Carbon storage and floristic dynamics in Peruvian peatland ecosystems

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Submitted in accordance with the requirements for the degree of
Doctor of Philosophy

The University of Leeds

School of Geography

September 2015

The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2:

Draper, F.C., Roucoux, K.H., Lawson, I.T., Mitchard, E.T.A., Honorio Coronado, E.N., Lähteenoja, O., Torres Montenegro, L., Valderrama Sandoval, E., Zaráte, R., Baker, T.R.. (2014). The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environmental Research Letters*, 9.

FCD, TRB, KHR,ITL and ETAM, designed the study; FCD, ENHC, OL, LTM, EVS collected data; ENHC EVS and RZ provided data; FCD analysed data and wrote the paper.

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Acknowledgements

First, many thanks to my supervisors Katy Roucoux and Tim Baker for their continued support, guidance and encouragement throughout this project. I’d also like to thank my third supervisor Ian Lawson for his many valuable contributions, particularly his guidance in bringing the thesis together. I would like to extend this thanks to Ed Mitchard, who supervised the remote sensing aspects of the project and provided useful guidance particularly in the preparation of Chapter Two for publication.

I would especially like to thank my field team Luis Torres, Julio Irarica, Hugo Vasques, Elvis Valderrama, Carlos Mogollon and Frans Ramirez and field assistants Sarah Pearl, Oliver Clark and Esme Shattock. Without their help in some exceptionally challenging environments this project could not have been completed. I’d like to extend this thanks to staff at IIAP including Ricardo Faroñay, Jhon del Aguila Pasquel and Dennis del Castillo Torres for their logistically support in Peru.

I would also like to thank Euridice Honorio Conorado, who provided guidance throughout the project, but also provided a lot of unpublished forest plot data that were crucial to this project. I also thank Outi Lähteenoja for making her peat data available and contributing to the manuscript of Chapter Two. Paul Fine, Nigel Pitman and Oliver Phillips generously provided floristic plot data for upland forests and Chris Baraloto and Ricardo Zaraté provided plot coordinates which were used in the remote sensing classification.

I would like to thank the Lab staff in the School of Geography, especially Martin Gilpin, Rachel Gasior and David Ashley who were exceptionally helpful in their assistance with soil and pollen analysis. I would also like to thank Gabriela López-González and Georgia Pickavance who provided assistance with the ForestPlots.net database. Duncan Quincey taught me the fundamentals of remote sensing and I thank him for his early input.

Many people in Leeds deserve a special mention; Greta Dargie, Tom Kelly and Fernanda Coelho de Souza in particular were a sounding board for ideas and provided useful input throughout the project. Dylan Young, Adriane Esquivel Muelbert and Martin Sullivan were a great help with statistical analysis and coding in R and William James provided help with GIS issues.

I would like to acknowledge NERC for funding my studentship (NE/J50001X/1).and for additionally funding two radiocarbon grants. Additional funding from the Quaternary Research Association, the Earth and Space Foundation, the Anglo Peruvian Society and the Royal Geographical Society contributed to fieldwork costs.

Abstract

In this thesis I took a novel interdisciplinary approach involving remote sensing, ecological and palaeoecological techniques to address some of the most fundamental gaps in our understanding of Peruvian peatlands. The existence of these peatlands was only recently confirmed and although they were known to store large quantities of carbon, initial assessments of carbon stocks were highly uncertain. In addition, little was known of their biodiversity or how they have developed.

Firstly, I used data fusion remote sensing and extensive field data to generate a high resolution, landscape scale map of peatland ecosystems in the largest peatland complex in Amazonia. This approach confirmed that peatland ecosystems in northern Peru are the most carbon dense ecosystems in Amazonia storing up to 1391 ± 710 Mg C ha^{-1}, and have a total carbon stock of 3.14 (0.44–8.15) Pg C, which equates to nearly 50 % of the total above-ground carbon stocks of the whole country.

Secondly, I established a new network of floristic inventory plots and described the composition and diversity of peatland tree communities. I demonstrated that peatland pole forest has the lowest alpha diversity of all tree communities in lowland Amazonia. In contrast, by comparing these data with three larger plot networks from other ecosystems in the region, I also showed that they have surprisingly high beta diversity, and harbour important populations of species that were previously thought to be restricted to other habitat types such as white sand forest.

Finally, pollen analysis was undertaken across eight peat cores from two sites to test the significance of historical processes in determining current patterns of composition and diversity. Both autogenic (internal biotic) and allogenic (external environmental) processes operating through time were important determinants of current floristic patterns. Demonstrating that such historical processes have an important role in determining the composition of tropical ecosystems is valuable as they are often overlooked – or in many cases impossible to study in such detail.

Overall this thesis shows that peatland ecosystems in the Peruvian Amazon have high conservation value both as a carbon store and for regional ecosystem diversity. In addition, peatland ecosystems provide an exciting opportunity to investigate the importance of fundamental historical and ecological processes for determining the composition and diversity of tropical forests.

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1. Introduction

1.1 Thesis background

Peatland ecosystems occur across the globe where anoxic conditions cause the rate of decomposition to be slower than the rate of litter input. This imbalance of input and output processes leads to the accumulation of partially broken down organic matter, which forms peat (Charman 2002). Peat can be defined as an organic soil made up of dead and partially decomposed plant remains that have accumulated in-situ under waterlogged conditions (Osaki *et al.* 2016). More specifically, peat soils are those with an organic matter content greater than 65% (Wüst *et al.* 2003). Peatlands provide a multitude of ecosystem services, but perhaps most importantly, peatlands are the largest store of terrestrial carbon on Earth, holding an estimated 530-694 Pg C (Yu *et al.* 2010). The majority (approximately 85%) of the global peatland area and carbon stock is thought to occur in the boreal and temperate regions of the northern hemisphere (Yu *et al.* 2010). However, a substantial number of peatlands are located in the tropics, where they occupy large areas and harbour globally significant amounts of carbon (Page *et al.* 2011).

Temperate and boreal peatlands have been researched intensively over the past 50 years, and many aspects of peatland ecosystems have now been well studied. Previous work has addressed themes such as carbon storage and dynamics; biogeochemistry; and ecology and development (Heinselman 1970; Harriss *et al.* 1985; Gorham 1991; Bedford *et al.* 1999; Glaser *et al.* 2004; Sheng *et al.* 2004; Bubier *et al.* 2007; Beilman *et al.* 2008; Bragazza *et al.* 2013; Tuittila *et al.* 2013). This high volume of studies means that many aspects of peatland ecosystem function in temperate and boreal regions are well understood. This has important implications, for example, by allowing the impacts of future climate change on peatlands and their carbon stocks to be predicted, using simulation models (Frolking *et al.* 2010; Baird *et al.* 2012).

Conversely, in tropical regions many fundamental aspects of peatland ecosystems remain poorly understood, and the literature surrounding them is comparatively scant (Lawson *et al.* 2014b). As a result, predicting the future trajectory of tropical peatlands is almost impossible, as tropical peat simulation models cannot be fully parameterised (Kurnianto *et al.* 2015). Peatlands are found in all tropical regions to a greater or lesser extent, but Southeast Asia is thought to be the most important peatland region, accounting for approximately 56% of global tropical peatland area, and approximately 77% of global tropical peatland carbon stock (Page *et al.* 2011). Southeast Asian peatlands have received greater attention than their African and Neotropical equivalents, and are comparatively well studied in terms of carbon storage and dynamics; (Page *et al.* 2002; Jaenicke *et al.* 2008; Hirano *et al.* 2009); ecology and palaeoecology (Anderson & Muller 1975; Page *et al.* 1999); and the impacts of land use change (Koh *et al.* 2011; Miettinen *et al.* 2011). However, few Southeast Asian peatlands remain intact. Decades of destruction have reduced peat swamp forests to 36% of their initial area (Miettinen *et al.* 2011), which in turn has led to significant carbon emissions (Page *et al.* 2002; Hooijer *et al.* 2010; Hooijer *et al.* 2012). If current levels of deforestation persist, peat swamp forests in Southeast Asia are predicted to disappear by 2030 (Miettinen *et al.* 2012).

Extensive peatlands in Amazonia were almost entirely unknown until relatively recently. There were sporadic reports in the literature of peatlands occupying 150,000 km^2, but these were based on little empirical data (Schulman *et al.* 1999; Ruokolainen *et al.* 2001). A set of four papers were the first to document extensive and deep peatlands in Amazonia (Lähteenoja *et al.* 2009a; Lähteenoja *et al.* 2009b; Lähteenoja & Page 2011; Lähteenoja *et al.* 2012). This collection of ground breaking studies confirmed that there are extensive peatlands storing a significant quantity of carbon (2- 20 Pg), underlying a range of different ecosystem types in the Pastaza Marañon foreland basin (PMFB) in northern Peru. An important distinction between these Amazonian peatlands and those of Southeast Asia is that currently Amazonian peatlands are almost entirely intact. These initial studies have led to subsequent investigations into the hydrology, geochemistry and long term ecosystem development of peatlands in Northern Peru (Roucoux *et al.* 2013; Kelly *et al.* 2014; Lawson *et al.* 2014a). Additionally, further studies have been carried out into peatlands in other areas of Amazonia (Householder *et al.* 2012; Lähteenoja *et al.* 2013).

Despite the progress these studies have made, many important research gaps and uncertainties remain. Although the peatland carbon stock is known to be large, current estimates range across an order of magnitude, from 2-20 Pg, and contain further sources of error that have not been quantified (Lähteenoja *et al.* 2012). In addition, remote sensing suggests that there is a range of distinct vegetation community types within the peatlands (Lähteenoja & Page 2011). However, their floristic composition and diversity is almost entirely undescribed. This is particularly remarkable as there is an abundance of floristic data for the surrounding region, which show that Northwest Amazonia contains some of the most diverse ecosystems on the planet (Gentry 1988b). The peatlands have also been confirmed to record their own vegetation history in the form of preserved pollen (Roucoux *et al.* 2013). Currently this study is the only published peatland pollen record in Amazonia, but indicates that there is a unique potential among Amazonian forests for gaining a historical perspective on how these ecosystems have developed.

1.1.1 Thesis outline

This thesis uses a multidisciplinary approach to address some of the key research gaps associated with peatland ecosystems in the PMFB. In Chapter One I introduce the relevant literature concerning the geological context of the PMFB; carbon storage in tropical forests and peatlands; floristic composition and diversity in tropical forests and peatlands; and palaeoecology and long term ecosystem dynamics in tropical peatlands. This literature review also contains an extensive discussion of relevant methods, as novel applications of methods are an important component of subsequent data chapters.

In Chapter Two I present a map of the spatial distribution of different ecosystem types within the PMFB, which was developed using a combination of data-fusion remote sensing and field sampling. Using this map alongside field data, I provide the most accurate estimates to date of the above- and below-ground carbon stock of the peatland ecosystems in the PMFB. In Chapter Three I use new floristic inventory data to provide the first description of floristic composition and diversity of peatland ecosystems in the PMFB. Placing these peatlands into the broader floristic context of western Amazonia using existing floristic plot data, I am able to make inferences about the underlying processes which determine patterns of composition and diversity at a landscape scale. In Chapter Four I combine this floristic data with eight new pollen records in order to understand how these peatlands have developed, and assess the importance of temporal processes in determining current spatial patterns of floristic composition and diversity. Finally, in Chapter Five I conclude the thesis by first providing an overview of the main findings, I then go on to discuss the interdisciplinary approach taken, and make some suggestions for possible future research directions. I finish by discussing some of the main implications of the research findings.

1.2 Study region

The study area for this thesis is the Pastaza Marañon foreland basin (PMFB), located in northeast Peru. Occupying an area of 120,000 km^2, the PMFB is the largest area of continuous wetland in Amazonia –if the seasonal and marginal Beni savanna is excluded (Figure 1.). Additionally, the PMFB is perhaps the largest area of inland Holocene aggradation globally (Rasanen *et al.* 1990; Rasanen *et al.* 1992; Lähteenoja *et al.* 2012). The basin was formed primarily during the Cenozoic following the uplift of the Andes – which peaked in this region ~23 Ma – and the subsequent foreshortening of the foreland basin (Rasanen *et al.* 1992; Hoorn *et al.* 2009; Hoorn *et al.* 2010b). The current basin relief was primarily formed during the Miocene-Pliocene (2.6-7 Ma), although the basin is still actively subsiding at present (Dumont *et al.* 1991; Dumont & Garcia 1991; Rasanen *et al.* 1992; Hoorn *et al.* 2010b).

