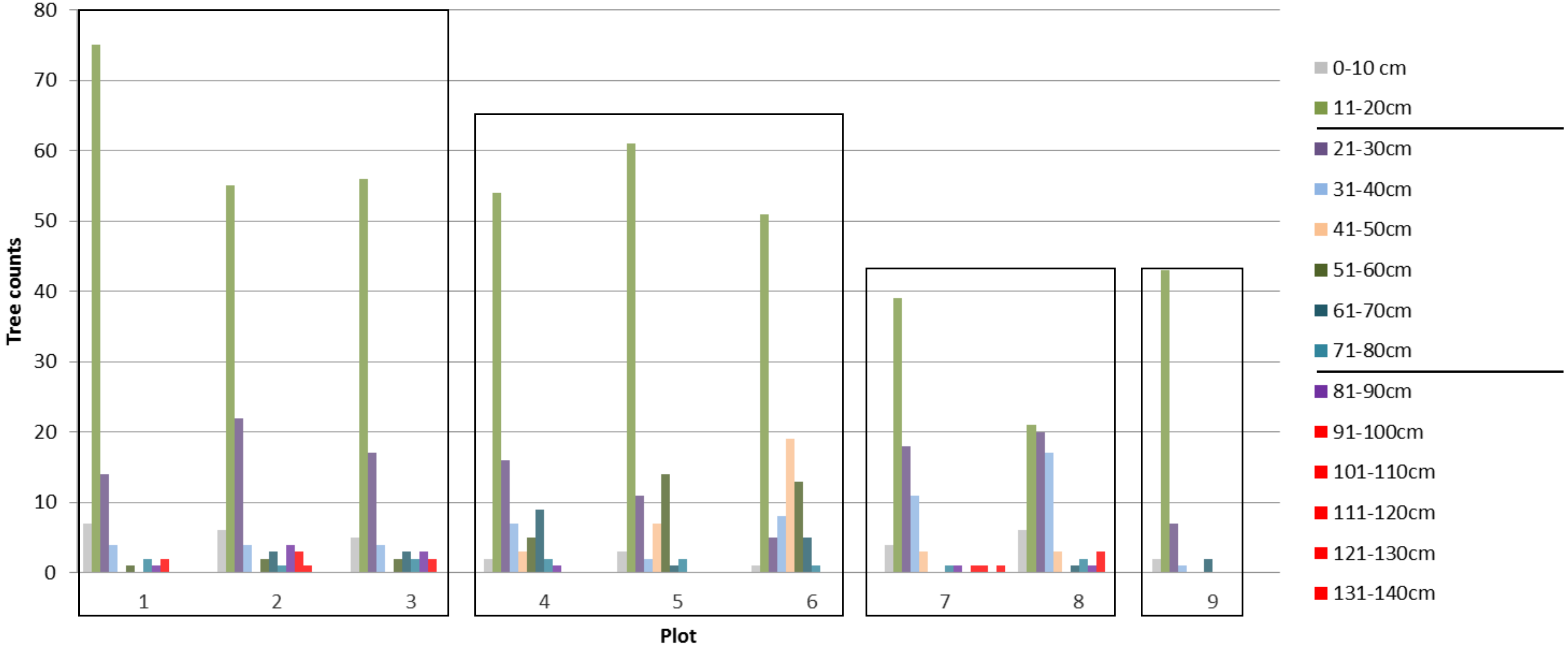


Figure 4-3: An illustration of the tree diameter distribution for each plot across 14 diameter classes. Four clusters can be obtained based on the relative presence of the upper canopy species of >80 cm dbh (light purple and red) and the most common species of lower canopy with less than 20 cm dbh (grey and green).

Through visual interpretation of the tree diameter class distribution patterns (Figure 4-3), it is possible to classify the plots according to their similarities. Plots 1, 2 and 3 could be grouped together on the basis of the presence of dominant trees >80 cm dbh; these plots are located adjacent to each other on the same transect (Site A).

Plots 4, 5, 6 can be placed in a separate group due to the lack of dominance of trees >80 cm dbh and these three plots also share the same transect (Site B).

Plots 7 and 8 form a separate group as they both have some dominance of trees >80 cm dbh and again share the same transect site (Site C).

On the other hand, plot 9 while sharing the same transect site (Site C) with plots 7 and 8, is apparently somewhat different due to the lack of species >80 cm dbh and a disproportionate number of species in the 11-20 cm dbh class compared to the nearby plots 7 and 8. Plot 9 is particularly different as the number of tree diameter classes is distinctively small in comparison to other plots i.e. it is represented by only five bar graphs.

4.2.2.4 Tree Structural Classification

The height division of tree stratification is based on Anderson (1963) with slight modification, as the structural division was made on the basis of tree girth. The upper canopy layer is described in this study as trees which attain >30 m height, the middle canopy ranging from 15 to 30 m and the lower canopy layer <15 m (Table 4-7). The decision on cut-off values was made for the purpose of simplicity as the Badas forest was found to have complex multi-strata features. In some areas, the tree heights exceed 45 m.

Table 4-7: Results of tree structural classifications at each site, in percentage.

Site	**5-14 m (lower)**	**15-30 m (mid)**	**30 m (upper)**
A	65.40	24.30	10.30
B	52.40	17.50	30.00
C	59.30	33.0	7.70

For all sites in Badas PSF, lower canopy species comprise of more than half of the total distribution of tree heights. The distinction is clear through observation and posterior analysis comparing the mid and upper canopy distribution of trees at each of the three sites.

With reference to Table 4-7, the lower, mid and upper canopy layers for each site were compared to identify the characteristics of canopies and their distribution at each site. For site A the results indicate that the mid-canopy layer is thick, about twice as dense as the upper canopy layer i.e. 24.30% and 10.30% respectively. The opposite is true for site B, where the mid canopy layer is fairly thin and, instead, the upper canopy layer dominates. The distribution ratio of canopies for the mid-canopy to the upper canopy layer in site B is about 1:2 (17.50:30.0). Site C on the other hand, similar to site A, has a sparse upper canopy layer i.e. about less than 10% of the tree species in site C formed the upper canopy. Instead, mid and lower canopy layers dominate site C. There were fairly abundant trees in the mid canopy layer in site C, nevertheless the ground would receive a higher penetration of light energy since species forming the mid canopy in this site were characteristically thin.

Shorea albida, Dryobalanops rappa and *Madhuca curtisii* form the dominant species of the upper canopy layer while *Diospyros evena, Lithocarpus dasystachyus, Syzygium acuminatissima* and *Garcinia sp.* are examples of the mid-canopy dominant species. In terms of physiognomy, trees of *Madhuca curtisii* do not generally reach the same height as *Shorea albida* but in this study both were described as upper canopy species. This is because a few of the *Madhuca* specimens based on the field survey results had attained a borderline tree height within the lower 30 m range, unlike the *Shorea* species that can reach a height range of >50 m.

4.3 Results on Plant Community

This section will describe and explain the results of ordination, classification, species association and common species of the PSF.

4.3.1 Ordination and Classification Results

Ordination was carried out in order to explore ecological gradients based on plant species space, and the ordination results revealed four distinct clusters (Figure 4-4). From left to right, plots 4, 5 and 6 belong to one cluster, plots 1, 2 and 3 to another cluster, and plots 7 and 8 to a further cluster while plot 9 exists in isolation. A cluster can be assumed to be a similar forest type, derived from shared characteristics in ordination (species) space. At site C, plots 7 and 8 are clearly distinctive from plot 9, as was also deduced from direct field observation, despite the fact that these plots shared the same transect.

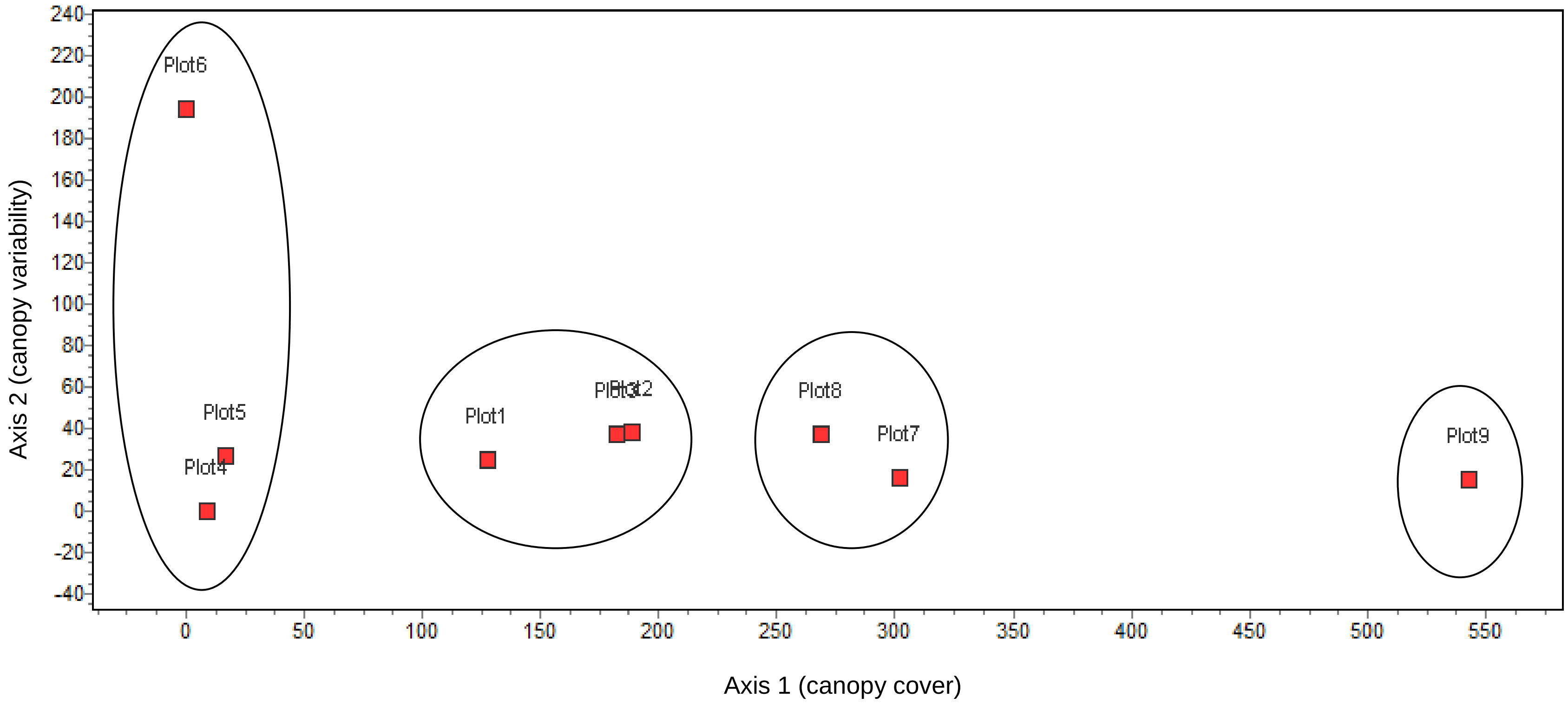


Figure 4-4: DECORANA showing ordination plot of plant species within the 9 plots separated into four groups.

Axis 1 represents changes in the tree canopy cover while Axis 2 (Figure 4-4) represents changes in variability/composition of the upper canopy species to true monodominant pattern. The general pattern is one of a change in canopy cover from intact and closed canopy gaps in plots 4, 5 and 6, to progressively more open in plot 9. Open canopy gaps are characteristic of plots 7, 8 and 9 as shown by a mixture of species dominating the upper canopy layer. On the other hand, in terms of variability, least variability in the distribution of canopy types/height was identified in plot 6.

Plots 4, 5 and 6 (site B) are located the furthest from plot 9 (site C) in ordination space, although the two sites were located fairly close to one another in geographic space. Plots 1, 2 and 3 are located adjacent to plots 7 and 8 in ordination space, although they form two fairly distinctive communities on the basis of species composition.

Plots 1, 2 and 3 (site A) are similar in terms of physiognomy to plot 7 and 8 (in site C), as the upper canopy species comprise of less than a quarter of the total species composition per plot (Table 4-7), again explaining their proximity on the first axis of the ordination space.

Similar to plots 7 and 8, trees of the Sapotaceae can also be found in plots 1, 2 and 3, but they usually occur as co-dominants (instead of dominants) in the mid-canopy layer.

Plots 4, 5, 6 belong to one group which is characterised by having a disproportionately thick upper canopy layer i.e. about 30% of the species distribution within plots 4, 5 and 6 is contributed by the *Shorea albida* family (Table 4-7). Moreover, the tree height mostly lies within the 30 m to lower 40 m range, which is lower than the maximum tree height for members of the

Dipterocarpaceae found in plots 1, 2, 3 and plots 7 and 8. The tree diameter sizes in plots 4, 5 and 6 are also small, a characteristic which may be partially responsible for enabling the large *Shorea albida* species to be densely packed, forming a large population within each of these plots. Despite the similarity of dominant species amongst plots 4, 5 and 6, plot 6 is distinctive in terms of the proportion of this species as is evident in the Axis 2 of the ordination space (Figure 4-4). In this plot the Dipterocarpaceae family monodominates, making up nearly half of the proportion of tree species. The co-dominant species found in plots 4 and 5 were mainly members of the Myrtaceae along with other species including a few Polygalaceae. In contrast, there is a strong pattern for members of the Polygalaceae family being co-dominant species in plot 6.

For species broadly separated (via ordination) on the basis of the implied presence of environmental gradients, plots 1 to 8 were grouped together as peat soil, while plot 9 was referred to as a heath soil plot, from which comparison on the plant species data were made. Plot 9 is distinctly separated in ordination space.

However, further in-depth groupings of PSF vegetation on the basis of the plant species pool data only indicated that there were four identified plant communities in the study area.

4.3.1.1 TWINSPAN Classification

TWINSPAN was applied in order to test for the association concept of plant communities based on the presence of constant and characteristic species.

The results of the TWINSPAN classification are shown in Figure 4-5, with the dendrogram being read from left to right. At the start, all species were separated based on the species absolute presence on either side of the dendrogram. *Agathis borneensis* was given a value of 1 since it has a strong preference for plot 9, being the only plot in which it was recorded. The next tier is separated on the presence/absence of *Austrobuxus nitidus* which is an indicator species for plots 4, 5 and 6 but is absent from all remaining plots. The negative sign next to *Austrobuxus nitidus* indicates that this species was found below the mean abundance value of the original ordination i.e. plot 9.

Further splits are characterised by the presence of another indicator species i.e. *Dactylocladus stenostachys,* which distinguishes plots 1,2,3,7 and 8 from plots 4,5,6 and 9. The positive sign next to *Dactylocladus stenostachys* indicates the abundance value is greater than the mean abundance value of the original ordination.