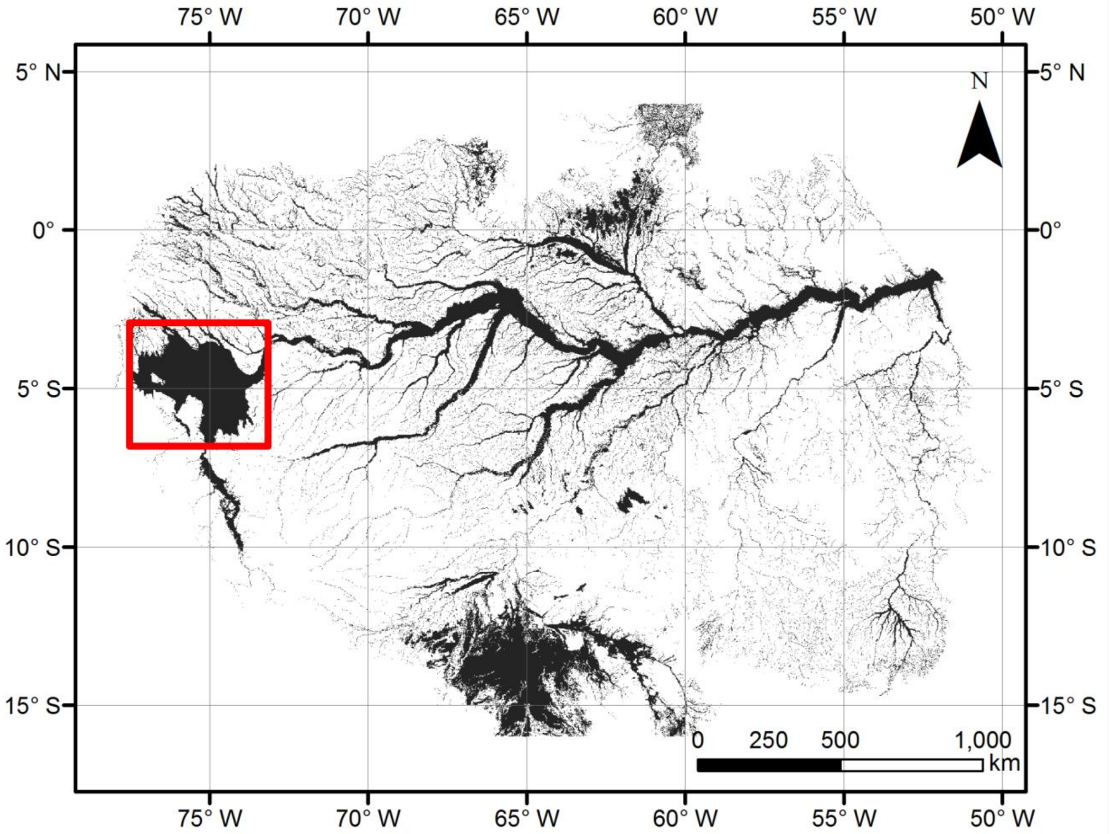

Figure 1.1. Floodable areas of wider Amazonia (as shown in black), the location of the PMFB is indicated by the red box. Data taken from Melack and Hess (2011).

The basin can be split into two distinct sub-regions that are divided by the Marañon River (figure 1.2) (Rasanen *et al.* 1992). The sub-region to the south of the Marañon (sometimes referred to as the Ucamara depression) is dominated by fluvial flood basin processes, within which the large sediment rich Marañon, Ucayali and Huallaga rivers are particularly influential (Rasanen *et al.* 1992; Kalliola *et al.* 1993). Despite the prevalence of these large white water (high sediment load) rivers, much of the interior of this sub-region is completely inundated by black water (low sediment load) during the wet season. In particular, the area between the Marañon and Ucayali rivers that now makes up the 20,800 km^2 Pacaya-Samiria National Reserve is flooded almost entirely by black water. from the smaller rivers (Pacaya, Samiria, Pucate and Yanayacu) in this area. This sub-region to the south of the Marañon has little topographic relief and is therefore hydrologically dynamic, with frequent lateral migration of rivers. Evidence of this lateral migration is particularly evident in satellite imagery, where numerous abandoned channels, ox-bow and serpentine lakes can be seen (Rasanen *et al.* 1992).

To the north of Marañon is the Pastaza Fan, a large (~ 60,000 km^2) alluvial fan-like depositional feature that dominates the second sub-region (Rasanen *et al.* 1990). The most important rivers in the Pastaza fan are the Pastaza, Tigre and Corrientes (figure 1.2). These rivers are relatively small in comparison to Marañon and Ucayali. Although they originate in the Andes as sediment rich rivers, by the time they reach the Marañon they are more mixed, due to the influence of local sediment poor rivers (Kalliola *et al.* 1993). The Pastaza fan has been dominated throughout the Holocene by the migration of the Pastaza River. The Pastaza was initially further west than where it occurs currently, and moved progressively eastwards, until it merged with the current Corrientes and Tigre rivers about 9000 Cal. yrs BP (Bernal *et al.* 2011). It has subsequently migrated back westwards during the mid-Holocene (Bernal *et al.* 2011). Small, locally originating rivers in this region typically occupy abandoned channels of the Pastaza and therefore meander little, flow from northwest to southeast and are separated by low inter-fluvial ridges (Rasanen *et al.* 1992).

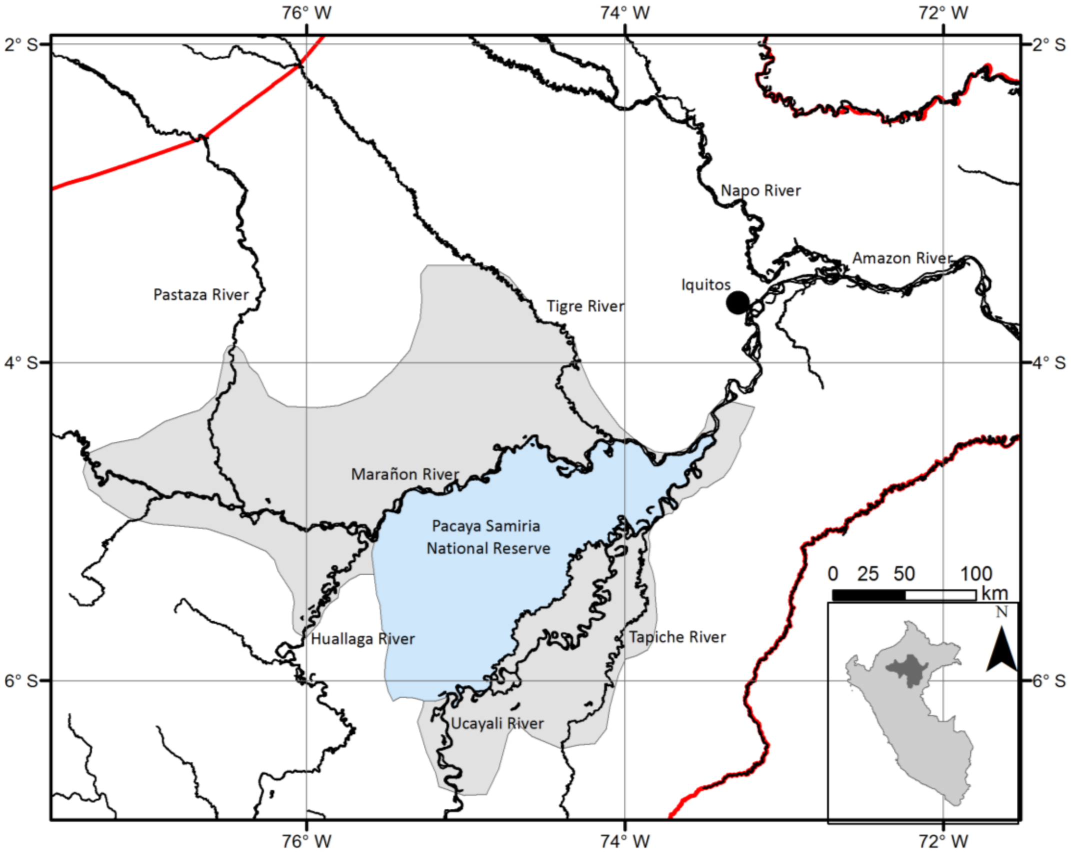

Figure 1.2 Map showing the location of the PMFB (shaded grey) the Pacaya Samiria national reserve (shaded blue) and the main rivers discussed in the text. The inset map indicates the location of the PMFB within Peru. National borders are in red, rivers are in black.

1.3 Peatlands in the PMFB

The PMFB has been shown to contain both high nutrient, minerotrophic peatlands (nutrient input from surrounding surface or ground water), and low nutrient ombrotrophic peatlands (nutrient input entirely from atmospheric deposition) (Lähteenoja *et al.* 2009a; Lähteenoja & Page 2011). This variation in nutrient input appears to be an important factor in determining vegetation composition, and a range of different peatland vegetation types have been qualitatively identified such as palm swamps, low stature pole forests, seasonally flooded forests, open herbaceous peatlands, and floating herbaceous mats (Lähteenoja & Page 2011). Of these vegetation types, forested pole forests appear to be restricted to ombrotrophic topographically domed peatlands, whilst the other vegetation types appear to be restricted to minerotrophic peatlands (Lähteenoja & Page 2011).

Peat depth is also variable, and a number of the sites identified as possible peatlands on the basis of remote sensing, contained little or no peat (Lähteenoja *et al.* 2012). The sites without peat were palm swamps or seasonally flooded forests (Lähteenoja *et al.* 2009b; Lähteenoja 2011). The deepest recorded peat depth measurement was 7.45 m, which was recorded in an ombrotrophic pole forest site in the northeast of the basin (Lähteenoja *et al.* 2012). Ombrotrophic pole forest sites consistently harbour peats > 2 m deep, whereas other ecosystem types appear to be highly variable (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012). Peatland stratigraphy is frequently complex, with numerous sites showing mineral intrusions through the profile. This pattern seems to be particularly prevalent in palm swamp peatlands (Lähteenoja *et al.* 2012). Radiocarbon dating suggests that peatlands in the PMFB have been a net carbon sink throughout the late Holocene (Lähteenoja *et al.* 2012). It remains to be seen if they have been a continuous carbon sink throughout their development, but new high resolution dating suggests some sites may have experienced a hiatus in peat accumulation (T.J. Kelly, pers. Comm.). Overall radiocarbon dating suggest that the peatlands are currently acting as a carbon sink (Lähteenoja *et al.* 2012), however, further data is needed to confirm this. Peat accumulation rates are broadly equivalent to those seen in Southeast Asian peatlands, and typically faster than rates in temperate and boreal peatlands (Lähteenoja *et al.* 2009b).

1.4 Carbon storage

1.4.1 Carbon storage of tropical forests

Tropical forests cover approximately 7-10% (1875 X 10^3 km^2) of the global land area and play a crucial role in the global carbon cycle, accounting for ~50% of the global terrestrial vegetation carbon stock (203 – 237 Pg C) (Malhi & Grace 2000; Lewis 2006; Saatchi *et al.* 2011; Baccini *et al.* 2012; Grace *et al.* 2014). Tropical forests are not only a substantial store of carbon, but are also significant sources and sinks of atmospheric CO_2. Intact tropical forests have been functioning as a carbon sink over at least the last ~30 years and globally are estimated to have increased in biomass by 0.5-1.3 Pg C yr^{-1} from 1990-2007 (Phillips *et al.* 1998; Baker *et al.* 2004a; Lewis *et al.* 2009; Grace *et al.* 2014). More recently, the Amazonian biomass carbon sink has declined primarily in response to an increase in tree mortality, particularly during drought years (Gatti *et al.* 2014; Brienen *et al.* 2015).

Over 50% of the area of tropical forests are not old growth, intact forest, but instead are naturally regenerating secondary forest (FAO 2010). Due to the recovering nature of these secondary forests, they are often a much larger carbon sink than old growth forests, particularly during early stages of regrowth. At a global scale, the regrowth of secondary tropical forests has been estimated to account for a carbon sink of 0.8-1.6 Pg C yr^{-1} (Pan *et al.* 2011; Grace *et al.* 2014). Conversely, deforestation and degradation of tropical forests is an important carbon source, accounting for global emissions of 0.8 to 2.9 Pg C yr^{-1} (FAO 2010; Malhi 2010; Pan *et al.* 2011; Harris *et al.* 2012). Despite substantial uncertainty, these results suggest that overall the tropical forest biome is a small net carbon source (0.1 Pg C yr^{-1}), or in net carbon balance (Pan *et al.* 2011; Grace *et al.* 2014; Lewis *et al.* 2015). Importantly, however, these studies have not included data from peatland forests specifically.

The importance of tropical forests in regulating the global carbon cycle and mitigating anthropogenic CO_2 emissions is now being recognised at governmental levels. This recognition has led to the development and implementation of a global tropical forest conservation initiative ‘Reducing Emissions from Deforestation and Degradation’ ($REDD^+$). The primary objective of this initiative is to provide financial incentives to help developing nations to reduce deforestation and degradation rates (Gibbs *et al.* 2007; Ebeling & Yasué 2008). Whilst REDD$^+$ is not currently operational as a large scale international programme, it was formally approved by the UN Framework Convention on Climate Change (UNFCCC) in 2009 (Ghazoul *et al.* 2010). Initial projects have already led to substantial investment in some tropical nations (Burgess *et al.* 2010), however, there have been numerous problems with the development, implementation and execution of REDD$^+$ (Murdiyarso *et al.* 2012; Visseren-Hamakers *et al.* 2012; Matthews *et al.* 2014). A key problem currently is the low price of carbon in existing markets, which results in part from uncertainty in accounting for carbon losses and gains (Asner *et al.* 2014a). Hence, the carbon stock of tropical forests has the potential to provide a plausible mechanism to protect tropical forests at large scales. However, in order for this to be successful, accurate carbon accounting in tropical forests is essential.

Over the past 20 years our knowledge of carbon storage in tropical forests has increased substantially (Grace *et al.* 2014). Specifically, the development of extensive networks of forest plots such as RAINFOR and AFRITRON have allowed for consistent above-ground carbon stock estimates to be made across continents in range of environments as well as providing a tool for continuously monitoring carbon fluxes (Phillips *et al.* 1998; Malhi *et al.* 2002; Malhi *et al.* 2006b; Peacock *et al.* 2007; Phillips *et al.* 2008; Lewis *et al.* 2009). In addition, the proliferation of satellite and airborne remote sensing products has provided new methods for estimating above-ground carbon stocks over large areas (Saatchi *et al.* 2007; Saatchi *et al.* 2011; Baccini *et al.* 2012), and at high resolution (Asner *et al.* 2010; Asner *et al.* 2012; Asner *et al.* 2014a). This has provided, for example, global estimates of tropical forest carbon stocks ranging from 203 – 237 Pg C (Saatchi *et al.* 2011; Baccini *et al.* 2012)

The forests of Amazonia are the most extensive area of tropical forest globally, accounting for approximately 50% of the area and carbon stock of all tropical forests, though there is much uncertainty surrounding these figures (Saatchi *et al.* 2011; Mitchard *et al.* 2013; Mitchard *et al.* 2014). Basin-wide estimates of total above-ground carbon stock have varied substantially from 58 Pg C (Olson *et al.* 1983) to 134 Pg C (Fearnside 1997), though more recent studies suggest a figure around 60 Pg C (Malhi *et al.* 2006a; Saatchi *et al.* 2011; Baccini *et al.* 2012; Mitchard *et al.* 2014).

1.4.2 Methods for determining tropical forest carbon stock

The discrepancies between different above-ground carbon storage estimates arise primarily from two sources. Firstly different methods are employed to both estimate the amount of biomass in a given area and then to scale these estimations up to the scale required. Secondly, different definitions of what level of canopy cover constitutes forest are used. The use of different definitions of forest can have an important effect on carbon stock estimates. For example, Saatchi *et al.* (2011) showed that using a definition of forest of either 10% or 30% canopy cover led to above ground carbon stock estimates for Latin America decreasing from 120 to 107 Pg C. Above-ground biomass (AGB) is typically estimated for a sample plot with a given area; in tropical forests, plots with an area of 1 ha have commonly been used (Malhi *et al.* 2006b). Within the sample plots the diameter at the standard height of 1.3 m (commonly termed diameter at breast height or dbh) is measured for all trees with a dbh >10 cm. Diameter measurements are then used in empirical allometric models to predict the amount of above-ground biomass (AGB), given in kg of oven dried matter, for each tree within the sample plot (Brown 1997). These empirical AGB models rely on the destructive sampling of tropical trees, and use regression models to quantify the relationship between the diameter measurement and the oven dry mass of the tree (Brown 1997). AGB allometric models have been shown to vary in quality and since their initial development much effort has been made to improve their performance by incorporating all key structural variables such as tree height and canopy dimensions (Chave *et al.* 2005; Feldpausch *et al.* 2011; Feldpausch *et al.* 2012; Goodman *et al.* 2012; Goodman *et al.* 2013; Chave *et al.* 2014; Goodman *et al.* 2014).

Active remote sensing products such as satellite based LiDAR and Radar can also be used to estimate AGB. Long wavelength radar backscatter has been shown to be sensitive to changes in forest structure (Castel *et al.* 2002; Mitchard *et al.* 2009). This relationship between forest structure and radar backscatter has been used to estimate AGB ‘directly’ from satellite based radar data in tropical forests (Englhart *et al.* 2011). However, this approach is flawed, as the backscatter signal is not directly related to AGB, and instead reflects more general structural properties of forests including the size and density of vegetation (Goetz *et al.* 2009; Woodhouse *et al.* 2012) Crucially, radar backscatter signals saturate in dense tropical forests with high carbon densities, making it impossible to accurately estimate more subtle changes in structure in these high carbon ecosystems (Woodhouse *et al.* 2012).

The use of full airborne waveform LiDAR provides the most accurate remote sensing method of estimating AGB (Asner *et al.* 2010; Asner *et al.* 2012; Asner *et al.* 2014a). This method does not saturate at high carbon densities and as it provides information on tree height, there is a strong relationship with AGB. However, the required use of an aircraft makes it expensive compared to satellite data, and therefore it is unavailable to many users. There is currently no satellite based full waveform LiDAR available, but the satellite based ICESat GLAS sensor provides LiDAR estimates for small patches of forest across the globe. Given sufficient coverage, interpolations can be made between these footprints, providing perhaps the most accurate method of generating large scale AGB maps (Saatchi *et al.* 2007; Saatchi *et al.* 2011; Baccini *et al.* 2012). An important drawback of using this ICESat GLAS data is that currently these methods have not effectively incorporated regional variation in biomass and wood density (Mitchard *et al.* 2014). This weakness has led to them showing a strong bias when compared with extensive ground data (Mitchard *et al.* 2014).

1.4.3 Carbon storage of tropical peatlands

Tropical peatlands are thought to occupy somewhere in the region of 441,000 km^2 (2.4% of tropical forest area), but are estimated to store 88.6 Pg (range 81.7-91.9 Pg) which equates to approximately 46% of the total estimated above-ground carbon stock in tropical forests (Page *et al.* 2011; Saatchi *et al.* 2011). Although the extent of peatlands may be relatively small when compared to other forests, peatlands store carbon at a much greater density. However, estimates of peatland area and carbon stock are poorly quantified and substantial uncertainties remain.

The vast majority of research on tropical peatland carbon stocks has focussed on Southeast Asia, as this region is known to contain the greatest proportion (approximately 77%) of the global tropical carbon store (66.3 -69.9 Pg C; (Page *et al.* 2011). Of the Southeast Asian countries that harbour peat, Indonesia is the most important in terms of peatland carbon, and alone accounts for 55-57.4 Pg C (Jaenicke *et al.* 2008; Page *et al.* 2011). The distribution of peatlands in Indonesia, and Southeast Asia more generally, has been comparatively well described (RePPProt 1988-1990). Tropical peatlands are well known in Indonesia because they occupy a high proportion of the total land area (approximately 11% (Page *et al.* 2011)). Despite Indonesian peatland carbon stocks being seemingly well described, substantial uncertainties remain. For example, separate studies have produced very different estimates of western Indonesian carbon stocks based on similar data but different methods, ranging from 23.1 Pg C (Dommain *et al.* 2014) to 33.3 Pg C (Wahyunto & Subagjo 2003; Wahyunto & Subagjo 2004). The disparity between these studies illustrates that even in the best studied region, uncertainty is high and further research and coordinated methods are required (Lawson *et al.* 2015a).

Given the high uncertainties in the relatively well studied and data-rich Southeast Asian peatlands, peatlands elsewhere in the tropics represent an even larger gap in our understanding of carbon stocks in tropical ecosystems. Extensive peatlands have now been confirmed across a number of locations across Central (Phillips *et al.* 1997; Sjoegersten *et al.* 2011) and South America (Lähteenoja *et al.* 2009a; Vegas-Vilarrubia *et al.* 2010; Householder *et al.* 2012; Lähteenoja *et al.* 2012; Lähteenoja *et al.* 2013). Of these Neotropical studies, only the peatlands of the PMFB in Northern Peru harbour extensive, deep ombrogeneous deposits (Lähteenoja *et al.* 2012). Outside the PMFB, the other peatlands confirmed are either small isolated patches of deep peat within river floodplains (Householder *et al.* 2012), more extensive but typically shallow peatlands (Lähteenoja *et al.* 2013), or smaller coastal peatlands (Phillips *et al.* 1997; Vegas-Vilarrubia *et al.* 2010; Sjoegersten *et al.* 2011).

Together Neotropical peatlands contain only a small fraction of the carbon stock of Southeast Asia (Page *et al.* 2011), however the carbon stock of Central and South American peatlands remains important for two primary reasons. Firstly, unlike their Southeast Asian counterparts, Neotropical peatlands are almost entirely intact. Peatlands in Southeast Asia have experienced decades of destruction as a result of legal and illegal logging (Miettinen *et al.* 2011, 2012), oil palm plantation development (Koh *et al.* 2011), peatland drainage (Hooijer *et al.*

2010), and increased fire frequency and intensity (Hoscilo *et al.* 2011; Turetsky *et al.* 2015). Such destruction has consequently led to exceptional carbon atmospheric and fluvial carbon losses (Page *et al.* 2002; Hooijer *et al.* 2010; Moore *et al.* 2013). Therefore, significant carbon losses from Neotropical peatlands in future may be prevented, whilst high emissions from many Southeast Asian peatlands in future appears inevitable.

Secondly, whilst models suggest Southeast Asian peatlands are likely to undergo substantial drying as a result of future climate change (Li *et al.* 2007), there is a much less clear prediction for South America. Some recent evidence suggests that overall, precipitation in the western Amazon is increasing (Gloor *et al.* 2013; Gloor *et al.* 2015). Additionally, whilst there is disagreement of how climate will change across the Amazon as a whole, most observed, modelled and predicted drought does not occur in north western Amazon (Espinoza *et al.* 2011; Lewis *et al.* 2011; Hilker *et al.* 2014). Any increase in drying is likely to lead to increased peat decomposition and substantial carbon fluxes (Hirano *et al.* 2009), as has been shown to have occurred across Western Indonesia throughout the Holocene (Dommain *et al.* 2014). Together these results suggest that carbon stocks of South American peatlands are currently intact and unlikely to be immediately impacted by climate change.

The peatland carbon stock of the PMFB is known to be large, but the only published estimate, apart from the new estimate developed as part of this project, ranges by more than an order of magnitude from 1.7 to 18.9 Pg C (Lähteenoja *et al.* 2012). Furthermore, this estimate does not incorporate any of the uncertainty surrounding the area of peatland. Given the rudimentary method used of estimating the peatland area for approximately half of the basin and then doubling this number (Lähteenoja *et al.* 2012), there is likely to be far greater uncertainty regarding the total carbon stock of the PMFB than expressed in their study. In order to understand why estimates of peatland carbon stocks are so uncertain and variable within and amongst studies, the difficulties and corresponding methods used for determining the four key peatland carbon stock parameters (peatland area, peat thickness, peat density and peat carbon concentration), are outlined below.

1.4.4 Methods for estimating peatland carbon storage

Mapping peatland area

Estimating the area of tropical peatlands is a substantial challenge for two reasons. Firstly, tropical peatlands are extensive and often remote, and therefore, collecting field inventory data on peatland boundaries is both expensive and time consuming. Hence, many published estimates of tropical peatland area are made using little original up to date field data, and often rely on a small number of older international inventories, which can be hard to verify (Page *et al.* 2007). Secondly, unlike, for example, forest savanna boundaries, the boundary between peatland forests and non-peatland forest is frequently poorly defined. This is reflected in national forest inventories, which typically have provided estimates of forest area based on extensive inventories but are not able to reliably distinguish peatland forests from its seasonally flooded or *terra firme* counterparts (Romijn *et al.* 2015). Indonesia is different in this respect as there have been a number of national scale inventories, which have specifically included peatland forests (RePPProt 1988-1990; Wahyunto & Subagjo 2003; Wahyunto & Subagjo 2004)

An approach combining remote sensing techniques and extensive field sampling is the most robust approach to defining peatland areas (Lawson *et al.* 2014b). Although peatland boundaries may not be obviously separable, peatlands have a number of characteristics which are likely to make them distinct from other forest types in remote sensing data.