However, separation of groups of plots into community types did occur, distinguishing plots 1, 2 and 3 as a distinct forest community type from plots 7 and 8 on the basis of the presence or absence of *Dactylocladus stenostachys* as an indicator species. This species was present in plots 7 and 8 but absent from plots 1, 2 and 3 (Figure 4-5). The similar sample clusters (Figure 4-4 and 4-5) have arranged the plots closer together such that plots 1, 2 and 3 are located close to plots 7 and 8.

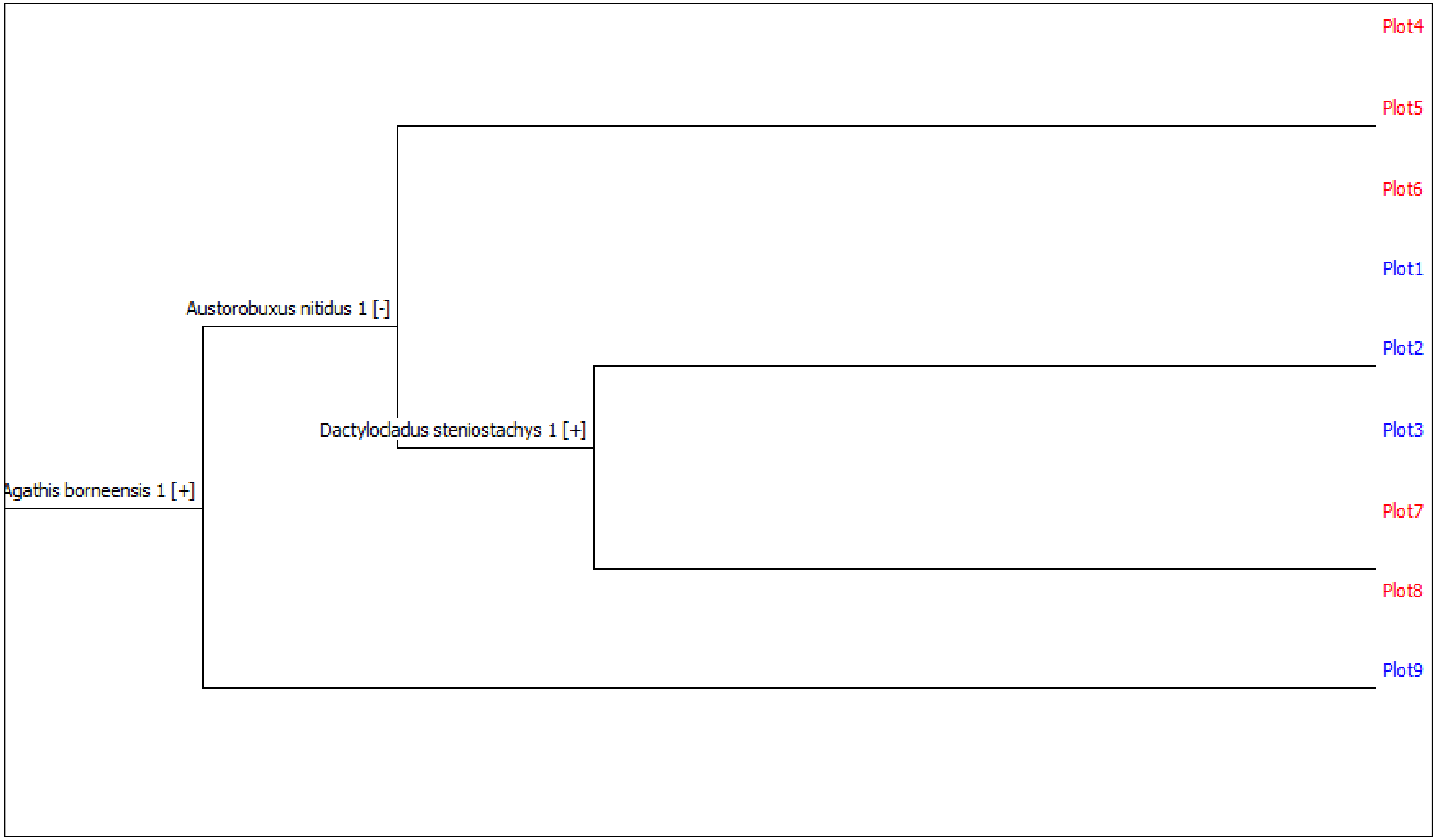


Figure 4-5: Results of the TWINSPAN analysis of the plot floristics data using a reciprocal averaging (RA) method.

4.3.2 Species Association

The results of the field survey and the vegetation floristic analysis on constant and characteristic species, tree structural variations, and common species between plots were used in order to derive a description of key community patterns (Table 4-8) for the Badas study site.

Table 4-8: Constant and characteristic species of the Badas plots.

Plot	Constant species	Co-dominant species	Characteristic species
1	*Shorea albida*	*Palaquium sp.*	*Polyalthia hypoleuca*
2	*Shorea albida*	*Gonystylus bancanus*	*Polyalthia hypoleuca*
3	*Shorea albida*	*Gonystylus bancanus*	*Polyalthia hypoleuca*
4	*Shorea albida*	*Syzygium acuminatissima*	*Austrobuxus nitidus*
5	*Shorea albida*	*Syzygium acuminatissima*	*Austrobuxus nitidus*
6	*Shorea albida*	*Xanthophyllum amoenum*	*Austrobuxus nitidus*
7	*Shorea albida*	*Madhuca curtisii*	*Dactylocladus stenostachys*
8	*Shorea albida*	*Madhuca curtisii*	*Dactylocladus stenostachys*
9	*Dryobalanops rappa*	*Horsefieldia crassifolia*	*Agathis borneensis*

Based on constant and characteristic species, community A, comprising plots 1, 2 and 3, can be described as a *Shorea albida-Gonystylus-Polyalthia* association.

Community B, comprising plots 4, 5 and 6, can be described as a *Shorea albida-Syzygium-Austrobuxus* association.

Community C, i.e. plots 7 and 8, appears to be a sub-community of PC 4 comprising a *Shorea albida-Madhuca-Dactylocladus* association. *Dactylocladus stenostachys* and *Gluta beccarii* are characteristic species of these plots.

Community D is a heath forest, which can be described as a *Dryobalanops rappa-Horsefieldia-Agathis* association. *Syzygium tawahense* is also abundant. The dominant PSF species *Shorea albida* is absent from this plot and dominance is replaced by *Dryobalanops rappa* of the same Dipterocarpaceae family. Moreover a characteristic large tree species *Agathis borneensis* is also found in this community which is absent from all other remaining plots. The decision to assign this to a heath forest type was based on references to previous literature for the Badas area and on the presence of *Agathis borneensis* and *Cotylelobium burckii* (Davies and Becker, 1996; Turner *et al.*, 2000) as well as *Dryobalanops rappa* (Newbery, 1991) which are distinctive to heath forest.

The characteristic species (Table 4-8) derived from TWINSPAN analysis for plots 4, 5 and 6 is *Austrobuxus nitidus* while for plot 9 it is *Agathis borneensis*. In Figure 4-5, TWINSPAN did not give a further indicator species type for these two clusters (plot 1, 2 and 3, and plots 7 and 8) and species lists were manually referred to which verified the absence of *Dactylocladus stenostachys* species in plots 1, 2 and 3. Hence, *Dactylocladus stenostachyus* is the characteristic species for plots 7 and 8 as this species was present for plots 7 and 8, but absent from plots 1, 2 and 3. The characteristic species of plots 1, 2 and 3 i.e. *Polyalthia hypoleuca* was identified manually from the species list.

4.3.3 Pattern of Common Species between Plots

The results of plant species comparison between plots with peat soil (1 to 8) and heath forest on sandy-peat soil (plot 9) will be described first, followed by comparison of plant species between sites i.e. Sites A and B, A and C, and B and C. Peat soil and heath soil plots were used in this analysis to illustrate the presence of spatial dependence separating the plots, as these plots are characterised by fairly contrasting environmental gradients based on the general observation of soil type in the field. The common species between sites were distinguished as verification of the identified characteristic species (Table 4-8), whereby the characteristic species are unique, and should not be present in the common species list between sites.

There are ten species in common for the peat and sandy-peat soil plots namely *Durio sp., Elaeocarpus mastersii, Ganua sp., Garcinia rostrata, Horsefieldia crossifolia, Madhuca curtisii, Naphelium lappaceum, Naphelium maingayi, Santiria laevigata* and *Syzygium zaylanicum.*

Thirteen species are in common for Sites A and B, namely *Baccaurea bracteata, Calophyllum sp., Diospyros evena, Elaeocarpus margiantus, Lithocarpus dasytachyus, Macaranga caladifolia, Madhuca curtisii, Naphelium maingayi,* *Palaquium cochlearifolium, Palaquium sp., Shorea albida, Syzygium incarnatum* and *Xantophyllum amoenum.*

For Sites A and C there are eleven species in common, namely *Diospyros evena, Madhuca curtisii, Mazzetia umbellata, Naphelium maingayi, Naphelium sp., Palaquium cochlearifolium, Shorea albida, Stemonurus scorpioides, Sterculia rhodifolia, Syzygium sp.* and *Syzygium zaylanicum.*

Twelve plant species are in common between Sites B and C, namely *Antidesma coriaceum, Campnosperma squamatum, Dalium indum L., Diospyros evena, Elaeocarpus mastersii, Garcinia sp., Gardenia chani, Lithocarpus sp., Madhuca curtisii, Naphelium maingayi, Palaquium cochlearifolium* and *Shorea albida.*

The number of species in common between the areas having presumed presence of spatial dependence, as well as among the different study sites, has a range value of between ten to thirteen species in common.

Syzygium spp. were also abundant throughout the plots, but different from one site to another. For example, S*yzygium incarnatum* was present at site A, S*yzygium acuminatissima* at site B and *Syzygium tawahense* at site C.

4.4 Results of Visualisation of Peat Swamp Forest Communities

The results in this visualisation section is divided into two parts which aim to address the research question on visualisation as a communication tool. The first part covers the research questions on how PSF is perceived through the species space. The species space are comprised of works on the PSF ordination and PSF tree diameter class. The second part is the PSF 3D tree model and pie chart of forest structure, which have been used to illustrate the inclusion of spatial elements and visual cues, in which the PSF communities were viewed from the perspectives of species and geographic spaces.

4.4.1 *PSF Communities from the Perspectives of Species Space*

The diagrams below (Figure 4-6) show the result of PSF ordination (top) and tree diameter class distribution (bottom), to illustrate the potential grouping of the PSF vegetation into four communities when viewed from the species space.

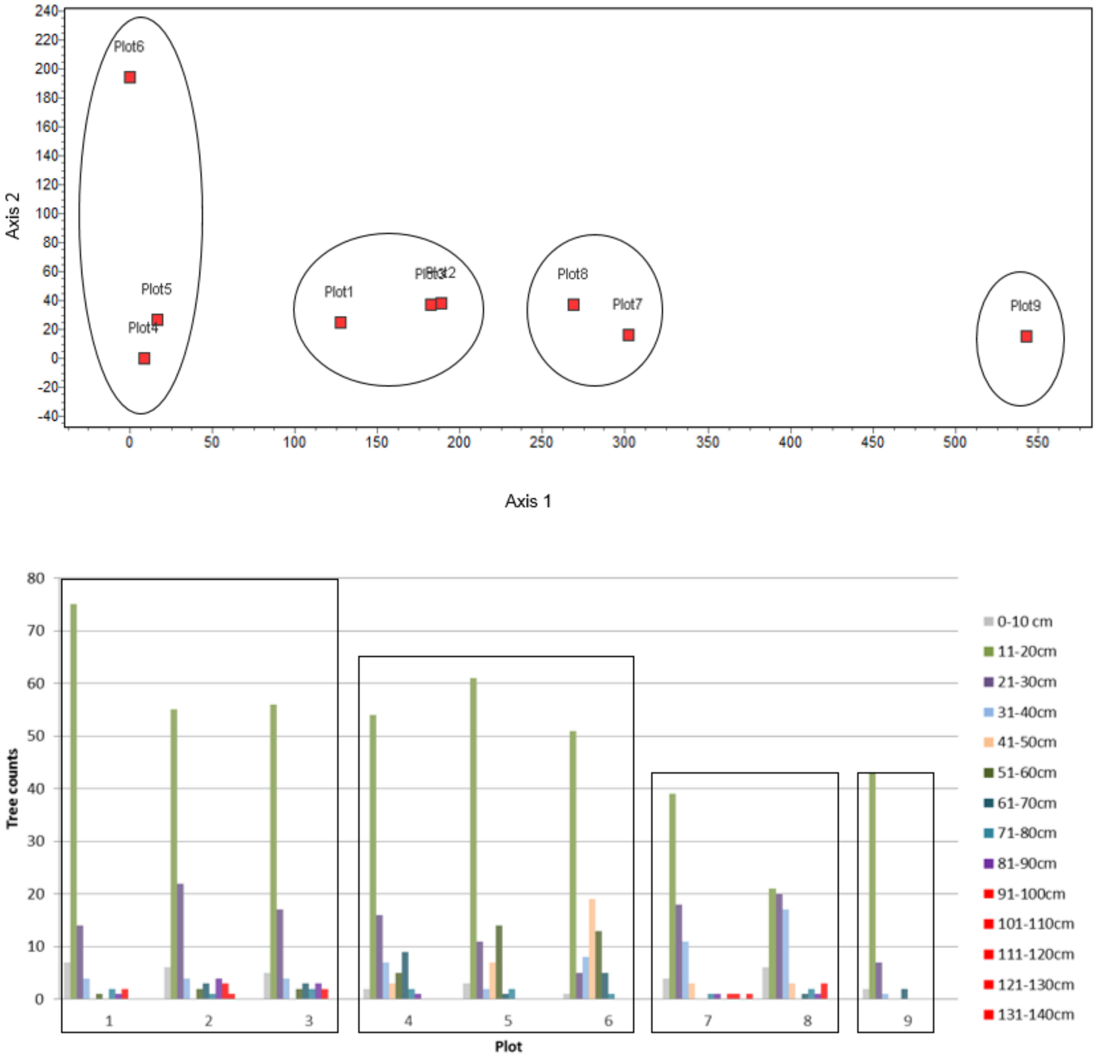


Figure 4-6: Diagrams showing four distinctive groupings on the basis of PSF ordination (above) and tree diameter class distribution (below).

Interestingly, the sole use of the species list identified four distinctive groupings by both ordination and tree diameter class distribution. Structural variations exist which are distinctive from one another, implying the diverse habitat of PSF, occurring even at a small scale.