Firstly, in terms of composition, peatland forests are thought to be less diverse than upland forests due to the extreme environmental conditions found in peatlands. Additionally, peatlands in the PMFB have been shown to hold a high proportion of palm species, particularly the emergent palm *Mauritia flexuosa*, which forms monodominant stands. Such compositional differences, are likely to be reflected in multispectral optical data, as different vegetation types are known to provide different reflectance values, principally in the red-to-near infrared region of the electromagnetic spectrum. As a result, Landsat, MODIS and SPOT satellite data have been used to map peatland areas successfully (Koh *et al.* 2011; Lähteenoja & Page 2011; Miettinen *et al.* 2011, 2012). Higher spatial or spectral resolution data are likely to perform even better. Emerging remote sensing technologies, such as ultra-high resolution data such as the airborne spectranomics system (Asner & Martin 2009; Asner *et al.* 2014a; Higgins *et al.* 2014), as well as freely available medium scale products such as the new European Union-led Sentinel 2 mission (Drusch *et al.* 2012), are likely to enhance our ability to map tropical peatlands accurately.

Peatland forests have also been shown to be distinctive from other forest types in terms of their structure. Typically, peatland forests are dominated by small trees, which is reflected in their low AGB. In some instances peatland forests have a highly stunted growth form, where individual trees are both exceptionally thin as well as being low in stature (Anderson 1983). Tropical peatlands have also been reported in areas of the PMFB which are almost entirely devoid of trees and instead form open, savannah-like ecosystems. Finally, the monodominant nature of some peatlands, particularly those dominated by *Mauritia flexuosa*, means that they are likely to be structurally distinct from other forests due to their homogeneous canopy.

Active sensors such as those that use Radar or LiDAR technologies are also useful in mapping peatlands based on their forest structure (Hoekman & Vissers 2007; Hoekman *et al.* 2010). Some active sensors such as the L band radar sensor (ALOS PALSAR) and the satellite based LiDAR ICESat GLAS have been used extensively as an indirect proxy of AGB by essentially providing a proxy measure of forest structure as discussed above. Open, low stature or uniform palm dominated canopies would all be expected to provide distinct radar back-scatter signals compared with taller denser and more complex *terra firme* forests. Essentially, polarised radar waves entering a more complex system are more likely to reflect off numerous surfaces than in a more simple system, which should result in a more scattered signal in *terra firme* than in peatland forests. High resolution airborne full waveform LiDAR data provides the most comprehensive structural information, and has been used very successfully to accurately estimate AGB of tropical forests at a landscape scale (Asner *et al.* 2014a).

Persistent standing water, especially during the dry season, is another indicator of peatland forest that can be used to define its area in combination with other factors. Active sensors such as ALOS PALSAR can also be used to detect regions where standing water is present underneath forest canopies, as water is more effective at scattering L-band radar waves than bare ground (Hoekman & Vissers 2007; Takada *et al.* 2009; Bwangoy *et al.* 2010).

Peatland forests are also often limited to specific geological and/or topographical features, which provide the necessary hydrological conditions for extended anoxia and subsequent peat formation. The PMFB provides a good example of such a feature. Initial field data suggests that whilst peatlands are extensive within the basin, sites with similar vegetation occurring just outside the basin do not harbour significant peat deposits, presumably because extended anoxia is not maintained (Lähteenoja *et al.* 2009a). At a regional scale, both active and optical medium scale sensors can be used to generate digital elevation models (DEMs) at a suitable resolution. For example, the optical ASTER sensor has been used to produce a global freely available DEM (ASTER GDEM). Alternatively, the active C/X band radar based sensor from the shuttle radar topography mission (SRTM) has also been used to produce a global freely available DEM. Both these DEMs have substantial drawbacks (Zhao *et al.* 2010). As an optical sensor, the ASTER data is sometimes not useful in tropical regions due to persistent cloud cover, and the dataset has lots of areas with missing data (Mitchard *et al.* 2012). Additionally, in forested regions such as tropical peatlands, this optical product does not provide an estimation of the actual elevation of the ground but instead an estimation of the tree canopy (Ni *et al.* 2014). SRTM data on the other hand is not affected by cloud cover. However, instead of being reflected by the canopy surface like the ASTER GDEM, SRTM penetrates the canopy to a variable depth depending on the density of the canopy (Miliaresis & Delikaraoglou 2009). Therefore, this SRTM DEM does not provide an accurate measure of surface topography in forested environments, but rather an approximate estimate.

Active sensors such as SRTM have also been used to map finer scale topographic features of peatlands, such as doming (Jaenicke *et al.* 2008). Such approaches are really only suitable on sites which either have an open bare peat surface or a consistent canopy structure. Inferring topographic structure at sites with a variable canopy is potentially misleading because of the inconsistent penetration of SRTM. LiDAR data provides a more robust alternative for understanding fine scale topographic differences as it fully penetrates the canopy to ground level. Both satellite based and high resolution airborne LiDAR data have been used to explore topography in tropical peatlands, as well as tropical forests more generally (Ballhorn *et al.* 2009; Ballhorn *et al.* 2011; Féret & Asner 2014).

These different factors all can provide useful indicators of peatland forests and whilst one indicator alone is probably always insufficient, if several indicators are present then far more robust inferences can be made. Crucially, however, any use of remote sensing data requires extensive field data, both for training supervised classification models and subsequently for testing the classifications (Olofsson *et al.* 2013). This crucial step allows for the performance of classifications to be assessed and for the error associated with the classification to be incorporated into any carbon stock assessment. In addition to using sufficient training and testing data, different classification algorithms should be explored in order to find the optimum method. Although computationally more demanding, more complex support vector machine (SVM) or neural network algorithms have been found to be more effective when developing supervised classifications using limited training data, as is often the case when assessing peatland area (Pal & Mather 2005; Mountrakis *et al.* 2011).

Estimating peat depth

Accurately measuring the thickness or depth of peat deposits is a fundamental step in determining the carbon stock of a peatland. However, as with estimating peatland area, estimating peat depth is not straightforward and numerous challenges must be overcome. Perhaps the most fundamental issue concerning peat depth is the definition of what constitutes peat. Typically, loss on ignition (LOI) data are used to define the minimum organic content required for a substrate to be defined as peat. However, different studies have often used different LOI values to define peat, ranging from a minimum organic content of 45 to 80 % (Wüst *et al.* 2003). Adding to this complexity, some studies also include a range of other organic substrate types that are not peat but contain large amounts of organic material; these substrates are usually termed ‘muck’ or simply ‘organic soils’ (Wüst *et al.* 2003).

At locations where there is a sharp transition from a mineral substrate to highly organic peat, such definitions are not important. However, in other peatlands the transition from mineral substrate to peat is often not so clear and mixing of mineral and organic sediments occurs. Equally, sites in fluvially dynamic regions may also contain thick minerogenic bands through the peat profile. The PMFB is a highly dynamic region and many of the peatlands confirmed contain large amounts of mixing and mineral bands are frequently observed (Lähteenoja *et al.* 2012). Therefore, the definition used to define how much of a core profile is peat in this region has the potentially to profoundly affect the estimate of carbon stock.

Estimates of peat depth, like estimates of peat area, are limited by a paucity of field data due to the same reasons of tropical peatlands being remote, large and expensive to access. Most commonly, a relatively small number of depth measurements are taken using an augur or peat corer, which can be a time-consuming and difficult process. These depth measurements are then extrapolated across entire peatlands, catchments or regions. This is a problem because peat depth varies both within and amongst sites, and therefore the small number of measurements may not be representative of the peatland as a whole. One solution is to increase the number of depth measurements by using a steel probe or rebar instead of a corer (Householder *et al.* 2012). This method provides an increased number of depth measurements as sampling is quicker and easier. However, as no information is provided on the organic content of the peat, where exactly the peat/mineral sediment interface is, or if there is substantial mixing, then there is a substantial loss of information, which can result in both under and over estimates of peat depth (Parry *et al.* 2014).

Another potential solution is to use ground penetrating radar (GPR) which is able to provide a much greater quantity of depth estimates at high resolution (Proulx-McInnis *et al.* 2013; Parry *et al.* 2014). GPR transmits an electromagnetic wave into the ground surface and then detects the reflectance of this electromagnetic wave. These reflections occur when the dielectric permittivity of the soil changes abruptly, predominantly as a result of the changes in moisture content found at the interface between peat and underlying mineral sediments (Parry *et al.* 2014). This method has only recently been successfully employed in tropical peatlands

(Comas *et al.* 2015), and like other methods has a number of drawbacks. Specifically, GPR signals tend to attenuate at depths over 5 m (Comas *et al.* 2015), meaning that GPR approaches may underestimate very deep peatlands. GPR is also less useful in peat deposits that contain substantial amounts of mineral sediments (Parry *et al.* 2014), as the radar signal can reflect off these mineral sediments before reaching the base of peat.

Once a dataset of depth values have been obtained, there are a number of further complications with extrapolating these depth values to the rest of peatland or landscape of interest. The most common method is to use a mean value of peat depth taken from one or more transects which move from the peatland margin towards the centre. This approach, however, is likely to overestimate the volume of the peatland, as a few deep values from the centre of the peatland are likely to be over-represented, whilst shallower areas towards the margin will be underrepresented (Householder *et al.* 2012; Lawson *et al.* 2015b).

One solution to this problem is to use remote sensing to constrain peat depth estimates, as vegetation often reflects the depth of the underlying peat (Page *et al.* 1999). For example, in Southeast Asian peatlands pole forest is consistently found growing on deeper peat deposits than mixed swamp forests (Page *et al.* 1999).Therefore, by constraining obtained values to mixed swamps or pole forests, more accurate values of overall peat carbon stock can be calculated. Similar approaches could be used in the PMFB, as forested peatlands, on average, are found on deeper peats than *M. flexuosa* palm swamps (Lähteenoja *et al.* 2012).

Another alternative to using a mean depth value is to conduct some form of spatial interpolation, and this method can be especially effective if a high density grid of depth measurements are obtained (Householder *et al.* 2012). However, this method may only be suitable for developing smaller scale carbon stock estimates and is not appropriate for landscape mosaics where peatlands are interspersed amongst *terra firme* forests. A similar method that is appropriate for large scale studies, creates a large number (2669) of GIS polygons that are distributed across a number of individual peatlands, each polygon is then assigned to a specific depth class, and the carbon stock is then quantified for each polygon separately (Dommain *et al.* 2014).

Estimating peat density

The next parameter required to develop an estimate of peatland carbon stock is the dry bulk density (DBD) of the peat matrix. Peat DBD values obtained from tropical peatlands have been found to be exceptionally variable. In the peatlands of the PMFB alone, DBD has been shown to vary by an order of magnitude within a single site (0.024 – 0.252 g cm $^{-3}$) (Lähteenoja *et al.* 2012). This variability appears to result from two factors. Firstly, and most importantly, sites with a high mineral content (particularly clay) have a much higher density, as mineral substrates typically hold much less water than organic substrates (Chambers *et al.* 2011). Secondly, as in northern peats the composition and the degree of decomposition of the peat also influences its density. Tropical peatlands, are typically made up of rapidly accumulating wood peats, which have both a fairly loose matrix and have had little time to breakdown the larger litter fragments. Peat that has been made up of herbaceous litter is typically better consolidated due to the lack of large wood and root fragments (Chambers *et al.* 2011).

Measuring peat density is difficult as a section of peat of a known volume must be extracted and transported to the lab where it can be dried and weighed. This is most commonly undertaken using a Russian style peat corer (Jowsey 1966), although due to the high wood and root content of tropical peatlands, this method is often imprecise. Other volumetric corers are available which can provide a more consistent sample (De Vleeschouwer *et al.* 2010). An alternative method involves digging a soil pit and extracted peat monoliths from the pit wall (Hooijer *et al.* 2012). Digging a soil pit though is likely to fundamentally alter the hydraulic status of the peatland and as water drains into the pit, the density of the surrounding peat will change.

As with estimates of landscape peat depth, estimates of peatland DBD are often made using only a small number of empirical samples, and in the worst instances no DBD samples are measured and instead values are taken from the literature. As DBD has been shown to be highly variable within and between sites and samples, best practice to both capture and reduce this uncertainty requires many measurements of site specific DBD (Lawson *et al.* 2015b). Finally, variation can result from the laboratory methods followed, although this can be avoided by following standard protocols (Chambers *et al.* 2011).

Estimating peat carbon concentration

The final parameter required to estimate peatland carbon stock is an estimate of the proportion of the peat which is carbon. Whilst there is some variation, values usually fall within the range of 30-60 % (Lawson *et al.* 2015b). Therefore, compared with the other parameters, which can vary by an order of magnitude or more, significantly less uncertainty is associated with carbon concentration. Two methods are used to determine carbon concentration. Elemental analysis, of homogenised peat sub samples is highly accurate and has been recommended as best practice (Chambers *et al.* 2011; Lawson *et al.* 2015b). Alternatively, there is a strong linear relationship between carbon concentration and LOI, so LOI can also be used to make reasonable estimates of C concentration (Turunen *et al.* 2002). As LOI is more straight forward and cheaper than elemental analysis, this method provides a viable option, particularly in tropical countries where access to elemental analysers may be limited.

Finally, a number of recent studies have used DBD as a proxy for estimating carbon content (Warren *et al.* 2012; Farmer *et al.* 2014). Whilst these studies have obtained convincing results in a small number of Indonesian sites, these equations are not applicable elsewhere as the equation assumes a positive relationship between density and carbon content. In the PMFB, for example, the opposite is true, as density is primarily driven by mineral content which reduces carbon content (Lähteenoja *et al.* 2012).

1.5 Floristic composition and diversity

1.5.1 Floristic composition and diversity of tropical forests

Tropical forests are famed for being the most biologically diverse ecosystems on Earth (Gentry 1992b; Gibson *et al.* 2011). With regards to tree diversity, Amazonia has often been thought of as the most important tropical region in terms of tree species richness, and maximum diversity in a given location (Gentry 1988b; Gentry 1988a; Valencia *et al.* 1994; Fine *et al.*

2009). However, a recent study has suggested that tree species richness in the Indopacific region is broadly equivalent to that in the neotropics (Slik *et al.* 2015).

Although the Amazon is now recognised as a crucial centre of tree diversity, fundamental questions regarding the organisation of the Amazon tree flora remain unanswered. For example, a recent study has extrapolated plot data to estimate that the Amazon harbours some 16,000 tree species (Ter Steege *et al.* 2013). However, the true number of tree species in the Amazon remains unknown, and of the 16,000 estimated, less than 30% have been described in this extensive dataset of 1170 plots (Ter Steege *et al.* 2013). Similarly, whilst strong patterns of diversity and tree composition have been identified across the Amazon (Gentry 1988a; ter Steege *et al.* 2000; Honorio Coronado *et al.* 2009), many of the processes that determine these patterns are poorly understood (Stropp *et al.* 2009).

In order to explore these patterns of diversity, a necessary first step is to define exactly what is meant by diversity, and how this meaning changes when considering diversity at a single location, diversity within a region and diversity amongst a number of locations. In a now seminal paper, Whittaker (1960) broke diversity down into three distinct alpha, beta and gamma components. Alpha diversity is defined as the species diversity of an individual stand or location. Beta diversity is the change in community composition across spatial gradients. Gamma diversity is the combined species diversity of a number of samples or locations, which span a range of environments, and therefore encompasses both alpha and beta components (Whittaker 1960). This diversity framework has been used for the past 50 years and has provided a useful basis for describing different facets of diversity. This thesis focuses only on the alpha and beta components and therefore gamma diversity will not be discussed further

1.5.2 Measuring alpha diversity

The alpha component of diversity can be measured relatively straightforwardly, most simply, the number of species in an assemblage (species richness) provides an intuitive measure of alpha diversity. However, species richness does not encompass the unevenness of assemblages or the relative abundance of different species (Magurran 2013). Therefore, a number of diversity metrics have been developed that incorporate both the species richness and species evenness of an assemblage. Perhaps the most widely used index of diversity is Fisher's α (Fisher *et al.* 1943). Fisher's α is a dimensionless constant: the slope of a log series distribution fitted to the relative abundances of species in an assemblage (Rosenzweig 1995). Some of the advantages of Fisher's α are that it takes into account the unevenness of species abundances, it can be calculated using species richness alone and it is theoretically insensitive to sample size (Rosenzweig 1995).

Two of the most widely used non-parametric alternatives to Fisher's α are the Simpson index of concentration (Simpson 1949), and Shannon entropy (Shannon 1948). These methods directly incorporate both the species richness and evenness elements of diversity. However, they are sensitive to sample size and require abundance data for each species in the dataset (Gotelli & Chao 2013). Additionally, they differ in their sensitivity to rare and common taxa, with the Simpson index sensitive to only the most common species, and Shannon entropy more sensitive to rare taxa and the evenness of a sample (Jost 2006). The numbers produced by these metrics are not particularly comparable or useful in their raw state. However, by using the exponential of the Shannon entropy and the inverse Simpson index, these metrics can be converted into two new indices, known as Hill numbers, that measure diversity in units of species richness (Hill 1973). Hill numbers, including species richness, provide more comparable and insightful measures of diversity (Jost 2006; Gotelli & Chao 2013).

One recurrent issue that affects all measures of alpha diversity to varying degrees is their sensitivity to sample size. In tropical forests it is never possible to completely measure the species richness of diversity of an assemblage, and therefore, inferences must be made using often only a small sample of the true diversity (Colwell *et al.* 2012). Some measures are less sensitive than others, with species richness being exceptionally sensitive to sample size (Gotelli & Colwell 2001), and Fisher's α being comparably insensitive (Rosenzweig 1995). In order to understand patterns of diversity through space, many samples are required. Sample sizes in tropical forests are almost never equivalent, as there is either variation in size of plots used or in the number of individuals in each plot, or both, making comparable estimates of diversity difficult.

Perhaps the most robust method for navigating this issue has been the use of rarefaction analysis (Sanders 1968), where statistical resampling methods are used to interpolate the relationship between the number of individuals and the number of taxa in sample (Gotelli & Colwell 2011). Using this relationship, ‘the rarefaction curve’, samples of different sizes can be standardised to provide an estimate of species richness at a constant number of individuals - the minimum number of individuals in any sample. Previously, the main drawback of this approach was that potentially lots of data is lost as samples need to be standardised to the minimum number of individuals (Rosenzweig 1995). More recently, statistical advancements have allowed rarefaction curves to be reliably extrapolated (Shen *et al.* 2003; Colwell *et al.* 2004; Chao *et al.* 2009; Colwell *et al.* 2012), meaning that it is no longer necessary to discard data in order to standardise across samples. Instead, samples can be extrapolated to an appropriate sample size, all data can be used and suitable diversity indices can be generated using this extrapolated species richness (Colwell *et al.* 2012; Colwell 2013).

1.5.3 Measuring beta diversity

Beta diversity, the variation in composition across gradients or through space, is perhaps the most conceptually complex and vaguely defined of the three components of diversity originally described by Whittaker (1960). This loose definition has led to a variety of interpretations, and subsequently beta diversity has become a much discussed concept in diversity studies (Vellend 2001; Tuomisto & Ruokolainen 2006; Tuomisto 2010a; Tuomisto 2010b; Anderson *et al.* 2011; Legendre & De Cáceres 2013). Anderson *et al.* (2011) provide a useful framework which splits beta diversity into two distinct components:(1) the turnover in species composition across a specific gradient, and (2) the variation in species composition amongst samples within a given spatial extent or habitat type. Both of these types of beta diversity are equally valid and are represented in the original outline of the concept (Whittaker 1960; Legendre & Legendre 2012a).

Numerous methods have been developed to measure beta diversity. Most broadly they can be split into methods which calculate beta diversity directly from measures of alpha and gamma diversity (Crist *et al.* 2003; Crist & Veech 2006; Jost 2007), and methods which use multivariate statistical approaches to examine pairwise compositional similarities of samples (Chao *et al.* 2005; Anderson 2006; Legendre & Legendre 2012a; Legendre & De Cáceres 2013). Multivariate analysis often proves to be the more informative approach, allowing for an assessment both of which samples are more similar (known as Q mode analysis), and also which taxa drive these similarities (known as R mode analysis) (Legendre & Legendre 2012a).

Multivariate analyses of compositional similarities among sites encompasses a multitude of different pairwise similarity or ecological distance indices, which have various mathematical properties and are suitable for different datasets (Legendre & Legendre 2012a). For example, if presence–absence data is available then the commonly used Jaccard or Sørensen indices are appropriate, whilst for abundance data the Bray–Curtis or Hellinger distances are suitable (Anderson *et al.* 2011). One of the key properties of large multivariate ecological datasets, particularly for tropical forests, is that there are many species absent from any given site, and most species have a strong unimodal distribution. These properties mean that species often only occur in small number of samples, leading to lots of zeros in the dataset. Some similarity indices (e.g. simple Euclidean distance) treat two zero values in the same way as two abundance values. This ‘double zero effect’ can lead to samples with completely different species being classed as similar based on the fact that the samples are missing many of the same species. Therefore, using a suitable similarity index is crucial, as poorly chosen metrics result in misleading results, and subsequently spurious interpretation.

Ordination methods provide an effective way of summarising and presenting multivariate data of compositional similarities. By reducing the data into the two or three dimensions which account for most variation within the entire dataset, ordinations can be used to summarise complex patterns, which would not otherwise be detectable. A variety of ordination methods are available, but perhaps the most commonly used methods are principal component analysis (PCA), principal coordinate analysis (PCoA) and non-metric multidimensional scaling (NMDS) (Legendre & Legendre 2012b). PCA is a powerful eigenvector based approach, however, PCA requires the use of a Euclidean distance metric, and therefore is sensitive to the double zero issue discussed above. Consequently, this method is unsuitable for many species composition datasets from tropical forests. Suitable transformations may sometimes be used in order to incorporate different distance metrics to be used in PCA (Legendre & Gallagher 2001). PCoA is also an eigenvector approach, but unlike PCA any distance measure can be used, allowing for greater flexibility (Legendre & Legendre 2012b). NMDS is not based on eigenvectors, and any ecological or distance measure can be used, therefore NMDS provides the most flexible ordination approach (Legendre & Legendre 2012b).

Multivariate distance based approaches have been used successfully as an exploratory tool to detect complex patterns in compositional data. However, they have a specific drawback in that they do not account for the strong mean-variance relationship of multivariate abundance data, meaning as the mean abundance of a species increases so does the variance (Warton *et al.* 2012). Not accounting for this property can lead to misleading results, particularly when inappropriate distance metrics are used (Warton *et al.* 2012). A promising improvement is the use of a model based framework in ordination analysis, which is able to specifically account for this mean–variance relationship in a given dataset (Hui *et al.* 2015). A number of distance based analyses have been used to test the significance of explanatory variables in determining abundance patterns, including canonical correspondence analysis (CCA) (Ter Braak 1987), PERMANOVA (Anderson 2001) and ANOSIM (Clarke & Warwick 2001). All of these approaches have been the subject of recent criticism, as they have been shown to lack statistical power, which could lead to incorrect interpretations (Warton *et al.* 2012; Warton *et al.* 2015). New model based methods appear to present a more powerful and flexible approach, which operates within the widely used generalised linear model framework (Warton 2011; Wang *et al.* 2012).

1.5.4 Determinants of diversity and composition

Being able to accurately measure the various alpha, beta and gamma components of diversity allows complex and large scale patterns to be identified. However, understanding the multitude of processes operating over a range of temporal and spatial scales that determine these patterns in tropical forest plant communities, presents an entirely different challenge. The conceptual model proposed by Ricklefs (2004) and expanded by ter Steege (2009) provides a foundation for reconciling these historical and ecological processes (figure 1).