4.4.2 3D Tree Model and Forest Structural Compositions of Peat Swamp Forest Communities

The visualisation of the 3D vegetation model shows distinct patterns in particular for the PC 4 Dipterocarpaceae and heath communities (Figure 4-7). The structural composition did not deviate much from the associated pie chart of each community, which was derived from the field data. For example, the upper canopy species sector (illustrated as the green sector on the pie chart) is the largest for the PC4 Dipterocarpaceae community and the 3D tree model clearly shows the continuous elongated row of dense upper canopy layers, in comparison to other PSF communities. In contrast, almost 90% of the pie chart (Figure 4-7) represents the lower canopy layer (the blue sector of the pie chart) in the heath community, which was also clearly shown by the sparse upper canopy layer in the 3D tree model for this particular community (Figure 4-7). The upper canopy species crown diameter for forest profile in this study is about 15 m, similar to the estimated crown diameter for *Shorea* species of PSF and hence offered a fairly representative model of the upper canopy. Comparison of species composition could not be offered through the use of pie chart alone.

The depiction of forest communities using 3D tree billboard is deemed sufficient for illustrating the concept of the structural diversity of the PSF, but such representativeness may not necessarily hold true for illustrating the diverse species composition of the PSF, due to the use of the non-tropical tree species from the available vegetation image library. Moreover the variation in species composition will be greater in reality due to the greater number of species found than those used in the 3D tree model, the presence of thick undergrowth and the various characteristic aboveground root structures of PSF species (e.g. buttress and stilt roots). However, as the 3D model with seamless integration with GIS environment is still in its infancy, there is potential for further conceptualisation of tropical tree species in the 3D tree model using other formats (i.e. other than billboard used in this study) such as through the use of SketchUp 6.0 and 3Ds max software that works with ArcMap v10.1 (ESRI, 2013). Rendering techniques and simulation of tree model growth have the advantage of creating profound visual impact and engagement, but may also be devoid of accurate species composition or location. However, geo-referenced points have the advantage of exploring PSF ecology through interaction, adjacency and comparison concepts which could be further developed in a GIS for the analysis of PSF patterns and processes.

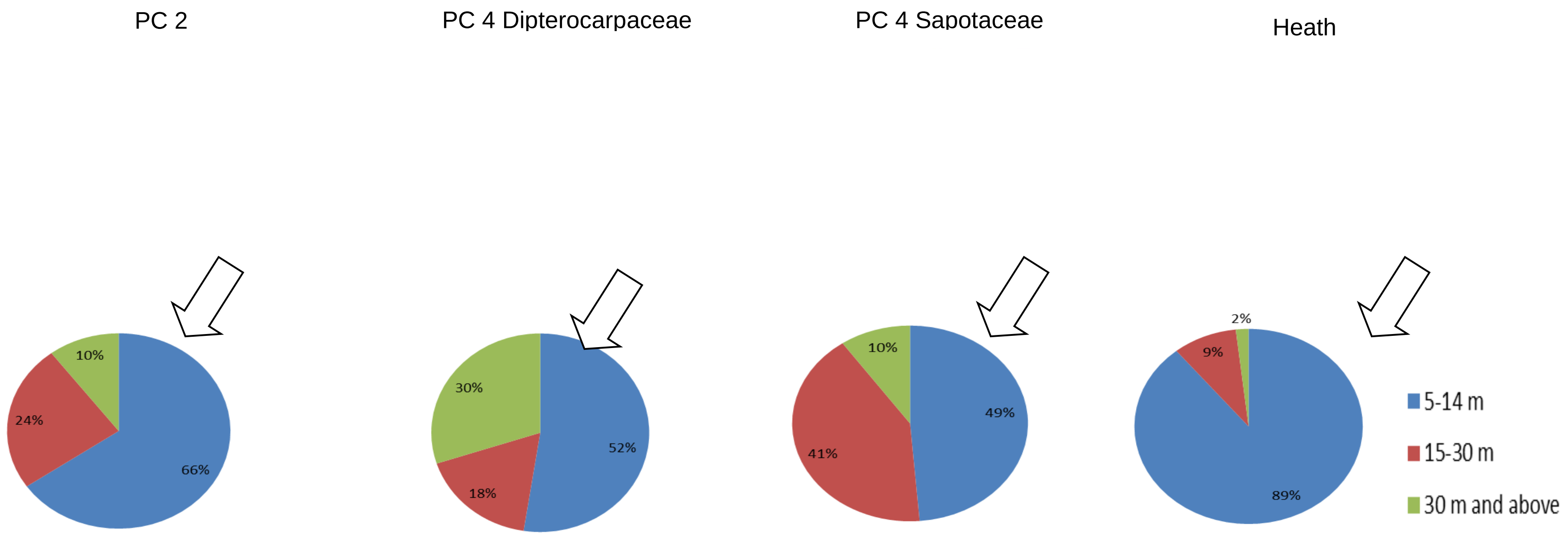


Figure 4-7: Structural compositions for the different peat swamp forest communities showing the lower forest layer of 5-14 m (blue sector), middle canopy layer of 15-30 m (red sector) and upper canopy layer of 30 m and above (green sector).

The vegetation profiles of each of the PSF communities, with 5 m breakpoint (solid line), for trees of over 30 m height and 50 m plot distances for all forest types are described and illustrated in the following sections.

4.4.2.1 Vegetation Profile of PC 2

The profile view for PC 2 shows a fairly complex forest, comprising of multiple strata (Figure 4-8).

Figure 4-8: Diagrams showing the vegetation profile and perspective views (inset) of the PC 2 community.

4.4.2.2 Vegetation Profile of PC 4 Dipterocarpaceae Community

The vegetation profile for PC 4 Dipterocarpaceae dominant was mainly composed of the upper canopy species of >30 m. There is an apparent gap in the mid canopy layer, which is also characterised by a sparsely distributed lower canopy species of <5 m (Figure 4-9).

Figure 4-9: Diagrams showing the vegetation profile and perspective views (inset) of plant community PC 4 Dipterocarpaceae dominant.

4.4.2.3 Vegetation Profile of PC4 Sapotaceae Community

The vegetation profile for the PC 4 Sapotaceae dominant community shows a complex forest. The mid and upper canopy layers provide much of the canopy cover (Figure 4-10).

Figure 4-10: Diagrams showing the vegetation profile and perspective views (inset) of plant community PC 4 Sapotaceae dominant.

4.4.2.4 Heath Community

The heath community has a sparse distribution of trees and the canopy is mostly dominated by the lower canopy species (Figure 4-11).

Figure 4-11: Diagrams showing the vegetation profile and perspective views (inset) of heath community.

The results of the interactive feature of the forest profile analysis shows the separation of a particular forest community into several forest layers (Figure 4-12). A particular species at each height layer could be identified through the Identity tool pointing at the features of interest, and supplemented with the associated spatial and attribute data. In this way, the pattern of species for each forest layer could be observed, while associated species and shade tolerant/intolerant species could also be inferred from such patterns. Therefore giving possible options for extraction of particular features of interest.

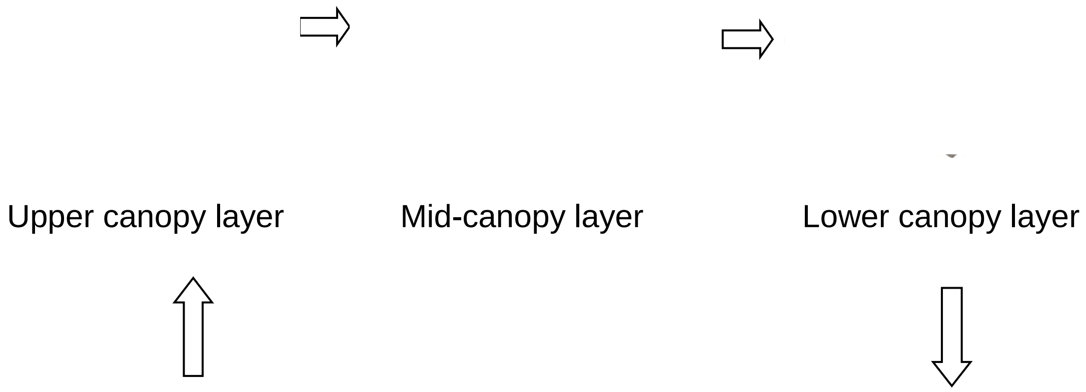


Figure 4-12: Illustration of structural compositions for the upper, middle and lower canopies of the peat swamp forest viewed from different perspectives.

4.5 Summary

The section on the ecological characteristics covered in this result chapter comprised of various elements of ecology; the species accumulation curve, rank-abundance curve, tree diameter class distribution, ordination, characteristic species and common species comparison table. On the other hand, communicating the ecological characteristics was explained through visualisation (in species and geographic space) which involved the use of a pie chart of tree structure as well as a 3D tree model of PSF communities that offered the use of visual cues and perspectives.

The research question of PSF ecology had seen the application of a diversity index to describe variations in tree species diversity amongst the study plots. The highest number of species richness comes from plot 9 while the lowest is plot 6.

The species accumulation curve has shown gentle increment of the slope of change of species number against the size of study area. This gentle inclining pattern is possibly an indication of a type of pattern of tree species changes with area for pristine PSF communities.

Diversity patterns at alpha and beta scale have been described in detail contributing invaluable information on the diversity index of the remaining PSF of Southeast Asia based on actual survey data. Issues on out-of-date data were solved to some extent with the provision of up-to-date knowledge based on available data on species diversity of the PSF in Brunei. As most field surveys on plant diversity were conducted in a small area using several plots, these results have shown the potential for further scope of work (of small area survey). For instance, this thesis demonstrates the analysis of forest structure and diversity patterns, and the interrelationship between them could be used as a rapid assessment tool for understanding the PSF community and ecology.

There were also some descriptive patterns of ecological dominance of PSF based on abundance value and basal area contributed in this results chapter. Abundance at plot, site and landscape level was calculated and analysed using the rank abundance curve, illustrating the different patterns in the distribution of dominant species. At a landscape scale the Badas PSF showed a binary pattern in the rank abundance model suggesting the presence of dominant and co-dominant species characterising the species arrangement and potentially also species interaction processes within the Badas PSF communities. In terms of abundance species within this study on Badas PSF, the most abundant species is *Madhuca curtisii* followed by *Shorea albida* where the abundance pattern was identified to be scale specific. Hence the apparent *Sapotaceae-Dipterocarpaceae* dominance at a landscape level in Badas PSF. Analysis of abundance in this study i.e. at plot, site and landscape level has given different dominant species based on abundance. The confinement to large scale study alone may hide differing tree species composition that might be found should floristic surveys be repeated at smaller scale. The use of abundance in defining dominance could not differentiate the abundance between the upper and lower canopy species.

Study on basal area patterns indicated two general divisions based on species diversity separating plots 1 to 6 from plots 7 to 9. A highly distinctive basal area amount may serve as an indicator of the unevenness or the monodominant traits of PSF, e.g. plot 6. Although basal area could not be used to form groupings of PSF communities, the use of basal area to describe dominance has also been able to distinguish PSF and non-peat forest. In contrast, the use of tree diameter class distribution was able to group four different PSF communities.

There was an inverse relationship between species diversity and dominance based on tree abundance as derived from field analysis. This may imply species relation with environmental conditions as well as biotic processes influencing such patterns.

The application of the ordination method DECORANA was fairly simple as it did not require the involvement of details on species structural variations as input, since the analysis was purely based on floristics. Furthermore, the result of the analysis suggested a strong correlation for species pool and shared communal structural traits, for example in terms of canopy structure (variability) and spacing between canopies which were related to the species in question. Through this way, distinctions between the different community types could be made.

DECORANA was useful in identifying the axis of species composition and the presence of the different PSF community types based on the species score and weighted data matrix. This indicated the presence of a potential environmental gradient underlying the distribution and presence of the community types.

The tree diameter class distribution results were similar to the phytosociologic approach classification results using DECORANA as both methods identified four separate groupings of plant community types.

Classification through indicator analysis (TWINSPAN) has been carried out to identify the characteristic species based on the Braun-Blanquet approach. The constant, co-dominant and characteristic species were used to identify that the plant species belong to a particular phasic community or forest community sub-type.

Based on the constant and characteristic species compared against a previous study (Anderson, 1963), identification of PC 2 was rather straightforward but PC 4 had more local variants, i.e. two sub-community types of PC 4. Also looking at other characteristic species for description of PC type is important, rather than sole reference to species association description from the previous studies e.g. Anderson (1963). A limitation of TWINSPAN is identified here whereby in the instances where second characteristic species was needed to be identified, posterior analysis will have to be carried out manually from the species lists.

Constant and characteristic species were more consistent to be used in the designation of PSF community types, in comparison to the use of co-dominant species which showed localized variation. Furthermore, common species between peat and heath, as well as between sites had identified a total of ten to thirteen species in common for these particular forest types.

Both ordination and classification methods result in the presence of structure in the data. Different forest structure and composition were related to different forest cover within the PSF phasic communities, as well as the possible presence of environmental gradients separating the vegetation types. Despite the small area used, this study implies the influence of small changes in the environmental conditions within a PSF in terms of peat depth, hydrology and microclimate.

The results of both ordination and classification in this study identified four community types namely PC 2, PC 4 Dipterocarpaceae dominant, PC 4 Sapotaceae dominant and heath forest.

The significance of ordination and classification is that they provide indirect methods for identification of the presence of environmental gradients and indicator/characteristic species, unique to individual community types.

The extent of monodominant pattern was found only in one plot in this study, in addition to the presence of different PSF communities based on the association concept, supporting the heterogeneous nature of PSF as identified from previous studies. Hence implying firstly, the need to further understand the possible relation of ecological gradients with a monodominant pattern and secondly the significance of incorporating a full range of PSF diversity in sustainable forest management.

Furthermore the results indicate the important role of the upper canopy layer as an umbrella species, hosting various middle and lower canopy species, some of which were sensitive to changes in microclimate conditions, indicated by the presence shade or flood tolerant/intolerant species. This was supported by a previous study (Shimamura and Momose, 2005) indicating the role of canopy gaps and drier hummocks in influencing the regeneration of PSF species.

In Badas PSF, it was found that high plant species diversity is accompanied by high forest stratification and vice versa. PC 4 Dipterocarpaceae dominant is associated with the least diverse forest structure, and the absence of mid-canopy layers.

The arrangement of the plant groupings were different when viewed from the perspectives of species and geographic spaces. This implies that two communities adjacent to each other may have different environmental gradients.

Hence, further understanding of the plant community characteristics can be explored through improved visualisation, replacing the traditional tree community bisect mapping.

Visualisation via the pie charts on forest structure and interactive forest profiles (species-geographic space) offered an alternative method (to forest bisect) of communicating the presence of distinctive PSF communities on the basis of horizontal (variation among communities) and vertical (multiple forest layers) data structures.