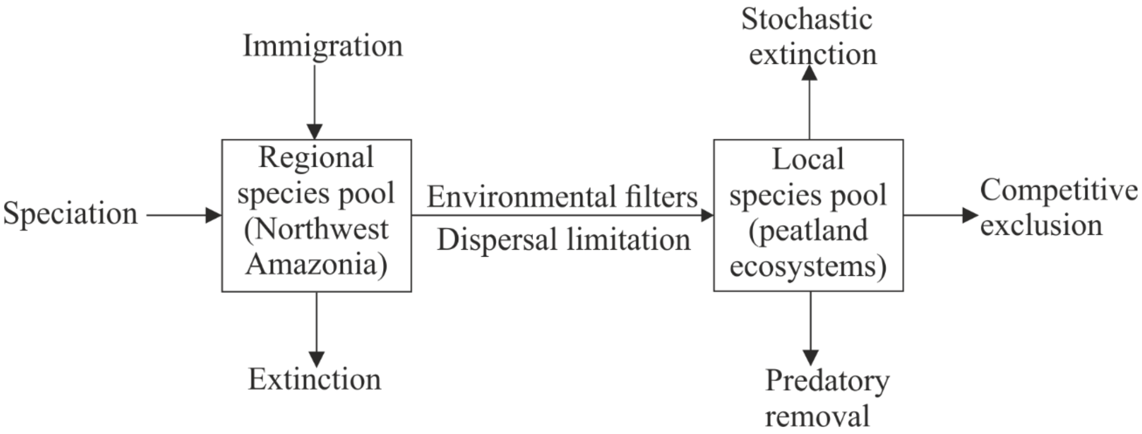

Figure 1.3 A conceptual model of the processes determining species composition and diversity operating at both long-term, regional and short-term, local scales. Adapted from ter Steege 2009.

This conceptual framework suggests that the species composition and diversity at any given location is first dependent on the species which are available in the regional species pool. This regional species pool is primarily determined by processes operating at large spatial and temporal scales: speciation, extinction and migration. From this large regional pool, species are able to disperse to any given location, limited by their dispersal abilities and the distance from the parent plant. Furthermore, at any given location there are a number of environmental gradients (e.g. fertility or climate) which will prevent a number of species from surviving - these are known as environmental filters (Keddy 1992). The local species pool is then composed of species from the regional species pool that could disperse and survive at the location. This local species pool is further modified by short-term small scale processes, including predatory removal, stochastic extinction and competitive exclusion.

Substantial evidence has now been obtained in support of all of these processes in Amazonia, although many of these processes have been most commonly studied in isolation without taking into account processes operating at different scales (Willis & Whittaker 2002; Ricklefs 2004). This lack of integration makes it difficult to separate the true effect of any given process, and in particular unmask the role of historical processes, at any given location (Ricklefs

2004). In order to simply this multitude of processes operating at different scales, here I have broken down these patterns and associated processes into their alpha and beta components.

Regional determinants of alpha diversity

Regional scale patterns of alpha diversity are largely driven by large scale processes acting over long timescales such as speciation, extinction and migration. In Amazonia, the major large scale pattern of alpha diversity is the higher diversity observed in the northwest region, compared with regions in the east and south (Gentry 1988a; ter Steege *et al.* 2000; Ter Steege *et al.* 2006; Stropp *et al.* 2009). There have been numerous explanations for this pattern and the most important are discussed below.

A number of studies have proposed that current climatic conditions are responsible for this diversity pattern, as regular droughts and strong dry seasons in the southern and eastern Amazon may mean that many wet-adapted species cannot grow in these areas (Clinebell *et al.* 1995; ter Steege *et al.* 2000; Ter Steege *et al.* 2003; Ter Steege *et al.* 2006). However, given that stronger relationships can be found between diversity and latitude than diversity and current climate, this current climate hypothesis is unsatisfying (Latham & Ricklefs 1993; Stropp *et al.* 2009; ter Steege 2009). An alternative explanation is that current climate to some extent reflects long term climatic stability which has allowed low extinction rates in western Amazonia, whilst climate instability elsewhere in the Amazon has led to increased extinction rates (Stropp *et al.* 2009; ter Steege 2009).

A further explanation is that the soils of western Amazonia are younger and more fertile than those further east in the basin (Quesada *et al.* 2010). This higher fertility has been shown to increase the productivity and turnover of trees (Phillips *et al.* 1994; Malhi *et al.* 2004; Quesada *et al.* 2012), leading to shorter generation times of lineages adapted to these conditions and rapid diversification rates (Svenning *et al.* 2008; Baker *et al.* 2014).

A final explanation for the higher diversity in the western Amazon is the Neogene uplift of the Andes and the subsequent effects on the wider landscape. The Andean uplift increased environmental heterogeneity, and nutrient supply in the form of alluvial deposits, and also brought about a wetter and less seasonal climate in western Amazonia (Gentry 1982; Hoorn *et al.* 2010b). It is quite possible that all of the explanations discussed above are correct, and the interaction of all these factors is responsible for the current patterns of diversity.

Determinants of local alpha diversity

Local alpha diversity first and foremost is limited by the size of the regional species pool (Harrison & Cornell 2008). This has been confirmed in the Amazon using a basin wide study in which regional diversity was found to be the most important factor in determining alpha diversity (Stropp *et al.* 2009). However, sites, or even neighbouring plots, within the same region can vary substantially in terms of their alpha diversity (Pitman *et al.* 2002; Valencia *et al.* 2004).

Much of the variation in alpha diversity among plots within regions can be explained by environmental filters. Low fertility white sand forests, swamp forests and floodplain forests consistently harbour fewer species than high fertility *terra firme* forests (Gentry 1988a; ter Steege *et al.* 2000; Kristiansen *et al.* 2011), and this pattern is maintained across fertility gradients in *terra firme* forests as well (Tuomisto *et al.* 2014). However, it has also been asserted that there is as yet little evidence of a causal relationship between environmental filters and diversity (ter Steege *et al.* 2000), and instead the low diversity of white sand forests, swamp forests and floodplain forests is due to their small area and isolated nature (ter Steege 2009; Pitman *et al.* 2014).

In contrast to these environmentally deterministic viewpoints, neutral theory puts forward that all species are functionally equivalent, and patterns of diversity are instead the result of demographic stochasticity (Hubbell 2001). Although this theory does not clearly represent an accurate view of the natural world (Hubbell 2005), it has been successfully used to describe several empirical diversity patterns (Hubbell 2001). Furthermore it has stimulated discussion, and provides a conceptual basis and a form of null model for expanding ecological diversity theory (Chave 2004; Wills *et al.* 2006). Neutral theory has predominantly been effective in explaining empirical diversity patterns within high diversity sites (Chave 2004), it is less useful in explaining robust spatial patterns of diversity that correspond to environmental gradients (Tuomisto *et al.* 2003). Furthermore, the well documented pattern of a relatively small number of species accounting a large number of stems at large spatial scales in Amazonia (sometimes termed ‘oligarchs’) (Pitman *et al.* 2001; Pitman *et al.* 2013; Ter Steege *et al.* 2013), runs against the predictions of neutral theory.

In addition to these extrinsic processes which determine which species are able to disperse and survive at any given location, there are a further set of interactions within the community which are important in determining local alpha diversity, including competition among species for resources (Wright 2002). The most prominent of these processes is the interaction between trees and host specific herbivores or pathogens, known as the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). This hypothesis states that mortality is higher for conspecific seedlings located close to parent trees, due to the increased density of host specific herbivores or pathogens. This negatively density dependent process essentially reduces the number of conspecifics which are able to occur in a single location, therefore promoting diversity. This process is now well documented, and is among the best explanations for the maintenance of high alpha diversity in tropical forests (Bell *et al.* 2006; Comita *et al.* 2010; Johnson *et al.* 2012; Bagchi *et al.* 2014).

Determinants of Beta diversity

Beta diversity in Amazonian forests has primarily been explained as resulting from two processes, environmental determinism and dispersal limitation (Condit *et al.* 2002; Tuomisto *et al.* 2003). Of these processes there now appears to be some consensus that often the most important driver is environment, but dispersal limitation, often represented by geographic distance, is an important but secondary process (Condit *et al.* 2002; Phillips *et al.* 2003; Tuomisto *et al.* 2003; Vormisto *et al.* 2004; Jones *et al.* 2006; Kristiansen *et al.* 2012). This has been shown to be variable over different scales, and over very large (continental) spatial scales, dispersal limitation is more important, whilst environmental determinism dominates over regional scales (Honorio Coronado *et al.* 2009).

Environmental conditions may not necessarily drive tree species composition directly, but instead, complex interactions with insect herbivores may determine composition. For example, in Amazonian white sand forests, *terra firme* species outcompete white sand specialists in the absence of herbivores, however, when herbivores are present the white sand species are dominant (Fine *et al.* 2004). Historical biogeography has also been shown to be an important process in determining compositional patterns in tropical forests, although these processes are rarely incorporated in beta diversity analysis. For example, secondary contact between historically isolated communities has been important in determining patterns of beta diversity in some west Amazonian tree communities (Dexter *et al.* 2012).

1.5.5 Floristic composition and diversity of tropical peatlands

Despite the high conservation importance of tropical peatlands as a carbon store, surprisingly little is known of their floristic composition and diversity (Posa *et al.* 2011). Almost all the floristic data published comes from Southeast Asia, but even in this relatively well studied region there is little published quantitative data. Perhaps the most detailed floristic work comes from the pioneering work of Anderson (1961, 1963, 1964, 1983), even though this work is predominantly qualitatively descriptive in nature. The quantitative data available suggest that peatland plots are less diverse than neighbouring *terra firme* sites (Momose 2002; Mirmanto *et al.* 2003; Gunawan *et al.* 2012). Additionally, peatland vegetation is often arranged in concentric formations of ‘phasic communities’ which differ in composition and diversity, reflecting the hydrology and nutrient availability across the peatland (Anderson 1964; Page *et al.* 1999; Poesie *et al.* 2010).

Southeast Asian peatlands are reported to harbour numerous (172) endemic tree taxa (Posa *et al.* 2011). However, the source of this data is not provided so this assertion is not currently verifiable. Interestingly, in contrast, Anderson (1964) states that there are probably few endemic species, and explains that many of the species found in the ombrotrophic centre are found in surrounding white sand ‘heath’ forests, whilst a number of species found towards the peatland margin are also found in fertile *terra firme* forest. The fact that there is little quantitative floristic data available has meant that it has not yet been possible to fully assess the factors that drive composition and diversity at local and regional scales in Southeast Asian peatlands.

Even less is known of the floristic composition and diversity of tropical peatlands in South America. However, remote sensing and geochemical analyses indicate that there is a diverse range of minerotrophic and ombrotrophic peatland ecosystems types within the PMFB (Lähteenoja & Page 2011). These ecosystem types include palm swamps dominated by the emergent palm *Mauritia flexuosa*, open herbaceous peatlands, and ’peatland pole forests’ which structurally resemble both the peatland pole forests described in Southeast Asia and Amazonian white sand forests (Lähteenoja *et al.* 2009a; Kelly *et al.* 2014).

1.5.6 Floristic composition and diversity of Amazonian wetlands

Amazonian wetland ecosystems more generally have received far greater attention than peatlands specifically (Dumont *et al.* 1990; Kahn & Mejia 1990; López Parodi & Freitas 1990; Junk 1997; Nebel *et al.* 2001; Wittmann *et al.* 2006; Junk & Piedade 2010; Junk *et al.* 2011). However, many of these studies have been strongly biased towards central and eastern Amazonia, despite the PMFB being perhaps the largest area of continuous wetland in Amazonia (Melack & Hess 2011). This bias is well illustrated by a recent paper (Junk *et al.* 2015) in which the wetlands of the PMFB are not only vastly underestimated in terms of extent, but also incorrectly labelled as white water Varzea forest.

Many of these studies have been concerned with producing vegetation classifications which can help to simplify the diversity of ecosystem types (Prance 1979; Encarnación 1985; López Parodi & Freitas 1990; Kalliola *et al.* 1991a; Kvist & Nebel 2001; Junk *et al.* 2011; Junk *et al.* 2015). These classifications have predominately not been quantitative classifications based on vegetation composition. Instead classifications have been produced based on flood water sediment load (white water vs black water), qualitative descriptions of common species, and assumed or measured hydroperiod (including flooding intensity and duration). Although predominantly qualitative, these studies have nonetheless provided a useful framework for describing these ecosystems. However, the lack of specific information on the presence of peat is a notable absence.

Most simply, these classifications distinguish between ecosystems which are seasonally flooded, and those which remain waterlogged throughout the entirety of the year. Seasonally flooded ecosystems tend to be forested, and are further split into those which are flooded by sediment rich ‘white’ water, and low sediment ‘black’ or ‘clear’ water. Various local vernacular names have been used for these two different types of flooded forest, but perhaps the most widely used are the Brazilian terms of Varzea (white water forest) and Igapo (black water flooded). In Peru, all flooded forests are typically known as Tahuampa, or Restinga for forests that are flooded for only a short time (Kvist & Nebel 2001). Permanently waterlogged ecosystems are called swamps, and this term is typically broken down further to identify forested or open swamps. In Peru, forested swamps are known as Aguajal and open swamps as Pantanal.

There is a general lack of information in the scientific literature surrounding the floristic composition and diversity of Amazonian swamps, but some fundamental properties of these communities have been noted. At local scales, swamps are typically less diverse than surrounding *terra firme* ecosystems (Dumont *et al.* 1990; Duivenvoorden 1996; Pitman *et al.* 1999; Duque *et al.* 2002; Pitman *et al.* 2014). The composition of swamps is dominated by palm species, particularly the emergent arboreal palm *Mauritia flexuosa* (Kahn & Mejia 1990; Kahn 1991; Pitman *et al.* 2014). Swamp vegetation composition and diversity are also known to be highly variable, both within and among sites (Pitman *et al.* 2014). Furthermore, although the composition of swamp forests appears distinctive (Kahn & Mejia 1990), >80% of species found in five Ecuadorian swamps were also found in surrounding upland vegetation (Pitman *et al.* 2014).

More recently, research in Amazonian wetlands has moved beyond floristic descriptions and classification and started to look at regional and local diversity patterns and the processes that may drive them. For example, the importance of the regional species pool and environmental filters in driving compositional patterns in Ecuadorian swamp forests has been shown (Pitman *et al.* 2014). Further examples can be found in the seasonally flooded forest literature, where environmental filters have be shown to be important determinants of both alpha and beta diversity (Assis *et al.* 2015). Additionally, large scale plot based studies have provided insights into regional patterns of diversity, composition and endemism (Wittmann *et al.* 2006; Wittmann *et al.* 2013). These studies have shown that the east to west diversity gradient seen in *terra firme* forests is also seen in seasonally flooded forests (Wittmann *et al.* 2006). Additionally, seasonally flooded white water forests are found to have low beta diversity over large spatial distances and a high number of endemics. It is suggested that these patterns reflect environmental filters and low dispersal limitation in these seasonally flooded ecosystems (Wittmann *et al.* 2006; Wittmann *et al.* 2013).

1.5.7 Floristic composition and diversity in Northwest Amazonia

Despite the lack of floristic data for the peatlands of the PMFB, there is an abundance of floristic data which reveal Northwest Amazonia to be one of the most important regions for floristic diversity in the world (Duivenvoorden & Duque 2010). Northwest Amazonia harbours some of the highest levels of site-level floristic diversity on Earth (Gentry 1988b) and a combination of Andean deposition and fluvial erosion has created a geologically heterogeneous landscape which is reflected in floristic composition (Higgins *et al.* 2011). White sand forests are an ecosystem of particular interest. These distinctive forests occur across this region on ancient cratonic sediments that have been exposed as a result of geological activity associated with late Miocene Andean uplift (Hoorn *et al.* 2010a). White sand forests are notable for their low stature and typically open canopy compared with *terra firme* forest in this region (García Villacorta *et al.* 2003). They have been of particular interest to ecologists though due to their exceptionally high levels of biotic endemism, and their associated role in promoting speciation in this region (Fine *et al.* 2005; Fine *et al.* 2010; Alonso *et al.* 2013).

White sand forests are relevant to this thesis as there appear to be structural and compositional similarities between white sand forests and the hitherto undescribed peatland pole forest ecosystems (Lähteenoja *et al.* 2009a; Kelly *et al.* 2014). Such comparisons have been made previously between white and pole forests in Southeast Asia (Anderson 1964). If many species are shared between peatland and white sand forests, this has important implications for understanding how peatland communities may have been assembled. Furthermore, if the white sand species found within peatlands are those thought to be specialists or endemics to white sand forests, this has implications for understanding the conservation significance of both ecosystems (Lähteenoja *et al.* 2009a).

1.6 Long term ecosystem dynamics

As peat accumulates through time, anoxic conditions preserve some biological material in sub-fossil form. By examining these sub-fossils, insights can be gained into past ecology and environments. Fossil pollen has proved to be particularly useful as pollen grains are highly abundant (even in small samples), often well preserved, taxonomically distinctive, and can represent vegetation at both local and landscape scales (Birks & Birks 1980). Pollen analysis has been used extensively in temperate and boreal peatlands to reconstruct past vegetation over the past century.

Over the past 30 years there has been a rapid increase in the number of palynological studies in lowland tropical forests. In Amazonia these studies have mostly come from lake records as opposed to peat records, largely because until recently substantial peat deposits were not thought to exist in Amazonia. The limited number of deep sediment rich lakes in lowland Amazonia has been an important limiting factor to the number of pollen records available. The primary focus of many of these studies has been to provide information on past climate (Behling 1998; Colinvaux & De Oliveira 2000; Bush & Silman 2004) and long-term responses of forest to climate change (Beerling & Mayle 2006; Bush *et al.* 2007a; Mayle & Power 2008) and human impact (Bush *et al.* 2007b; Carson *et al.* 2014). One particularly important outcome is the number of pollen based studies which have documented the extent of forest throughout glacial cycles, and subsequently been widely considered to provide a refutation of the refuge hypothesis (Colinvaux *et al.* 1996a; Haberle & Maslin 1999; Colinvaux *et al.* 2000). The refugia hypothesis posits that current patterns of biodiversity in Amazonia can be explained by lower temperatures and rainfall during the Pleistocene leading to much of Amazonian forests being replaced by savanna (Haffer 1969; Van der Hammen & Absy 1994).

Few studies have used pollen records to address questions related to the ecological processes that govern vegetation development in tropical peatlands (Roucoux *et al.* 2013). Of these studies an even smaller number have attempted to integrate these temporal patterns with spatial patterns of vegetation composition (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997). Palaeoecology presents an important and, in the tropics, currently neglected method for understanding ecological processes operating over long timescales that drive current patterns of composition and diversity (Jackson & Blois 2015). Although it is now well acknowledged that historical processes need to be better incorporated into ecological studies (Ricklefs 2008), only evolutionary processes, such as speciation, which act over geologically long time scales are typically considered. Environmental filters, for example, are largely assumed to be temporally static in diversity studies, even though environmental conditions are known to change through time.

1.6.1 Succession and development in peatlands

One way in which environmental filters can change through time is through the process of succession. Succession has been defined in a number of ways, most loosely as the change in vegetation through time at a given location. This definition is of limited usefulness, as vegetation can change through time for a number of reasons. A more restricted definition of succession refers to an orderly, directional and predictable process of vegetation change though time, which results from the modification of the physical environment by the vegetation community, and which results in a more stable ecosystem (Odum 1969). Aspects of this more specific definition have been criticised, as succession has been found to be highly variable and does not necessarily lead to a more stable community (Walker *et al.* 2010a; Prach & Walker 2011). In this thesis, succession refers specifically to the autogenic process of vegetation change though time that results from the modification of the physical environment by the vegetation community.

Succession is especially relevant to peatlands because the process of peat accumulation typically leads to changing environmental filters (such as lower nutrient availability) and therefore, potentially, to changes in vegetation composition and diversity. The importance of succession in determining patterns of vegetation composition and diversity in northern peatlands has been known for some time, and is encapsulated in the conceptual model of hydroseral succession (Tansley 1939; Walker 1970). The initial conceptual model states that as organic material accumulates in lakes they move from aquatic environments to dry woodland environments, moving through a number of distinct vegetation types. The initial model was established based on the assumption that patterns of vegetation assemblages through space were a result of vegetation development patterns through time; this space for time substitution is known as a chronosequence. Subsequent palaeoecological analysis has shown that there is far more variability in successional pathways than originally proposed, and that the final suggested transition from a raised bog to a forest is not represented in empirical data (Klinger 1996).

These inconsistencies between the original hypothesis and the observed data have led to a number of authors dismissing the ‘classical’ model of hydroseral succession and going on to propose alternative models (Heinselman 1963, 1970; Van Breemen 1995; Klinger 1996). Certainly it has been repeatedly shown that inferring succession from apparent chronosequences is a flawed approach, and palaeoecological investigation is required (Johnson & Miyanishi 2008; Walker *et al.* 2010a). The autogenic process of succession takes place within environmental settings that change due to external allogenic factors such as climate change or disturbance by river migration. Furthermore, even if environmental conditions are constant, community assembly is also in part a stochastic process, therefore, succession would be expected to be variable. Despite this variability, when many studies of hydroseral succession are taken together, there is a clear pattern which appears to fulfil the criteria of succession in that it is orderly, predictable, caused by autogenic processes and results in a stable community.

Understanding general but consistent patterns in peatland vegetation development, such as hydroseral succession, are important for developing models of peatland development and function (Frolking *et al.* 2010; Tuittila *et al.* 2013). Such models are required to better understand how peatlands will function in response to future global change, and to assess how any changes in peatland function could affect the global carbon cycle (Farmer *et al.* 2014). As developmental changes in vegetation will affect crucial properties of peatland function, e.g. litter input, models need to accurately simulate vegetation succession. Currently, models of tropical peatland development and function are in the early stages of development, and have only been used to simulate Southeast Asian peatlands, using the little data available to parameterise the model (Kurnianto *et al.* 2015). However, as these models are applied more widely across the tropics, a thorough understanding of peatland development will be required in order to adapt models to local contexts and test their performance.

Hydroseral succession is closely related to the peat development process of terrestrialisation, which is the gradual infilling of a water body with organic matter (Charman 2002). The two processes are not synonymous. Hydroseral succession refers to the changes in vegetation, whilst terrestrialisation refers to the physical process of infilling (Klinger 1996). The alternative peat development process to terrestrialisation is paludification, which is a process whereby peat develops directly over a mineral substrate without an aquatic phase (Charman 2002; Rydin & Jeglum 2013). Paludification can occur as a result of climate change and has sometimes been associated with lateral encroachment at peatland margins (Heinselman 1963). In general it appears that many more peatlands are formed through paludification than terrestrialisation in temperate and boreal ecosystems (Sjörs 1983; Charman 2002).

1.6.2 Succession and development in tropical peatlands

Although there are comparatively few pollen records from tropical peatlands, many of these have established site-specific patterns of vegetation succession and peatland development (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997; Anshari *et al.* 2001; Morley 2013; Roucoux *et al.* 2013). The majority of these studies have been confined to Southeast Asia, where a number of studies have found that successional development can account for spatial vegetation patterns found above ground (Anderson & Muller 1975; Morley 1981; Anderson 1983). Typically, these successional pathways have moved from minerotrophic flooded forests to ombrotrophic domed low diversity forests. However, there are a number of differences in the development of peatlands found towards the coast, and those inland, with coastal peatlands developing in saline mangroves and inland peatlands initiating in upland podzolic forests that become anoxic (Morley 2013). A study of a coastal peatland in Panama revealed a similar successional pattern to the coastal peatlands found in Indonesia, with modern-day spatial vegetation patterns found to reflect the temporal successional patterns (Phillips *et al.* 1997).

The only published pollen record from a continuous peat core in Amazonia comes from Quistococha, a palm swamp just downstream from the PMFB and close to the city of Iquitos (Roucoux *et al.* 2013). The Quistococha record shows very different development patterns compared with those of Panama and Southeast Asia. In many ways this is unsurprising, as Southeast Asian and Panamanian peatlands have formed in response to coastal dynamics and changes to past sea level (Dommain *et al.* 2014). Conversely, Amazonian peatlands are associated with inland fluvial dynamics. The Quistococha peatland has a complex developmental history, with evidence of a number of reversals and repetitions in the pattern of vegetation change (Roucoux *et al.* 2013). The overall pattern of vegetation development can be interpreted as moving from a lake, to a marginal/floating mat herbaceous community, to a flooded forest and finally to the current vegetation type, palm swamp (Roucoux *et al.* 2013). This lake to palm swamp developmental pathway found at Quistococha, shares features with a chronosequence based successional model that was developed based on observations of current spatial patterns in Amazonian swamps (Kalliola *et al.* 1991a; Kalliola *et al.* 1991b). This chronosequence suggests a sequence from open water to a floating macrophyte community, to a herbaceous community, to a shrub swamp, to a palm swamp to a forest swamp (Kalliola *et al.* 1991a; Kalliola *et al.* 1991b).

Despite the lack of pollen records from Amazonian peatlands, there are a number of records from Amazonian wetlands that contain thin lenses of peat and provide some insight into palm swamp succession (Frost 1988; Ferraz-vicentini & Salgado-Labouriau 1996; Behling *et al.* 1999; Weng *et al.* 2002). Whilst these records share some features in common with the Quistococha peatland, there are also clear differences that have developed in fundamentally different environments. For example, in some cores, palm swamps appear to follow flooded forests (Behling & Hooghiemstra 1998), whilst in others the reverse is true (Frost 1988). Identifying any consistent patterns related to peat development is difficult, as peat accounts for only a fraction of the sequence, which instead is mostly made up of minerogenic sediments.