The application of 3D tree model in this study has illustrated an interactive feature with, most importantly, the seamless integration of resultant 3D tree models within a GIS environment. In addition to interactivity is the use of visual cues in delivering the concept of comparison (similarities and differences) and adjacency, in order to communicate the ecological characteristics of PSF properties. These features could be harnessed for multiple stakeholders, in particular for educational and conservation use, since it provides general knowledge of PSF ecosystems where a stand level approach is deemed appropriate in this context.

The following chapter offers a discussion of results on species diversity index, ordination and indicator/characteristic species analysis and visualisation.

CHAPTER FIVE

5 Discussion of Results

5.1 Introduction

This chapter centres upon forest classification methods at a fine level i.e. at forest community or forest sub-type level. The previous chapter detailed the results of modelling and communicating the ecological characteristics, while the objective of this chapter is to discuss such results.

Forest classification in Brunei has previously been performed either at a large scale e.g. into distinctive classes of PSF or mangrove forest (FRA, 2005), or at a smaller scale, e.g. to identify forest phasic communities based on floristic composition but also with additional description of the vegetation structure (Anderson, 1963). The national classification level is used for various purposes and serves well as a general reference but it is limited for the purposes of studying the vegetation ecology of PSF since it hides the inherent PSF sub-types, i.e. different phasic community types.

A mixed approach to forest classification was used in this study which combines both phytosociologic and physiognomic information. Specifically, this study uses vegetation pattern analysis from the perspectives of both species and geographic spaces to illustrate diversity and variations within the PSF communities.

Discussion focuses on the relationship between diversity and dominance (abundance) of PSF species, investigating the implications of the differential basis of plot sizes for diversity derivation and the different study scales as a basis of dominance, approached via comparative studies with other studies of PSF in Southeast Asia. This information subsequently informs the basis of dominance used for defining constant species in PSF phasic community theory, and also the use of visualisation methods in vegetation science.

The discussion section is divided into three parts. This chapter will first discuss the results of analysis on plant diversity and dominance, which is followed by discussion on the derivation of peat swamp forest communities in this study. The final part of the discussion revolves on the visualisation of the PSF communities.

5.2 Plant Diversity and Dominance

For all study sites in Badas, examples of upper canopy species are *Shorea albida*, *Dryobalanops rappa* and *Gluta beccari*. The tree canopies are large in breadth and volume. The mid canopy species examples are *Gonystylus bancanus*, *Dactylocladus stenostachys, Lithocarpus dasystachyus* and *Austrobuxus nitidus* a few of which sometimes exist as a dominant species for certain PSF communities. But while the focus of this study was on tree species, it is important to also recognize that the PSF provides a suitable environment for other plant forms. For example, the presence of a few epiphytic species implies the dependant nature of non-tree species on upper canopy tree species which provide these plants with suitable environmental conditions (Figure 5-1).

Figure 5-1: Compound diversity for the upper canopy species as shown by the presence of epiphytes in the upper canopy layer.

In the undergrowth non-tree species included spiky *Pandanus andersonii* species of about 1 metre in height, with greater presence where canopy gaps exist. A further characteristic herbaceous plant species was *Nepenthes bicalcarata* which was randomly distributed on the ground. The physiognomy of this insect-catching pitcher plant has helped it to survive the nutrient poor environment by its water filled sac, which collects nutrients from trapped ants or other insects. On the forest floor, the tree roots in a PSF community also vary, comprising a mixture of characteristic low wing, creeping buttresses and for plots located near to the river, stilt or pneumataphore types were also found (Figure 5-2). These tree physiognomies are clearly related to the environment and are adaptations to changing conditions such as tolerance to flooding which possibly restricts the habitat range.

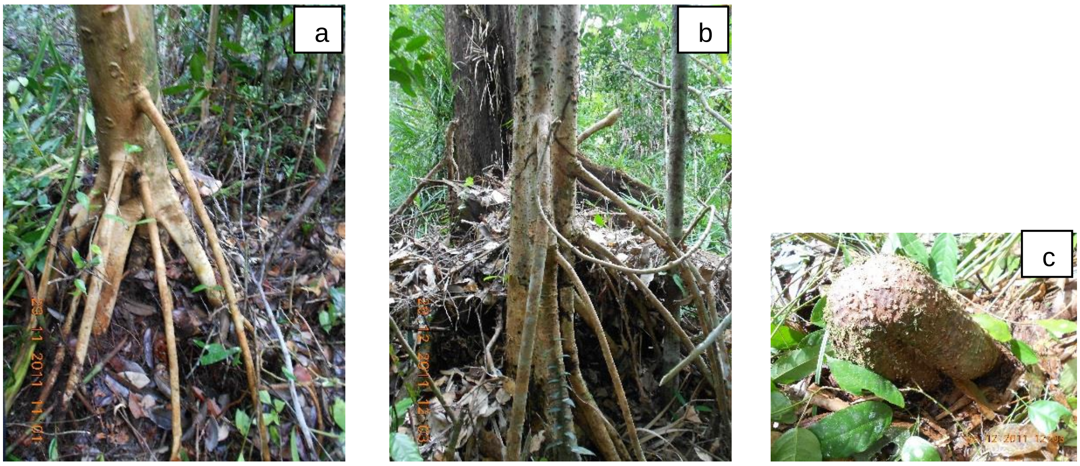


Figure 5-2: Some of the varied root types in PSF; stilt (a and b) and knee like pneumatophores (c), implying the different environmental conditions on which these plant species were adapted to.

The study by Yamada (1997) on Brunei PSF has provided invaluable information on the physiognomy, tree stratification and species composition of PSF in Brunei including details on dominant species and basal areas. Nevertheless, the approach employed in his study was subjective and the potential offered by current methods of vegetation analysis remained untapped. Similarly, Stoneman (1997) did not address how the species assemble into different community types, as could be allowed through posterior analysis using statistics i.e. either the species composition or tree structures, using, for example, ordination techniques used for the identification of forest types. Further correlation studies and multivariate analysis of species and environmental gradient relationships could also be performed in the future.

5.2.1 Species Diversity Index

In terms of a comparison of the number of species at the plot level within Brunei, a relatively small 100 X 100 m plot in a mixed PSF can have some 58 different species per plot, although this diversity is not as high as can be found in plots of the same size and same minimum tree diameter used for sampling in forests on mineral soils, which can have about three times as many species (Yamada, 1997). However, within the Brunei PSF there is limited knowledge on species diversity of the different PSF communities, as well as at a wider level of observation in the Southeast Asian region. Therefore a comparison is made both of the PSF communities within Badas as well as beyond Badas in order to explore the extent of tree diversities. This is perceived to offer further insight into the implied environmental conditions/spatial dependency related to the variations in PSF species i.e. via the application of the H’ Index.

The H’ Index of the Badas PSF varies among all the study sites. The H’ Index in sites A and B does not differ greatly. The H’ Index for the site A plots ranges from 1.90 to 2.05 while for site B it is 1.70 to 2.19. Site C plots have the highest H’ Index values, ranging from 2.11 to 2.99. Within site C, the highest value of 2.99 is for the heath (*Kerangas*) forest in Plot 9. Site C comprises a mixture of the PSF and heath forests, which may indicate a transitory stage between forest on deep peat and heath forest on shallow peat overlying sandy podzol. The differences in the H’ Index across the different soil types i.e. peat soil (PSF) and peat-sandy soil (heath forest), may indicate a spatial dependency effect, while the almost similar H’ Index values between sites A and B may indicate the effect of spatial autocorrelation or ecological characteristics of the plots.

The results presented in Table 5-1 below show that within Borneo Island, the highest plant diversity in PSF is recorded in Brunei followed by Sabah and Central Kalimantan with H’ index values ranging from 1.42 (Sabah) to 2.99 (Badas). This comparison includes both previously degraded (burnt) and intact forests, but the results are broadly comparable as the plot sizes used are fairly similar i.e. 50 X 50 m for Brunei and Central Kalimantan, and 40 X 40 m for Sabah. By comparison with Borneo, the PSF communities described from Sumatra island appear to be distinctively more floristically diverse with recorded H’ values for most communities described by Gunawan *et al.* (2012) exceeding 3.00 (maximum 3.60), even with the use of a smaller plot size (25 X 25 m).

Table 5-1: Plant diversity index for PSF of Southeast Asia.

Plots	H'	Status	Plot size	Reference source
a) Klias Peninsula PSF, Sabah	1.98	Intact	2X2 to 40X40m	Phua *et al.* (2008)
	1.85	Burnt once		
	1.42	Burnt twice		
b) Province of Riau	2.75	Primary forest		Istomo *et al*. (2009)
Block A, Central Kalimantan	2.34	Logged over		Istomo *et al*. (2009)
c) Raja Musa PSF Reserve, Selangor	2.40	Unburnt	50 X 20 m	Ainuddin and Goh (2010)
	1.62	Burnt		
d) Sebangau PSF, Central Kalimantan		N/A	50 X 50 m	Mirmanto (2010)
Plot 1	1.68			
Plot 2	1.66			
Plot 3	1.58			
Plot 4	1.50			
Plot 5	1.47			
Plot 6	1.59			
Plot 7	1.53			
Plot 8	1.62			
e) Giam Siak Kecil- Bukit Batu Biosphere Reserve, Riau, East Sumatra		N/A	2X2 to 25X25 m	Gunawan *et al.* (2012)
Plot 1	3.37			
Plot 2	3.60			
Plot 3	3.56			
Plot 4	3.60			
Plot 5	3.31			
Plot 6	2.70			
f) Badas PSF, Belait		All intact	50X50 m	This study
Plot 1	2.02			
Plot 2	2.05			
Plot 3	1.90			
Plot 4	2.19			
Plot 5	2.08			
Plot 6	1.70			
Plot 7	2.96			
Plot 8	2.11			
Plot 9	2.99			

Despite the limited number of studies available for comparison, it is clear that the use of the Shannon-Wiener Index has the potential to be used for comparative studies of PSF on a regional basis (Phua *et al.* 2008) and as a way to increase further understanding of the changes in the biodiversity of PSF that occurs as a result of forest disturbance and recovery. A drawback to this approach is that not all species from previous studies have been identified up to the species level. The interplay of various disturbances, such as logging and fire with their consequent secondary successions, on the plant species diversity of PSFs across the region requires further investigation. For this purpose, the acquisition of data from intact forests (i.e. control sites, such as the Brunei PSFs), will have an important role to play in future conservation and rehabilitation strategies (e.g. Page *et al.*, 2009).

There has been an increase in the body of knowledge on the extent of PSF diversity at various levels which can facilitate a concerted conservation effort through an increased understanding and awareness of species composition and distributions. Analysis at the landscape level has revealed that PSF not only has unique species, but its diversity is also high in certain areas. This knowledge has indirectly geared a shift of focus on forest depletion at recent times towards a focus on discovering the patterns of the diversity and dominance status of some of the remaining PSF in Southeast Asia. The indices constructed were all fairly recent thus highlighting the significance of this study which can serve as baseline information for future studies amid imminent threats to the PSF such as from unfavourable events e.g. droughts (Nilus *et al.*, 2011), and recurring fire (Phua *et al.*, 2008).

Information on richness and diversity are useful in the assessment of plant diversity as they both enable comparisons to be made between studies. The diversity index provides more detailed information, as it acknowledges the contribution of each species to diversity within an area. Owing to its region-wide application and ease of use, it has the potential as an enabling communication tool for understanding diversity at a regional level, further implying potential applications in education and conservation. A drawback, however, is the need to identify the vegetation at the species level, which requires time, effort and expert knowledge. Nevertheless, recent research has seen further applications of the Shannon-Weiner diversity index to the assessment of forest structural diversity by calculating the proportion of vegetation recorded at each vegetation height level, in order to create a foliage height diversity index (Simonson *et al.*, 2012).

5.2.1.1 Species-Area Relation

Previous studies of tree species diversity in PSF have shown variations in terms of the minimum tree diameter selected and the size of plots used, in part because the objectives of the studies were different. These factors may greatly influence the total number of species recorded and thus direct comparison is unwise. Other factors, such as the shape of the ecological plots, whether located along transects or contiguously, and the presence of different community types may also account for the variations in the total number of species recorded. Table 5-2 shows the change in the number of PSF tree species per unit area across three studies at a regional level (N.B. minimum tree diameter (dbh) differs between locations).

Table 5-2: Some of the studies in PSF showing the number of tree species in Southeast Asia based on area surveyed. Note: Different minimum tree diameter (dbh) size used at different locations.

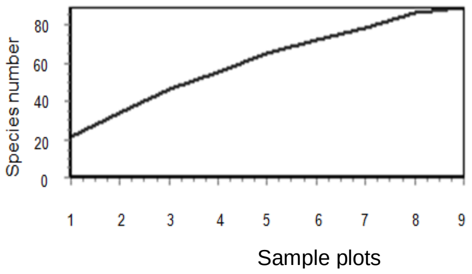
Location	**Area (ha)**	**Total no. of species**	**Min. dbh**	**Reference source**
Sambas regency Kalimantan	total 1.05 ha 105 X 0.01 ha	86 sp.	>10 cm	Siregar and Sambas (2000)
Badas	total 2.25ha i.e. 9 X 0.25 ha plots	89 sp. (tree species)	≥10cm	this research
Giam Siak Kecil-Bukit Batu, E. Sumatra	total 3.0 ha i.e. 6 X 0.5 ha plots	135 sp. (tree species)	3-10cm	Gunawan *et al.* (2012)
Pahang state, Malaysia	total 5.0 ha i.e. 125 X 0.04 ha plots	132 sp. (tree species)	≥5cm	Ibrahim (1997)

In view of the lack of standardisation in sampling, only general patterns based on the available data so far can be deduced in terms of the species area relation. Increasing the size of area sampled resulted in an increase in the number of species recorded in Badas PSF in this study (Table 5-2), supporting one of the four primary reasons proposed by Gaston and Spicer (2004) i.e. sampling factor of species-area relation. This is due to the effect of the increase in the number of individuals with increase in the size of study area, and therefore subsequently results in an increase in the number of species recorded (Gaston and Spicer, 2004). A similar trend is apparent when the species area relation is compared to elsewhere within the Southeast Asian region e.g. Badas compared to Pahang (Table 5-2) where doubling the area sampled was similarly followed by an increase in the number of species recorded from 89 to 132 species. Only a small increase in total study area between Badas (2.25 ha) and East Sumatra (3.0 ha) results in an increase in the number of species recorded (from 89 to 135 spp.), although this is likely an indicator of floristically different and more species-diverse PSF communities in Sumatra compared to Borneo.

The rapid increase in the species-area relationship indicates different communities in locations such as Badas and East Sumatra (Table 5-2). This is supported by earlier analysis of communities at the landscape level for these two areas. In Badas there is an apparent dominance (abundance) of *Sapotaceae-Dipterocarpaceae* (Table 4-4), while in East Sumatra there is apparent dominance (basal area) of the *Calophyllum* family at a landscape level, and for the association of *Shorea-Palaquium-Calophyllum* for Sumatra, at a large level of study (Table 2-1).

The comparison of the Malaysian study and the Sumatran study indicates, however, that the number of species recorded does not necessarily reflect the increase in the size of the study plots. For example, the Malaysian study has a lower total number of species i.e. 132 species in comparison to the Sumatran study, i.e. 135 species, despite the fact that the size of area surveyed is much bigger at 5.0 ha in comparison to Sumatra with 3.0 ha (Table 5-2), although to some extent this result may be influenced by the selection of a smaller minimum tree diameter in the Sumatran study which could have resulted in a greater number of trees being recorded.

In a study of Mixed PSF in West Kalimantan shown in Figure 5-3, the species area curve showed a gentle inclining pattern (Siregar and Sambas, 2000) indicating a similar trend to the Badas PSF.



Key:
MPSF= Mixed peat swamp forest (Siregar and Sambas, 2000)
PNm, SNm, Pse, PSp, SSp, PGp, PTp1, PTp2, STp, SBs, Sin = eleven other PSF in Kalimantan, from various studies.

Figure 5-3: Species-area curve of primary Mixed PSF in West Kalimantan (left) and Badas PSF (right). Image source (left): Siregar and Sambas (2000;159).

However, when comparison was made using the species-area concept for PSF, the results disagreed with this pattern where doubling the size of the study area i.e. 1.05 ha in West Kalimantan (Table 5-2) and 2.25 ha in Badas (this study) resulted in no appreciable increase in the number of species recorded i.e. 86 and 89 respectively, with minimum tree diameter being constant i.e. >10 cm dbh for both studies. Various mechanisms govern the species-area relation at various scales (Léps, 2005) such as colonisation/extinction and speciation/extinction dynamics, in addition to habitat diversity (Gaston and Spicer, 2004). As illustrated, habitat diversity is the most likely factor affecting the species area relationship. The Mixed PSF type in West Kalimantan is therefore particularly diverse. However, Mixed PSF was not encountered in Badas (the Mixed PSF is usually located at the edge of the main peat dome). Knowing that the Mixed PSF is particularly diverse, the same type i.e. the Mixed PSF type for both West Kalimantan and Brunei is foreseen to give a comparable result in respect of the species-area relation for the same PSF community, should the analysis be repeated in the future.

This brief assessment indicates that species-area comparisons for the purpose of PSF species diversity evaluation across the Southeast Asian region need to take into account variations in the sampling methods used. In order to improve cross-site comparisons, it is recommended that nested plots could be used (i.e. plots of increasing size) to better understand the nature of the change in species number with area sampled, in relation to the species-area curve.

5.2.2 Species Dominance Patterns

Rank abundance curve and species association require information on abundance to describe a dominant/constant species. A measure of dominance based on tree density has the advantage of allowing the ecologist/botanist to identify the different forest communities e.g. Anderson (1961) used tree stem counts to identify the different PSF communities.

Information on basal area will also be valuable for the purpose of visualising forest types as differences may be related to resource functions (e.g. water balance and nutrient cycling), indicating the axis of the environmental gradient separating each forest type. The data presented in Figure 4-8 suggest that the variation in tree diameter class may be related to the presence of an environmental gradient.

It is necessary to identify dominant species based on basal area for comparative studies with other forest types, as well as within the region's PSFs. Despite knowledge of the heterogeneous nature of PSF at a regional level (Page and Waldes, 2005), similarity in forest types was noted to some extent such as for northern Borneo, i.e. Sarawak and Brunei. Through this knowledge it was hoped to further our understanding of the species distribution patterns of the dominant species which may indicate possible links with ecological processes such as species interactions and competition for light. Moreover these data provide an avenue for further study of PSF ecology such as peat accumulation and litter formation at local, regional and biogeographic levels.

Dominance based on basal area may reveal different patterns of species dominance ranking according to the scale of study. At the landscape level, the dominant tree in the species count, i.e. the most abundant (*Madhuca curtisii*), does not necessarily dominate the ground space as illustrated by the dominance in terms of basal area by *Shorea albida*. Information on forest structure can also be used as a proxy for the microclimatic variations within the PSF community e.g.

as a result of different degrees of canopy shading. Specification of the basis of dominance is therefore important.

Baseline data were obtained from the literature for comparative analysis across the Southeast Asian region. Data on the dominant species of PSF were compiled from various sources (Table 5-3), although this was rather problematic as information was found to be inconsistently recorded at family, genus and species level making direct comparisons challenging. This information suggests a need for a unifying approach for descriptions of the plant species data, to enable comparisons at the regional level. Thus, additional information was made to the existing plant species record in order to identify the species pattern based on commonly available, aggregated plant species information i.e. at the family level. The most common family is Dipterocarpaceae.

Table 5-3: Dominant tree species of PSF at a regional level in Southeast Asia by family, genus and species.

Location		**Dominant family**	**Reference source**
Central Kalimantan		Dipterocarpaceae	Mirmanto (2010)
		Clusiaceae	
		Myrtaceae	
		Sapotaceae	

Location	**Dominant genera (Indonesia)**	**Dominant family**	**Reference source**
Kerumutan, Sumatra	Koompassia, Durio	Fabaceae, Malvaceae	Momose and Shimamura (2002)
Bukit Batu 1, E.Sumatra	Diospyros, Calophyllum	Ebenaceae, Calophyllaceae	Gunawan *et al.* (2012)
Bukit Batu 2, E.Sumatra	Eugenia, Shorea	Myrtaceae, Dipterocarpaceae	Gunawan *et al.* (2012)
Bukit Batu 3, E.Sumatra	Palaquium, Diospyros	Sapotaceae, Ebenaceae	Gunawan *et al.* (2012)
Bukit Batu 4, E.Sumatra	Eugenia, Madhuca	Myrtaceae, Sapotaceae	Gunawan *et al.* (2012)

Location	**Dominant species**	**Dominant family**	**Reference source**
Suaq Balimbing, Gunung Leuser National Park, S.Aceh	*Gluta renghas*	Anacardiaceae	Purwaningsih and Yusuf (1999)
	Eugenia sexangulata	Myrtaceae	
	Shorea palembanica	Dipterocarpaceae	
	Parinarium corymbosum	Chrysobalanaceae	
Riverbanks of Lahei, Central Kalimantan	*Semecarpus longifolius*	Anacardiaceae	Simbolon and Mirmanto (1999)
	Shorea balengaran	Dipterocarpaceae	
Sebangau river, Central Kalimantan	*Palaquium leiocarpum*	Sapotaceae	Simbolon and Mirmanto (1999)
	Syzygium densinervium	Myrtaceae	
Tanjong Puting National Park, C. Kalimantan	*Gluta wallichii*	Anacardiaceae	Simbolon and Mirmanto (1999)
	Neoscortechinia philippinensis	Euphorbiaceae	
Mensemat-Sambas, West Kalimantan	*Blumeodendron elatriospermum*	Euphorbiaceae	Siregar and Sambas (2000)
	Cyathocalyx biovulatus	Annonaceae	
	Blumeodendron tokbrai	Euphorbiaceae	
Tanjong Puting National Park, Kalimantan	*Ganua motleyana*	Sapotaceae	Yeager *et al.* (2003)
Central Kalimantan (logged over)	*Combretocarpus rotundatus*	Anisophylleaceae	Istomo *et al.* (2009)
Province of Riau, Indonesia (primary forest)	*Gonystylus bancanus*	Thymelaeaceae	Istomo *et al.* (2009)

Location	**Dominant species (Malaysia)**	**Family**	**Reference source**
Kuala Langat North PSF, Selangor	*Nothaphoebe coriacea*	Lauraceae	Ibrahim and Lepun (1999)
	Gonystylus bancanus	Thymelaeaceae	
	Dacryodes rostrata	Burseraceae	
	Shorea platycarpa	Dipterocarpaceae	
Selangor (unburnt)	*Macaranga hypoleuca*	Euphorbiaceae	Ainuddin and Goh (2010)
	Eugenia sp.	Myrtaceae	based on abundant value
	Canarium sp.	Burseraceae	
	Shorea bracteolata	Dipterocarpaceae	
Selangor (burnt)	*Macaranga hypoleuca*	Euphorbiaceae	Ainuddin and Goh (2010)
	Behschmiedia sp.	Lauraceae	based on abundant value
	Adenanthera paronina.	Fabaceae	

5.2.3 *Tree Diameter Class Distribution Patterns for Peat Swamp Forest and Other Forest Types in Brunei*

Basal area values for each tree species were calculated for species in each plot and arranged in tree diameter class in order to identify dominant species and analyse the tree diameter distribution patterns for the upper, middle and lower canopies. A previous study on the tree diameter class of PSF in Riau province, Sumatra (Gunawan *et al.,* 2012) showed negative, J-shaped, gently sloping curves (with the exception of one plot, post selective logging in plot 4) shown in Figure 5-4.

Figure 5-4: Negative J-curve shape of diameter class distribution of Mixed PSF (plots 1-4) and Bintangur forest (plots 5-6) in Riau, Sumatra. Source: Gunawan *et al.* (2012;7).

On the other hand, the Badas PSF data show a distribution curve that is highly skewed to the left, with a distinctive peak for the 11-20 cm dbh class for each group (Figure 5-5, below).

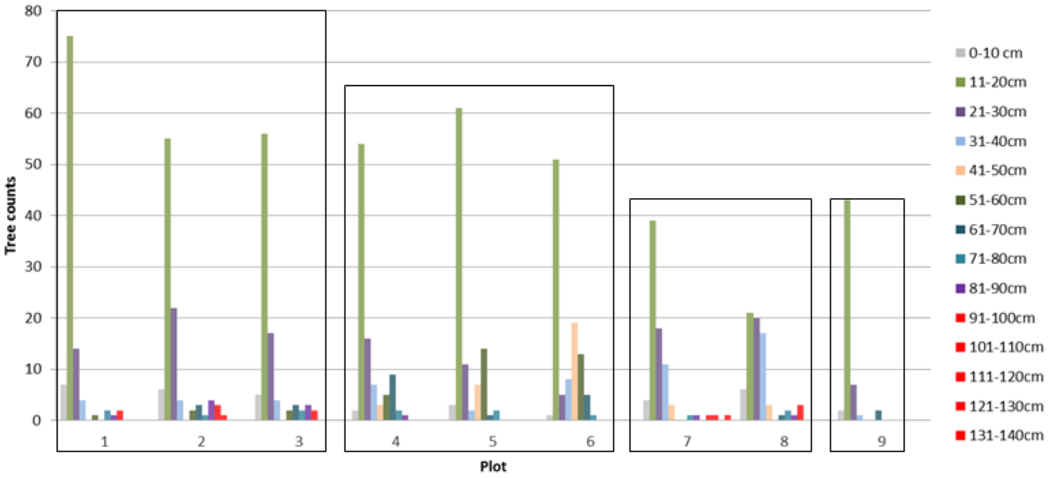


Figure 5-5: Tree diameter distribution pattern of Lowland Dipterocarp Forest. Image source (above): Hédl *et al.* (2009; 126). Badas PSF (below) illustrates the trees are mainly comprised of the 11-20 cm dbh (green).

A study on tree diameter classes for Mixed PSF in West Kalimantan (Siregar and Sambas, 2000) showed a similar reverse J-curve shape to that of Gunawan *et al.* (2012) in Figure 5-4. Unlike the data for Badas PSF, neither studies show a high abundance value for the 11-20 cm dbh class. Furthermore unlike the Badas PSF the number of trees with diameter >80cm dbh for both studies in the West

Kalimantan and Riau Sumatra was also insignificant. Thus the observed variations in patterns of tree diameter classes in the PSFs of Badas, West Kalimantan and Riau could be used to provide an initial indication of the presence of different PSF community types, even without prior knowledge of the floristic details.

One of the most thorough studies of PSF structure was made by Yamada (1997) who investigated the forest response to disturbance by lightning damage and caterpillar attack i.e. *ulat bulu.* He further suggested that the *Shorea albida* double layered root system is a direct predictor in explaining the distribution of PSF community types as they play a key role in competition for the absorption of nutrients which would then lead to the dominance of such species (Yamada, 1997). But this study did not further explore the spatial locations of the dominant species in relation to each other. Hence there needs to be further focus on dominance in addition to studies of species diversity and forest structure. Further study on the diversity of the root types of PSF, and the possible interaction at different trophic levels is also lacking; however this was beyond the scope of this study.

A study of non-peat forest i.e. lowland dipterocarp forest (LDF) in Kuala Belalong, Brunei (Hédl *et al*., 2009), used a smaller plot area of 1 ha compared to this study (2.25 ha). Although the maximum tree diameter class for LDF was found to be slightly higher than for the PSF i.e. 152.8 cm dbh (Hédl *et al.*, 2009), the number of trees with a large diameter was only a few. In comparison to PSF, LDF has a slightly lower total number of tree counts for trees with large trunks such that there was only 7 trees per ha with diameter of 80 cm dbh or greater, but for PSF the number is 11 trees per ha (Table 4-6). For the purpose of comparison, LDF has 1318 tree stems per ha but PSF only has 361 tree stems per ha. The selection of tree diameter may also influence to a lesser extent the tree stem density whereby for LDF a minimum tree diameter of ≥5 cm dbh was used but for the PSF the minimum tree diameter used was larger i.e. ≥10 cm.

Referring to Figure 5-5, a similar pattern to PSF exists for LDF types, where the diameter class distribution shows a distribution that is skewed to the left even though its most common dbh class size is smaller i.e. 5-10 cm (Hédl *et al.*, 2009) than the Badas 11-20 cm in this study. Comparison of Badas with LDF type and also within the same PSF types elsewhere has shown that the dominance of 11-20 cm dbh is distinctive to the Badas PSF.

5.2.4 Species Dominance and Diversity Relation in Peat Swamp Forest

A distinct feature within the peat swamp forest plots is the rough peat surface microtopography and ecological dominance by only one or few species, of mostly the Dipterocarpaceae family. *Shorea albida* has the highest maximum tree diameter and its presence and spacing are thought to influence the presence of other nearby species (Figure 5-6). For example, as a result of the organic matter dynamics through root and leaf litter production, individuals of *Shorea albida* form large hummocks which will have a subsequent influence on the presence or absence of species with various flood tolerance ranges (Shimamura and Momose, 2005), e.g. least flood tolerant species will establish on the drier hummock surfaces. It is assumed that the competition factor (Watt, 1947) for space and natural resources is greatest in this PSF community, which limits the distribution of species.

Figure 5-6: Photo showing buttress root of *Shorea albida* species at Badas Site A, which spread sideways forming an elevated mound over the ground surface. Many pole-like trees of much smaller diameter were found surrounding it.

In addressing the research question on the relationship between diversity and dominance of PSF species, we can refer to the results of the PSF tree richness and density patterns (Table 4-1). The dominance-diversity link, as illustrated in Figure 5-7, shows an inverse relationship between diversity and tree abundance which may also be related to the presence of dominant and co-dominant species. The interaction between these dominant species may create a dependency, i.e. particular co-dominant species are found in relation to the presence of dominant species, leading to an overall reduced diversity. This is despite the high tree abundance which is dominated by the presence of co-dominant species (usually trees of small diameter). This interpretation is supported by the lower tree abundance that is associated with increased species diversity in one of the plots (plot 9, on the edge of the forest). This may be a consequence of reduced dominance and co-dominance which provides a more favourable environment for a wider diversity of tree species to establish there.

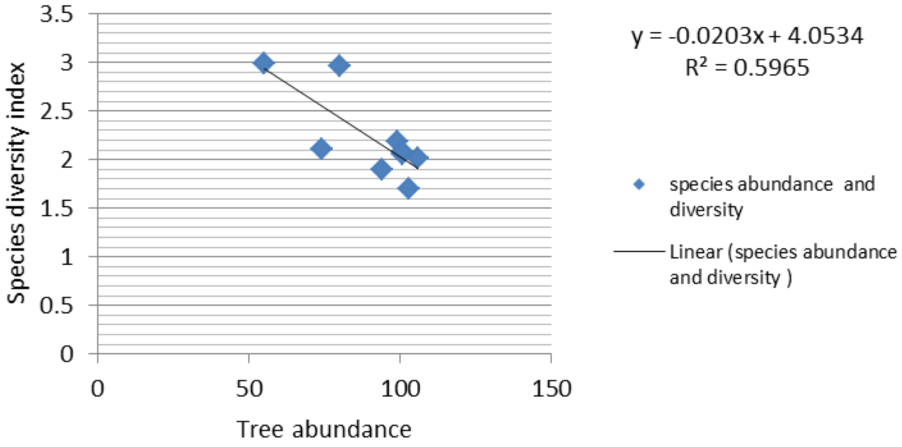


Figure 5-7: Diagram showing inverse relationship between species diversity and dominance (based on abundance) relationship with r = 0.60.

Thus the results of this study in one area of PSF suggest that species richness and density (stem count) are related to the forest structure and the arrangement of species within a plot. A low species diversity may suggest an uneven distribution (e.g. due to the ecologically dominant species, that occupies almost all the upper canopy layer) of tree species within an individual plot. Where one or more species are dominant as identified by their aggregated basal area values (Table 4-5), other species have a low dominance (in terms of basal area) or are excluded, presumably through competition for space and light. In areas with high species diversity the contrasting scenario prevails where no single species dominates. In these situations, the species distribution is therefore more even and characterised by trees with similar physiognomy, occupying free spaces on the ground. As a result, the lack of dominant species has allowed numerous different tree species to occupy the available area and increase the species diversity. To illustrate, the lack of dominant species occurring in plot 9 (Figure 4-2) was related to a low tree density of 220 stem/ha and a high species diversity i.e. H’ value of 2.99 (Table 4-1).

5.3 Peat Swamp Forest Communities

Based on the literature review on studies on the floristics of Southeast Asia PSF communities (Chapter two), a crude estimate is that there are more than 30 PSF communities identified for all Southeast Asia combined. The review also indicates that there is also sub-community variation, with the mixed swamp forest community appearing to be particularly diverse. In the Malaysian peninsula, for example, up to 5 sub-types have been classified within one Mixed PSF community (Jusoff *et al.*, 2007). This result supports the view of Posa *et al.* (2011) who state that tropical PSF supports some of the highest community and hence plant diversity amongst all other peatlands across the world (Posa *et al.*, 2011).

Information on the structure of PSF communities may be linked to diversity through the degree of evenness in a community. For instance, an uneven canopy structure such as found in the lowland mixed dipterocarp forest type in Brunei was associated with a high species diversity in contrast to the less varied structure of the PSF environment, which in some sub-communities dominated by *Shorea albida*, has the general pattern of an almost pure stand. At a finer scale however, PSF is comprised of multiple structural characteristics which usually underlie the dominant trait associated with the different phasic communities. Trait (physical appearance) composition as implied by forest structure has been argued to be much more important than diversity (as indicated by species number), especially when considering how species gains and losses relate to the functioning of communities (Lepš, 2013). Understanding these variations will be valuable not only for academic use but also for conservation efforts aimed at preservation of the PSF native biota.

The vegetation analysis of Badas PSF identified four communities on the basis of species using indirect ordination (DECORANA) method i.e. Site A, Site B, Site C peat soil and Site C sandy-peat soil. The first axis in DECORANA separated the vegetation on the basis of canopy gaps while the second axis do so on the overall forest structure/variability.

The ordination result implied the presence of spatial dependence i.e. there was an environmental gradient structuring the plant species data in the Badas PSF.

A Non-Metric Dimensional Scaling ordination technique was previously used in recent examples to describe such species-environmental relationships in the ordination axis e.g. Mediterranean Oak forest (Simonson *et al*., 2012) and in Dipterocarp communities in Brunei (Sukri *et al*., 2012). However, how and why PSF communities in Brunei respond to a particular environmental gradient has not been established. The PSF communities are described in detail in the following sub-sections.

5.3.1 Community Types of Site A

Plots 1, 2 and 3 closely resemble Anderson's PC 2. Tree species of the Sapotaceae family were also found to be abundant in these communities.

With the exception of *Gonystylus bancanus,* which was not found in plot 1, plots 2 and 3 showed a stronger degree of similarity between them compared to plot 1 and so the plots were located close together in ordination space (Figure 4-4).

All three plots (plots 1, 2 and 3) shared the same characteristic species thus plot 1 was grouped in the same community.

Polyalthia hypoleuca was identified as the characteristic species of PC 2 community in this study. The decision to allocate this community to PC 2 rather than PC 3 was based on the absence of *Tetractomia holtumii* and *Cephalomappa paludicola* which were not found in plots 1, 2 and 3, but which Anderson (1963) noted are characteristic of PC 3. Furthermore, the description for the maximum height of *Shorea albida* was not as tall as those described for PC 3. The description of floristics and tree physiognomy for plots 1, 2 and 3 in this study therefore corresponded most closely to PC 2.

The separation of plots on the basis of TWINSPAN (Figure 4-5) indicator species analysis supported previous floristic analysis via DECORANA (Figure 4-4) whereby plots 1, 2 and 3 were floristically distinctive to plots 7 and 8 on the basis of the absence of *Dactylocladus stenostachyus* in plots 1, 2, and 3. However, the characteristic species could not be identified by using the TWINSPAN method alone, and reference to the species list was needed for the verification stage, confirming the absence of *Dactylocladus stenostachyus* in plots 1, 2 and 3.

5.3.2 Community Types of Site B

The characteristic low height of *Shorea albida* in these plots resembles the description of Anderson's PC 4. Additionally, however, plot 6 more closely resembles the sub-community type of PC 4 called Alan Padang by Yamada (1997), which comprises a pure *Shorea albida* stand.

The arrangement of species in species ordination space from TWINSPAN and DECORANA illustrated some similarities in floristics and physiognomy in that the sample clusters were arranged close together based on their degree of similarities, and yet distinctive enough to form separate cluster groups (Figure 4-4 and Figure 4-5). For example plots 1, 2 and 3 were located close to plots 7 and 8 in species space of TWINSPAN and DECORANA, despite the fact that these clusters were separated some 3.5 km in geographic space. Plots 1, 2 and 3 and plots 4, 5 and 6 were located adjacent to one another in species space, have similar constant upper canopy species amongst them, distinct from other plots 7, 8 and 9 that have fairly mixed upper canopy species. The species composition, in particular the upper canopy species, may be related to canopy evenness and spacings, where pure stands are more even and intact, as opposed to mixed canopy stands, as indicated by DECORANA.

A monodominant pattern at the plot level was found only in plot 6. The almost pure *Shorea albida* stand i.e. near 50% coverage in this plot, was related to the lowest H' index among all plots surveyed i.e. 1.70. This finding was similar to Yamada's (1997) description of the Alan padang community (Table 2-4) which resembled PC 4 in species composition, Dipterocarpaceae dominance at about 50%, small tree diameters and low species no./plot. Although plot 6 was different, in terms of the number of trees per plot recorded, which was high, i.e. 412 stems per ha (Table 4-1).

Furthermore, plot 6 (as well as plots 4 and 5) was different from PC 3, since following the description of PC 4 (chapter 2), the *Shorea albida* species in the plot had a pole like appearance, were small in diameter and relatively low in height in the range 30 to 40 m. While some trees reached the upper 40 m, none of the trees in these plots exceeded 50 m high. These plots were also different from PC 2 as the characteristic species *Gonystylus* or *Stemonurus* were not found here. One significant characteristic of these plots is where the upper canopy Dipterocarpaceae species comprise more than a quarter of the species composition found in a plot, including a particularly higher proportion of these species for a plot with an inherent monodominant trait. DECORANA analysis clearly showed the axes of differences within Badas PSF, where the plot of true dominant form (as indicated by plot 6) was located the highest in Axis 2. On the other hand, plots 4, 5 and 6 were located in the further left hand side of the ordination space along Axis 1, indicating intact and tightly spaced upper canopies characterising these plots, supporting previous description of PC 4 (Anderson, 1963). Hence, plots 4, 5 and 6 belong to PC 4 Dipterocarpaceae dominant.

The results from this study closely resemble those of Yamada (1997), for example in the designation of PC 4 sub-community types to either the Dipterocarpaceae or Sapotaceae dominant. The description of PC 4 based on data collection over a large area, where the species association was derived from PSF in both Brunei and Sarawak combined i.e. *Shorea albida-Litsea-Parastemon* (Anderson, 1963), resulted in the presence of the co-dominant (*Litsea*) which was absent in PSF of Badas in this study.

In terms of co-dominant species, *Litsea* species (Anderson, 1963) did not prevail, rather either the Sapotaceae or Dipterocarpaceae family co-dominates PC 4 in Badas (this study), forming distinctive communities as indicated by the application of DECORANA, as well as based on earlier field observations (Yamada, 1997). The other characteristic species identified by Anderson (1963), i.e. *Parastemon*, was found only in certain PC 4 types i.e. PC 4 Sapotaceae dominant in this study, while it was absent from a similar PC 4 community (Padang Alan) described in the previous study by Yamada (1997). Both Yamada (1997) and this study found other characteristic species namely *Combretocarpus* and *Calophyllum* species, which are also indicated by Anderson (1963) as other characteristic species used for describing PC 4.

However, apart from the use of characteristic species in identification of PC 4, other structural descriptions and the dominant species fit the description of PC 4. This implies the localised association of constant and characteristic species forming the sub-community types of PC 4.

As for the case of PC 4 Dipterocarpaceae dominant, *Austrobuxus nitidus* was found to be the characteristic species of this study as supported by Yamada (1997) where this species could be found in large numbers for this particular PC type (Table 4-8). According to Yamada (1997), the distribution ratio of Dipterocarpaceae: *Austrobuxus nitidus* in this community is about 50:30 percent within a plot while in one plot of PC 4 Dipterocarpaceae dominant in this study, a comparable ratio of 45:21 for Dipterocarpaceae: *Austrobuxus nitidus* was recorded.

Thus plots 4, 5 and 6 resemble closely the description of PC 4 Dipterocarpaceae dominant provided by Yamada (1997).

5.3.3 Community Types of Site C (Peat Soil)

Plots 7 and 8 were almost similar in species ordination space to plots 1, 2 and 3, however they were different due to the absence of *Gonystylus* or *Stemonurus* species that characterise plots 1, 2 and 3.

Plots 7 and 8 are not identified as PC 3 *Shorea albida consociation* due to the presence of other upper canopy species other than *Shorea albida*. Upper canopy species of the Anacardiaceae family, i.e. *Gluta beccari,* are only found in plots 7 and 8, which makes these plots distinctive.

Further sub-community PC 4, i.e. PC 4 Sapotaceae dominant in this study resulted in some 40% Sapotaceae and 5% Dipterocarpaceae for both plots 7 and 8 combined, which has some resemblance to the findings of the previous study by Yamada (1997), where a highly disproportionate 65:8 percent ratio for the distribution of Sapotaceae to Dipterocarpaceae family was recorded for this particular PC type.

Thus the floristic differences in terms of general species composition and characteristic species indicate that plots 7 and 8 belong to PC 4 Sapotaceae dominant.

5.3.4 Community Types of Site C (Heath)

The presence of *Agathis borneensis* did not fit any of the previously described PC types of PSF by Anderson (1963), thus this plot was assigned as a heath community (section 4.3.2).

From the results in Table 5-4 below, it can be deduced that the species associations (Table 4-8) were related to some extent to the community types described from previous literature (chapter two). The summary is given in Table 5-4 below:

Table 5-4: Summary table of the PC types identified from previous study compared with this study in Badas PSF region.

Yamada	This research
PC 1	--
PC 2	PC 2
PC 3	--
PC 4 Dipterocarpaceae dominant	PC 4 Dipterocarpaceae dominant
PC 4 Sapotaceae dominant	PC 4 Sapotaceae dominant

Previous studies have shown the differences in dominant species (based on abundance) for constant and co-dominant species, as well as overall species composition distinguishing the different PSF communities.

5.3.5 Characteristic Species

The application of the TWINSPAN method to explore the characteristic species of the Badas PSF, revealed *Dactylocladus stenostachys* as characteristic species of plots 7 and 8. This species was identified by Anderson (1963) and also Page and Waldes (2005) as a characteristic PSF species from vegetation surveys in other parts of Brunei. Anderson (1963) regarded this species as the principal dominant (constant species) along with *Gonystylus bancanus* and four types of *Shorea* species for PC1. However, *Dactylocladus stenostachys* was not the principal dominant in either PC 5 (*Tristania-Parastemon-Palaquium* association) or PC 6 (*Combretocarpus-Dactylocladus* association) as illustrated in Table 2-4 (Anderson, 1963), although it was found in large amounts in both communities. The findings of this study indicate that *Dactylocladus stenostachys* has a restricted range as it was only found in the PC 4 Sapotaceae community in plots 7 and 8, thereby explaining its existence as a characteristic species. Being a characteristic species of these plots based on TWINSPAN analysis, this species was absent from all other plots in this study. To date, this species was known to have a random distribution within the PSF, and studies including this study, have shown that this species exists in dual form either as dominant (constant) or characteristic species.

Therefore this similarity highlighted the potential benefit derived from this previously unexplored PSF classification method in the identification of characteristic species of Brunei PSF. In addition, TWINSPAN could serve as a rapid assessment tool for the study of vegetation ecology including but not limited to the diversity and the presence of different phasic community/sub-community types, from phytosociology perspectives of constant and characteristic species. However, a limitation to this method is where only one characteristic species can be identified while there could be more than one within a plot (as identified through posterior analysis in this study), e.g. *Gluta beccarii* in addition to *Dactylocladus Stenostachys* in plots 7 and 8.

The results of the floristic analysis in this study revealed that repetitive distribution patterns of constant and characteristic species did occur forming an association (chapter two), which were possibly related to environmental gradient, although with some exceptions. In other words, there were exceptions to the general rule whereby some species exist in an individualistic manner, irrespective of their relation with the dominant species or the environmental gradients. Despite the fact that actual environmental data were not used in vegetation pattern analysis in this study, the presence of spatial dependence or environmental gradient (Legendre and Fortin, 1989) was implied through indirect gradient analysis (ordination). Gradients were implied by direct field observation of soil conditions and the site condition i.e. distance to river, as well as consultation of the previous literature.

Furthermore, the findings showed that an individualistic (generalist) species may alternatively exist as a characteristic species for a particular phasic community, depending on its abundance value, as has been explored through the application of indicator species analysis using TWINSPAN in this study. One example of an individualistic species is the widely distributed *Dactylocladus stenostachys* which is a unique species found in all phasic community types of Brunei and Sarawak (Anderson, 1963). It exhibits versatility within the PSF environmental conditions and supports the continuum concept of plant distribution. This is further supported by Yamada (1997) whereby this species was found in all community types (except PC 1). However, *Dactylocladus stenostachys* could only be found in PC

4 Sapotaceae dominant community in this study, and hence it became a characteristic species for such PSF community.

In view of this dual characteristic/individualistic nature, the conceptual diagram illustrating individualistic species I (Figure 2-3) might not altogether show a smooth lateral line throughout the PSF communities. A peak line (indicating abundance) will likely be shown instead, accordingly representing the species significant presence for a particular community, which subsequently declines and reverts to a lateral solid line to illustrate low abundance, yet persistence through the progressively different communities. This individualistic nature is in contrast to the more rigid characteristic species hypothetical distribution, in a sense that there is an almost absolute absence of characteristic species beyond the (discrete) community partition (Figure 2-3). Localised abundance of *Dactylocladus stenostachys* had also been recorded for PC 5 and PC 6, within which this species represents a characteristic species of PC 6 (Anderson, 1963). Hence, a localised peak in the conceptual diagram of plant association of species-environment relation (chapter two) is favourable, in order to account for the simultaneous characteristic/individualistic nature of certain PSF species based on actual survey data.

5.3.6 Common Species

In a comparison of common species between the peat soil and the sandy-peat soil (heath) plot, the characteristic species of the heath community i.e. *Agathis borneensis* was found to be absent from the peat soil plots. All characteristic species for site A (*Polyalthia hypoleuca*), Site B (*Austrobuxus nitidus*) and Site C (*Dactylocladus stenostachys*) and Site C (*Agathis borneensis*) were also absent in the list of common species between sites, therefore verifying these characteristic species' presence as distinctive to each community type.

Plant species which are found in common on the peat soil and sandy-peat soil could be assumed to either exist in a continuum or in transitory stage (chapter two), as the species were able to survive irrespective of the different environmental gradients. The small number of species in common implies the floristically distinct communities of peat and sandy-peat soils (as further indicated by the indirect ordination method), that these common species co-exist in a transitory stage between these plots.

However, common species between such plots are not always synonymous with individualistic species. True individualistic behaviour of these common species can only be revealed through analysis of persistent presence for a particular species across a wide area comprising the different environmental gradients, and preferably involving more than one sandy-peat soil plot. By default, the common species is in a transitory stage between the overlapping boundary lines of plots (Figure 2-3), which accompanied the changing environmental conditions in a subtle rather than abrupt manner. To illustrate, the sandy-peat soil was drier than peat soil plots in terms of their soil moisture contents. Furthermore, the sandy-peat soil plot was located on a slightly elevated micro-topography (sand ridge) (Figure 5-8) with further implications for reduced water retention capacity and species adaptations to such conditions. While this study focused exclusively on floristic and structural attributes of the PSF communities, further field study could encompass the abiotic field conditions.

Figure 5-8: Photos showing the environmental conditions in plot 9, illustrating a different soil conditions to all other plots, as underneath the peat layer is sandy soil. Partially decomposed leaf litters forming mound could also be seen.

Madhuca curtisii became a common species for all phasic communities in this study implying an individualistic behaviour of this species in PSF, in addition to the previously discussed *Dactylocladus stenostachys* species. Despite the similarity, it was not a characteristic species based on the indicator species analysis, but instead became a co-dominant for certain PSF communities, on the basis of tree physiognomy and frequency. This individualistic behaviour similarly implies that certain co-dominant species exist in a continuum. Revised taxonomy determined *Madhuca curtisii* to be synonymous to *Ganua curtisii* (WCSP, 2014), the species Anderson (1963) described as having a restricted range in Badas PSF (chapter two), although it has subsequently also been found in hill habitat at about 457 m altitude in Peninsular Malaysia (Kew, 2014).

5.3.7 Structural Variations of Peat Swamp Forest Communities

Constant species i.e. *Shorea albida* may also be first thought to exist in a continuum state as it is generally associated with the PSF. But further analysis indicated the presence of subtle structural physiognomic differences of this constant species in this study, and in association with co-dominants and characteristic species, they represent the different phasic community types (chapter two). Thus it is imperative that superficial similarities on the basis of floristic accounts must be supplemented with tree physiognomy details for further study on the vegetation/ecology of this particular forest type.

Apart from floristic details, there were other community traits that could potentially be used to provide conceptual descriptions of the PSF communities. Such examples are the variations in terms of the stratification of the upper and lower canopy layers which can be built into a visualisation of forest communities of the PSF.

5.3.8 Species Adaptation to the Wetland Environment

Ordination and classification can be utilised to improve our understanding of the relationship between PSF species and the changing environmental conditions such as forest cover which may affect microclimate (Ludang *et al.*, 2007) and surface water table level (e.g. through its effect on throughfall and evapotranspiration). The presence of a particular forest community implies various underlying environmental conditions partially responsible for dictating the distribution of certain plant species. This baseline information can be used in intervention management approaches for example after forest disturbance by logging or fire, to identify suitable regenerating species while also offering knowledge of the conducive environment for successful regrowth of PSF species.

Changes in forest cover also have implications for species adaptation and the presence of shade tolerant and intolerant species. *Gonystylus bancanus* is known to prefer a low light environment (Graham, 2009), which is associated with a thick canopy. This was confirmed by its absence from forest plots with an open canopy (the axis of differences was identified through DECORANA), for example (its absence) in site C in this study. In contrast, *Agathis borneensis* is found on peat and sandy soils in Kalimantan and Sumatra (Istomo, 2002 cited in Graham, 2009) and is intolerant to shade during its early stages of growth (Meurs, 1947 cited in Graham, 2009). This species was found in the plot with sandy-peat soil in Badas which was characterised by a fairly open canopy, i.e. confirming that this species is less tolerant to shade. The results from this study shown that the spatial distribution of *Gonystylus bancanus* and *Agathis borneensis* species potentially repel each other due to the contrasting types of forest cover which affects the forest microclimate. With greater study coverage in the future, presumably this pattern may be repeatedly found in other places as well.

The presence of flood tolerant species in PSF is also well known e.g. *Combretocarpus rotundatus* and *Pandanus spp.* (Dommain *et al.,* 2010). Furthermore, *Diospyros evena* and *Gonystylus bancanus* are a type of climax species that can live in waterlogged conditions where flooding exceeds 3 months per year and there is a dense canopy cover of more than 50% (Giesen and Van der Meer, 2009), implying conditions which favour rates of low evapotranspiration. Fairly dense canopy cover was characteristic of plots 1, 2 and 3 as indicated by Axis 1 in DECORANA, implying a lower evapotranspiration rate and waterlogged soil, which coincides with where these two species could be found (Table 4-8).

5.4 Visualisation

5.4.1 Peat Swamp Forest Communities from the Perspectives of the Species and Geographical Space

The use of 3D tree model has the advantage of providing multiple perspectives to describe the structural diversity of the PSF compared to the use of aerial photos. A further advantage of 3D tree models over photographs of plot areas is the interactive feature, where each tree is associated with spatial and attribute data, and which can also be viewed in several desired forest height layers (turned on or off) and from multiple perspectives. Interactive queries can be made through the identity tool in ArcMap, upon which the accuracy of the feedback to the user will depend on the rigour of the data cleaning process, following the data entry stage. There is further potential use for habitat mapping such as prediction of the diversity/density of avian species, with relation to foliage height diversity (Karr and Roth, 1971) and relation to repeat occurrence of fire in Borneo (Slik and Balen, 2006). A further example is carried out in a wetland reserve, Malaysia whereby three variables namely vegetation structure, composition and microclimate were found to be influential in determining the occurence of wetland avian species (Rajpar and Zakaria, 2011).

Another previous example of visualisation was a study on tree diameter change over time for lowland dipterocarp forest in Brunei (Hédl *et al*., 2009), in which ESRI ArcScene v8.3 and 3D Analyst were used in the creation of a 3D model of an undulating landscape. However, in that case, the trees were represented by differing tree diameter sizes (dbh) by the use of circles. Therefore the application of a 3D tree model in this study is perceived to add value through perspectives and the interactive GIS features, for existing related forest studies conducted at a plot level. In this way, a combined approach of both above ground and Digital Elevation Model (DEM) features are considered appropriate for further forest related studies. Moreover, the use of a wireframe DEM e.g. as used by Stoneman (1997), could be further explored using an image draping technique, in order to represent the hummocks and hollows of the PSF floor, and the different rooting environments of the trees. As for the case of representativeness of canopy image, e.g. draping of the Digital Surface Model (DSM), a serious issue lies with the low number of under canopy discrete return LiDAR readings, with resultant wrong canopy shape/volume i.e. the blanketing effect of DSM draped over canopies (Lee *et al*., 2001; Zimble *et al*., 2003). A further limitation is contributed by the sheer complexities of the PSF forest canopies e.g. strong canopy overlaps, which did not permit the identification of individual canopies, as is usually required in the study of PSF ecology, e.g. Figure 2-6.

5.4.2 Addressing Visualisation as a Communication Tool on Peat Swamp Forest Ecology

Mietner *et al*. (2005) identified 3D visualisation as a form of communication tool that is potentially cogent, which according to their study was as a result of this technique's close resemblance to human vision and relation to the common feature encountered on a day to day basis. For example in this study, the profile and perspective views of forest at the plot level are arguably easier to comprehend than the aerial view of the forest, where details on multiple forest structure and their relation to forest diversity were not readily apparent. In this respect, 3D visualisation can be harnessed as a tool to extend an understanding of scientific information, which is complex e.g. through advanced realism and interactive features (Mietner *et al*., 2005). The authors of this study further state that the interaction in bivariate or multivariate forms for factors such as topography and distribution of plant species, when expressed via visualisation, is where the ultimate contribution to understanding of complex forest ecosystems potentially lies.

5.5 Summary

In addition to the purpose of providing comparative studies on PSF communities (Page and Waldes, 2005), is the need to address the issue on the nature of available data of the PSF vegetation. The dominant species of PSF in Southeast Asia have also been analysed in this study, and data standardisation issues have been recognised which impeded direct comparisons of ecological studies of PSF at regional level. Interestingly, in some cases, the species did not increase with increase in areal extent when the concept of species area curve was analysed at regional level, suggesting the presence of diverse habitat at this level.

The small scale study of Badas PSF indicates that it is possible to classify PSF communities from either the species pool (phytosociologic) or species tree diameter class distribution (physiognomic), whereby both approaches have resulted in groupings of the species into four distinctive PSF communities. The limitation identified from the use of the species phytosociologic approach is that the characteristic species can either exist in continuum (widespread) or for that particular community only, depending on the scale at which the observation was made. In addition to this, further posterior analysis can be applied where manual reference in some instances needs to be made to the species list in order to identify the characteristic species (previously not identified through the sole use of TWINSPAN). Further drawback is where the species name or forest structural variations were not known through the sole use of this method. The use of both phytosociologic and physiognomic approaches therefore implies field data collection as an indispensable route to ecological knowledge.

The species diversity is inversely related to forest variability which acts as a surrogate to the environmental gradient of microclimate. High diversity was found in plot 9 which largely comprised of trees with a highly diverse structure, further backed up by the pie chart of tree structure which clearly separated the lower, mid and upper canopy layers. On the other hand, low diversity (H’) was found in plot 6 which exhibited a monodominant trait. However other factor of variations in tree structure were not taken into account, which could potentially also exist as a result of disturbance and subsequent regeneration of new species.

The use of models to enhance the understanding of species diversity is accentuated through the improved visualisation method. While the use of a bisect sketch model potentially gives a fairly accurate representation of forest communities, these are static and limited to a snapshot in time. On the other hand, the use of a 3D tree model integrates the use of both spatial and attribute data (species-geographic space), and given the wealth of information readily available this could be tailored to a particular area of interest in the study of PSF ecology. GIS also allows regular updates of data, in addition to the manipulation of data from various ways such as profile and perspective/ multiple orientated views of forests layers. However, this method is still in its infancy and hence are limited in terms of representativeness of tree species as it is based on the available tree image library, in addition to the lack of environmental data from actual field survey, but which could be incorporated in the future.

This chapter has discussed the elements of diversity and PSF communities' derivation and the visualisation of PSF communities in species-geographic spaces. The subsequent chapter will conclude the findings of this thesis describing the contribution to knowledge and the way forward.

CHAPTER SIX

6 Conclusion

6.1 Introduction

This chapter provides the synthesis of the previous chapters whereby a general discussion of research findings will be given, followed by the contributions and limitations of the research. The final section describes future recommendations that arise from this research.

6.2 Key Findings and General Discussion of Results

A number of findings have emanated from this research. The research questions cover peat swamp forest ecology, visualisation and GIS, as described in chapter one.

6.2.1 Peat Swamp Forest Ecology

- *What are the plant communities within Badas from the perspective of plant species space?*

The indirect ordination and indicator analysis methods had identified four PSF communities based on the species pool (chapter four). The constant and characteristic species had been identified and used to define the community as per the species association concept. The plant communities are PC 2, PC 4 Dipterocarpaceae dominant, PC 4 Sapotaceae dominant and heath forest. The separation of PC 4 communities into two types bears a close resemblance to the PSF communities identified in a previous study in the Badas forests (Yamada, 1997).

The groupings of plant communities through the ordination analysis correspond well with the patterns of tree diameter distribution classes, from each of the study sites (chapter four). Thus, the results from this study suggest that the PSF community could be identified on the basis of data on either the species pool (phytosociology) or tree diameter class distribution (physiognomy) as both approaches resulted in groupings of species data into four PSF communities.

Further analysis of common species identified a few distinctive species between sites, as a verification process on the extent of similarities and differences of species between each site. It was found that the transition of species between communities was gradual rather than abrupt, which suggests that with the gradual change in environmental gradients that certain species are able to adapt or tolerate the changed conditions.

- *What is the relationship between species diversity and dominance of the PSF?*

The relationship between plant species diversity and dominance in the Badas PSF was discussed in chapter five. The Shannon-Weiner diversity Index (H' Index) for the pristine Badas PSF was found to be high, ranging from 1.70 to 2.99. This H' Index is comparable to other previous H' index values recorded for the PSF of Southeast Asia, but the H' for pristine Badas PSF is among the highest in Borneo. In the wider Southeast Asian region, the H' Index values indicate that PSF in Sumatra is particularly diverse with index values higher than those of the PSF in Borneo. Dominance was defined in two ways in this study to represent ecological dominance and abundance. Ecological dominance for a particular study site (based on both basal area and frequency of occurrence of species) was used to define a constant species, following the species association concept. On the other hand, the species count per plot, i.e. abundance, was used as an alternative way to describe dominance in this study. The result of the correlation analysis between plant species diversity and dominance (abundance) for all plots in Badas, was an inverse relationship, with a regression coefficient score of R^2= 0.60.

In addition to the species diversity index (describing species richness per plot), the PSF communities were also found to be structurally diverse, which indicates the extent of ecological dominance patterns. Hence, an analysis of tree diameter class distribution at 10 cm class intervals served as an exploratory data tool, to further aid the understanding of the data structure of the Badas PSF. The results revealed distinct patterns for the 11-20 cm and >80 cm dbh, specifically of the Badas PSF, at each study site, which were associated with the lower and upper canopy layers respectively. Furthermore, comparative analysis with other PSFs in Southeast Asia indicated structural heterogeneity, i.e. the presence of distinct regional differences on the basis of the distribution of tree diameter classes.

An earlier review of the limited literature on the PSF plant communities in Southeast Asia by Page and Waldes (2005) highlighted the apparent need for continued work to be put in place, as a way to provide a more detailed account of the PSF vegetation of this region. These authors stressed the significance of such information in enabling comparative studies of PSF vegetation at different scales, with the potential to establish conservation strategies for PSF at a regional level, but also as a fundamental guide for localised forest restoration measures. The information presented in chapter four provides a contribution to this knowledge and, in particular, presents some of the first detailed floristic information on the species diversity of the Badas PSF in Brunei, which was previously poorly documented. The study of the Badas plots adds to the knowledge that intact PSF shows considerable variation even at the small scale of a single site. When included in regional comparisons, the Badas data contribute to the broader view that PSF in Southeast Asia does indeed show considerable regional variation, thus supporting the earlier interpretation by Page and Waldes (2005). If comparison was made at a more detailed scale such as at a species level, it is sensible to suggest that the similarly high diversity follows at an aggregated plant community level in the region.

6.2.2 GIS Visualisation

- *How can an ecological understanding of PSF be visualised and communicated to a range of stakeholders for sustainable management of this ecosystem?*

An understanding of the characteristics of PSF communities was approached by the exploration of the forest ecological characteristics and species composition. This knowledge was communicated visually via the interactive 3D tree models which bridge the visualisations of the non-geographic (ordination/clustering) and geographic data (geo-referenced tree species) as described in chapter one. The emphasis of model designation was on conceptual understanding and model flexibility/interactivity elements.

The 3D visualisation of vegetation structure offered multiple assessments from the profile, plan and perspective views. The ecological characteristics offered improved cognition through the use of visual cues of comparable tree structural distribution patterns within the PSF community. The interactive feature in GIS enabled further spatial and attribute knowledge such as in conceptualising the species association pattern of a PSF community, which would otherwise be difficult to analyse or comprehend in a 2D view. The use of photorealistic tree billboards of various species, placed on the geo-referenced points from field data, had the advantage over other visualisation methods (not used in this thesis) e.g. discrete return LiDAR visualisation of PSF communities. Furthermore, the actual canopy form as well as the interactive features e.g. manipulation of specific tree height layers/species, for visualisation use were limited by using LiDAR.

Further advantages of the 3D tree model over forest bisect and photo approaches are the interactive and dynamic elements whereby plant attribute data such as tree height, diameter, frequency of occurrence and characteristic species could be identified through visualisation and query functions on-the-fly in GIS.

6.3 Contribution and Limitation of Research

An alternative way of knowledge production was demonstrated through the integrated approach of the three core themes in this thesis, namely peat swamp forest ecology, visualisation and GIS. The integrated approach was introduced for the first time and was novel in relation to conventional approaches to studying

PSF communities in Brunei or Southeast Asia more generally, which were mostly based on field data techniques. This new approach aims to advance the knowledge on plant communities from the perspectives of both patterns and processes (Watt, 1947).

One of the strategies identified in the implementation of the Convention of Biological Diversity in Brunei, is concerned with enhancing the foundation for scientific knowledge, among which, is the provision of ‘literature on vascular and non-vascular plants’ (Forestry Department, 2010; p.15). The vegetation survey conducted within the Badas PSF is aligned with this purpose whereby 89 tree species were identified within the nine plots of the Badas PSF. A further review was made in this thesis, not only on the PSF communities in Brunei, but also the PSF communities in Southeast Asia. In addition, a comparative (Southeast Asian regional) analysis of ecological characteristics and floristic accounts was made to address the knowledge gaps in these areas. The provision of vernacular references along with the Latin equivalent of the Brunei PSF plant species list in this thesis has added value, in terms of taking into account the (transferrable) traditional local knowledge. Such knowledge is a type of cultural ecosystem service as identified by the MEA (Millennium Ecosystem Assessment, 2005b). Strategies for forest conservation in Brunei include enhancing educational awareness, in pursuance of which various measures have been carried out such as the World Forestry Day and Mass Tree Planting (Forestry Department, 2010). Familiarity with species in the local context has also been identified as lacking; temperate forest environments are more commonly used in biodiversity education in comparison to the local examples of *kerangas* (tropical heath), *kerapah* (the waterlogged equivalent) and peat swamp forest in Brunei (Rasidah, 2014). In accordance with this strategy, the PSF communities, the ecological characteristics as well as the literature review on the PSF of the neighbouring regions covered in this thesis, have advanced the knowledge on PSF, within the context of the Southeast Asian region, and emphasised the particular conservation value of PSF within Brunei.

A number of items were presented in this thesis, which add to the existing wealth of knowledge on the peat swamp forests, and each theme will be described in turn.

On the species diversity theme, this thesis has provided an overview of measures of diversity and dominance of the PSF communities. The diversity index provided some indicators on the level of variations of species composition within a particular PSF community. The H' Index used could play a role as an easy to understand communication tool with regard to the relative diversity index of the PSFs in other Southeast Asian regions, where this index has commonly been used. However a high diversity index was also recorded in some regions where the forests were no longer pristine, e.g. due to the contribution of successful regeneration, where in many cases, the native species were being replaced. Thus a drawback of this method is its inability to distinguish the native and regenerating species without a knowledge of the ecological history of the study area. The distribution of species of either the native or regenerating forest is perceived as having implications for the species dominance patterns, microclimate, PSF nutrient cycling processes, seed dispersal and foraging behaviour of mammal and avian species. Hence, this research has instilled new understanding of diversity at a plot scale that was compared against diversity operating at the landscape level in SE Asia.

A further contribution is through the ordination work which was found to be useful in implying the presence of environmental gradients of microclimate and light energy based on canopy spacing and variability patterns, in addition to the possible groupings of PSF communities through ordination method. Increasing forest complexities were identified as being a characteristic of highly diverse forests. The variations in forest structure identified a number of shade tolerant and intolerant species of the PSF, from a review of existing literature (albeit limited) on the PSF ecology. At the plot level analysis used in this thesis, the distributions of the plant species were suggested to be as a result of environment constraints, in particular light availability. Dense canopy implies the low amount of light energy penetrating into the forest floor, in particular for PC2 and PC4 Dipterocarpaceae identified in this thesis. On the other hand, it was found that PC4 Sapotaceae dominance are less dense in terms of canopy cover than the PC4 Dipterocarpaceae. The canopy for heath forest is more open and highly variable, and despite the fact that the number of heath forest identified in this thesis is limited to a single plot, it is interesting to note that this particular forest type also coincides with the high diversity index found among all other plots. Hence, an implication which arise from this thesis in which light energy (which is related to the ecological characteristics of PSF) is a factor that determine the plant species distribution for the different PSF communities, adds to the existing knowledge on other important environmental factors, i.e. hydrology and peat depth, identified as being influential to the plant species distribution and diversity in PSF.

A further contribution was made in this thesis through the identification of heterogeneous pattern of the PSF communities as well as the identification of the different types of such communities on the basis of the tree diameter class distributions. The finding of this thesis indicates that apart from the conventional phytosociologic approach, the Brunei PSF can be categorized into several groupings based on the patterns of the combined upper and lower canopies of the PSF, which are distinctive from other tree diameter class distribution patterns of the PSF in SE Asia in particular.

In addition to non-geographic visualisation, the PSF communities were explored spatially through the use of visualisation in the form of a 3D tree model using GIS. This has provided a novel exploration of PSF data in a user-friendly environment with the added advantage of enhanced cognition of a familiar environment which people encounter in their daily lives. The novel application of photorealistic tree stratifications also offered numerous advantages in ecological studies of the PSF replacing the traditional tree bisect i.e. through the interactive query, manipulation of scale, orientation and perspective as well as comparative features available in GIS.

The potential, nevertheless, is not without limitations, with the use of non-PSF species and planimetric ground deemed as major drawbacks. Despite this, the model has served the purpose of illustrating the structural differences including canopy spacing and canopy variability patterns (which indicates the degree of complexities) of the PSF communities. An added advantage is the seamless integration of georeferenced data in a GIS environment, which render it valuable for improved knowledge on spatial pattern ecology. There is a further avenue for building a tropical PSF tree species library to fine tune the existing model, with accurate illustrations of the tree physiognomy, tree form, canopy diameter, tree diameter, root types and non-tree species. The digital collection of tree species with botanical coherency is perceived to serve as a platform or as a form of engagement to instil love for nature though the digital arts domain e.g. plant factory software (E-on software, 2014). Moreover, the product could be applicable to other forest types, in addition to being used as a supplement prior to fieldwork or other excursions for educational or research purposes. In a wider context, digital representations of PSF could also be used to engage with policy makers to promote enhanced awareness of the conservation priorities for PSF.

To reify species diversity is regarded as a fundamental issue (Dale and Fortin, 2014). Moreover, understanding the patterns of species richness is regarded as ‘one of the most fundamental problems in ecology’ (White *et al*., 2010; p.3633), as diversity varies across space, scale and time. The knowledge of plant species diversity patterns was presented in this thesis via a spatial approach, in order to assess the spatial patterns of the plant species diversity of PSF (at community level). Therefore, further knowledge was added in this thesis, concurrent with the ecosystem approach for sustainable management of forests. Additionally, there is also the possibility of further longitudinal study; as White *et al*. (2010) argued, the incorporation of the time factor into geographical analysis will greatly improve our understanding of species richness patterns.

6.4 Future Directions

Some of the future works that could be derived from this research are described as follows:

- A conservation approach that takes into account a range of variations in the PSF from the perspective of phytosociology and physiognomy differences/diversity. In addition to this is the maintenance of intact areas and spatial connectivity between the PSF communities.
- Further improvement in the literature on PSF ecology of native species e.g. after Graham (2009), incorporating important elements such as phenology and ecological tolerances.
- Diversity survey (including non-tree species) for other PSF communities, in relation to simple or complex forest structures occurring in either natural or regenerating environments (succession) e.g. from disturbance.
- Indirect ordination identified four PSF communities concurrent with tree diameter class distribution patterns. The relationship between results derived from the phytosociology and the ecological characteristic measure/physiognomy, as identified in this thesis, could be extended further to other PSF communities and other forest types.
- Time-series modelling of plant species diversity change.
- Application of a 3D visualisation of ecological characteristics to other forest types, and non-tree species with improved capabilities such as interactive visualisation, animation and immersive rendering.
- Application of 3D digital nature theme to encourage creative learning, and nurture transferable skills in creative industry. In addition, the application could also be foreseen to engage stakeholders with an interest in the preservation of diversity and ecosystem services.

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APPENDICES

Appendix One: Tree Species and Family Lists Including Vernacular Reference of Badas Peat Swamp and Heath Forests

For this study, uncertainties on species with *cf*. e.g. *Syzygium cf. zeylanicum, we*re counted as one with its same type (without *cf)*.

Based on Latin species references;
(A) = Species identified by Anderson (1963) (Brunei only).
(S) = Species identified by Stoneman (1997).

Appendix Two: Species List Based on Tree Structural Division

Upper canopy species (≥30 m)

Mid canopy species (≥15-29 m)

Lower canopy species (≥5-14 m)

Appendix Three: Total Basal Area (BA) Per Tree Family for All Badas Plots (Arranged Alphabetically)

Family	**Total BA**	**Frequency**
Anacardiaceae	11.69	9
Anisophylleaceae	1.15	1
Annonaceae	21.63	21
Apocynaceae	14.47	14
Aquifoliaceae	4.04	4
Araucariaceae	1.35	1
Bombaccaceae	2.04	2
Burseraceae	1.24	1
Celastraceae	5.02	5
Chrysobalanaceae	2.03	2
Combretaceae	1.03	1
Crypteroniaceae	4.13	4
Dipterocarpaceae	193.73	150
Ebenaceae	59.81	59
Elaeocarpaceae	9.14	9
Euphorbiaceae	47.87	47
Fagaceae	63.1	62
Gentianaceae	2.03	2
Guttiferae	43.63	43
Icacecaceae	11.15	11
Lauraceae	1.02	1
Leguminosae- Caesalpinioideae	5.07	5
Malvaceae	6.07	6
Myrisinaceae	2.12	2
Myristicaceae	7.27	7
Myrtaceae	82.14	80
Polygalaceae	23.94	23
Rhizophoraceae	1.01	1
Rubiaceae	6.07	6
Rutaceae	4.06	4
Sapindaceae	18.58	18
Sapotaceae	208.22	200
Thymelaeaceae	6.35	6