Of the few records available in tropical peatlands it appear that both terrestrialisation and paludification have been important processes. In Southeast Asia, coastal peatlands appear to have undergone a form of terrestrialisation, from aquatic mangrove ecosystems to domed ombrotrophic peatlands (Anderson & Muller 1975; Morley 2013). Alternatively, some inland ‘kerapah’ peatlands appear to have developed through paludification, initiating under freshwater swamp conditions (Morley 2013). In the neotropics, a coastal Panamanian peatland has developed following a similar terrestrialisation process as seen in Indonesian coastal peatlands (Phillips *et al.* 1997). The one continuous record from an Amazonian peatland appears to show a pattern of terrestrialisation that is occasionally deflected by allogenic river influence (Roucoux *et al.* 2013). Peats in other Amazonian wetlands appear to have initiated through paludification (Ferraz-vicentini & Salgado-Labouriau 1996). This suggests that tropical peatlands can develop following a range of different processes, but as yet it is not clear how common or important are terrestrialisation or paludification processes. If paludification is indeed an important process in Amazonian peatland formation, this would have important implications as it suggests that there is likely at least some climatic influence on peat accumulation (Charman 2002).

1.6.3 Pollen analysis in Amazonia

Pollen analysis is an immensely useful tool for understanding past vegetation communities. However, there are a number of important limitations to using this approach in Amazonia. Many of these limitations stem from the vast diversity of plant species found in Amazonia, which has been discussed in section two.

Pollen analysis was originally developed in European temperate and boreal ecosystems where plant diversity is low. This meant that pollen reference collections could be built up relatively easily and that a pollen grain could quickly be accurately identified, often to genus or even species level, and a palaeoenvironmental inference could be made on the basis of the current distribution of that species. In Amazonia the huge diversity of plants means firstly, that pollen grains of many species have not been described; and secondly, due to the much greater number of species and often small morphological differences between pollen grains from congeneric species, grains can often only be accurately identified to genus or even family level, and the amount of palaeoecological information that can be deduced is correspondingly reduced. Some genera contain hundreds of species, which may be trees, shrubs, lianas or herbs, and which may be found in a range of environments from the high Andes to lowland swamps. An example is the large genus *Miconia* in Melastomataceae (Gentry 1994), which is not only often ecologically ubiquitous but also often can only be separated from the rest of the Melastomataceae with difficulty and some uncertainty, even under ideal conditions of preservation. Other genera, however, can be immediately indicative of a specific environmental condition. For example, *Symmeria paniculata*, a member of the Polygonaceae and the only species in its genus, has distinctive pollen grains and is considered a good palaeoenvironmental indicator of seasonally flooded black water forests (Absy 1979; Gentry 1994).

In addition to this huge diversity of species, there is substantial variation in how different species are represented in pollen assemblages due largely to variation in their pollination strategy. Unlike in boreal or temperate ecosystems, the vast majority of tropical forest tree species (>95%) are zoophilous (animal dispersed pollen strategists) rather than anemophilous (wind dispersed pollen strategists). Anemophilous species produce far greater quantities of pollen than zoophilous taxa, and are therefore much more abundant in the pollen rain. The lack of anemophilous taxa initially led to the feasibility of pollen analysis in the tropics being doubted (Bush 1991). However, it has since been shown that there is a vast range of zoophilous strategies, and some zoophilous species in fact produce large quantities of pollen and are well represented in the pollen rain, whilst others produce very little (Bush 1991, 1995; Bush & Rivera 2001).

The consequence of this range of pollen production rates means that some species are overrepresented in the pollen rain opposed to the contemporaneous vegetation assemblage, whilst other are underrepresented or do not appear at all in the pollen assemblage, and are sometimes referred to as “palynologically silent”(Bush 1995). The only detailed study to look specifically at differences between the modern pollen rain and the contemporaneous vegetation in lowland Amazonia found that 75% of trees in a one hectare plot were not represented at all in the pollen assemblage (Gosling *et al.* 2005). Of the taxa that were represented in both the vegetation and pollen data, there was little correspondence between vegetation and pollen abundance data.

A further distinction between pollen analyses in tropical forests compared with temperate or boreal ecosystems, is that most pollen in tropical forests reflects a very local signal rather than a regional signal. This is again largely due to the high proportion of zoophilous taxa in tropical forests, which have been shown to mainly disperse pollen within a radius of approximately 50 m from the parent tree (Bush & Rivera 2001). The effect of this is that only 20% of taxa disperse more than 40 m from the parent tree in tropical forests (Bush & Rivera 1998), and of the 20% which manage to disperse further away most species were anemophilous. This means that pollen assemblages predominantly represent local taxa, but the taxa that are likely to represent a more regional signal are also more likely to be over-represented. The pollen rain in forests also represents a more local signal than in open areas (e.g. lakes, fens, and herbaceous peatlands), because pollen travels less far in forest due primarily to decreased wind turbulence (Moore *et al.* 1991).

Together these limitations make pollen analysis in tropical forests a challenging prospect and must be taken into account when interpreting the meaning of down-core pollen records. It is necessary to have an understanding of the ecology and distribution of each taxon recorded in the pollen record. Where pollen identification is only possible to genus or family level, then it is important to also understand the ecology and distribution of other species in that clade. For example, a number of genera which occur frequently in montane Andean environments have been used as an indicator of past cooling in the Amazon (Bush *et al.* 1990; Colinvaux *et al.* 1996a; Colinvaux *et al.* 1996b). However, many of these taxa are also abundant in lowland swamps, which could also account for their abundance in pollen records (Householder *et al.* 2015).

It is equally important to take into account the pollination strategies of taxa where possible. For example, grass (Poaceae) pollen has often been used as an indicator of open savanna-like environments. However, all Poaceae are anemophilous, and Poaceae pollen has been shown to be more abundant in lake environments than some savanna environments (Bush 2002; Gosling *et al.* 2009). This is in part due to the fact that many Amazonian lakes contain floating mats of grass species. Lakes are also more open than savannas and therefore contain more regional anemophilous pollen (Tauber 1967; Prentice 1985). Additionally, as pollen data are typically presented as proportions, if there are several anemophilous taxa present at a site the contribution of Poaceae will be diminished. Alternatively, if Poaceae is the only anemophilous taxon present, Poaceae will likely be overrepresented (Bush 2002). This ‘percentage effect’ will also affect other abundant anemophilous taxa such as the pioneer tree genus *Cecropia*.

Despite the limitations discussed above, pollen records hold a great deal of extremely valuable information on past floristic composition, which can provide valuable historical perspectives when analysed carefully. In the context of this thesis, pollen records in peatlands have the potential to provide novel insights into ecological processes operating through time that may help to explain current patterns of diversity. In order to address questions related to ecological processes, such as succession, it is necessary to be able to identify different ecological communities based on their pollen rain. This problem of identifying communities from pollen assemblages can be broken down into two interconnected parts: firstly, differentiating between different pollen assemblages based on the pollen composition, and secondly, assigning these assemblages to a specific ecological community based on the relationship between the pollen composition and the vegetation composition.

Differentiating communities based on pollen composition is theoretically similar to the issue of looking for patterns of compositional similarity amongst ecological data (discussed in section two). Comparable with neo-ecological datasets, these patterns in palaeoecological datasets are typically complex, and multivariate statistical analyses have been used extensively for discriminating between neotropical pollen communities since Bush (1991). There has been some controversy surrounding the ability of multivariate approaches to differentiate between ecosystem types in modern pollen data (Bush *et al.* 2001; Burn *et al.* 2010). However, these results are confounded by the fact that inappropriate statistical approaches have often been used. Specifically, Euclidean or log transformed Euclidean distances have been used with PCA or DCA, which are highly likely to provide misleading results due to the ‘double zero problem’ (Legendre & Gallagher 2001).

The second part of the problem of assigning pollen assemblages to a specific community or ecosystem type requires a thorough understanding of the relationship between vegetation and pollen assemblages. To understand this relationship, modern pollen surface samples must be taken within forest plots where the floristic composition is known. Multivariate approaches can again be used to assess the similarity between this modern pollen assemblage and fossil pollen assemblages (Burn *et al.* 2010), this approach is known as the modern analogue technique (Guiot 1990). A drawback of this approach is that multivariate analyses will be dominated by the most abundant pollen types, and these abundant pollen types may not be particularly indicative of any specific community or ecosystem type. Therefore, abundant but ecologically ubiquitous taxa may mask the signal of rare but ecologically meaningful taxa.

Alternatively, a more subjective approach can be taken whereby taxa that are known to be both ecologically meaningful and present in the modern pollen assemblage can be used as indicators of specific communities or ecosystem types (Gosling *et al.* 2009). However, this approach requires extremely thorough understanding of the ecology and distribution of these ‘indicator taxa’. Ideally indicator taxa should be identified to species level, and only to genus if that genus is especially indicative of specific environmental conditions. Indicator species can also be identified using multivariate analysis (Dufrêne & Legendre 1997), however, these approaches are limited as they do not incorporate any knowledge of the ecology and wider distribution of the taxa outside the dataset being examined.

1.6.4 Linking palaeoecology and ecology

A key element of this thesis is linking ecological and palaeoecological approaches. A recent publication summarised the research questions that a number of leading palaeoecologists perceive to be priorities in palaeoecology (Seddon *et al.* 2014). Of the 804 suggested questions, 40% were associated with methodological approaches and 18% were focused on community, species or diversity dynamics (Seddon *et al.* 2014). This priority question exercise suggests that there is a demand for using palaeoecological approaches to answer ecological questions, and developing or using new methods to allow this to happen. Equally, among ecologists there is a growing appreciation for the importance of historical processes in determining ecological patterns (Ricklefs 2008; Jackson & Blois 2015). However, there has typically been little interaction between ecologists and palaeoecologists, although the disciplines are closely linked (Rull 2010; Birks 2012; Rull 2014). Many reasons have been suggested to account for this lack of interaction, including methodological differences and departmental isolation (Rull 2010; Birks 2012; Rull 2014).

Recently, there has been an increase in the interaction between palaeoecology and biodiversity conservation studies (Willis & Birks 2006; Willis *et al.* 2007a; Willis *et al.* 2007b; Froyd & Willis 2008; Cole *et al.* 2015; Jeffers *et al.* 2015b). However, interactions between palaeoecology and pure ecology (community ecology, theoretical ecology etc.) are scarce (White *et al.* 2010; Jackson & Blois 2015), even though the mutual benefits available have been known for some time (Schoonmaker & Foster 1991; Birks 1993; Bjune *et al.* 2015).

One of the main differences between the two disciplines is the approach used to collect and analyse data. Over the past 30 years, ecology has become increasingly focused on hypothesis testing, often model-based approaches (Zuur *et al.* 2007; Bolker *et al.* 2009). whilst much of “ecological palaeoecology” – the branch of palaeoecology concerned with the effect of environmental change on communities – has remained predominantly descriptive (Birks 2012). Although there are clear exceptions, the work of John Birks in particular has involved developing innovative and cutting edge numerical approaches to analysing palaeoecological data over the past 30 years (Birks & Birks 1980; Birks & Gordon 1985; Birks & Line 1992; Birks *et al.* 2012). One of the main ways that the gap between palaeoecology and ecology can be crossed is by using robust statistical methods, within a hypothesis testing framework, to test ecological patterns e.g. (Jeffers *et al.* 2011; Blois *et al.* 2014; Jeffers *et al.* 2015a). There is also a broad literature which uses palaeoecological proxies to reconstruct past climate, this is often highly numerical and model-based (Fritz *et al.* 1991; Birks *et al.* 2010), but is less relevant to the issues addressed here.

1.8 Thesis aims and objectives

The discussion above has shown that the PMFB peatlands are underexplored, important in the context of regional C cycling, and floristically of great interest. The central goal of this thesis is to improve our understanding of these ecosystems. The review above also identified knowledge gaps, methodological problems, and possible avenues for research. On the basis of that review, and taking into account logistical constraints, the following aims and objectives were developed.

Aims

This thesis has three broad aims:

1. To estimate the size and distribution of the peatland carbon stock in the PMFB.

2. To investigate patterns of floristic diversity and composition through space in the peatland ecosystems of the PMFB.

3. To investigate patterns of floristic composition through time in the peatland ecosystems of the PMFB.

These aims consist of a series of more specific objectives which I have listed below. These three sets of aims and objectives have been addressed in the following three data chapters, which are presented in the form of three scientific papers, one of which is already published.

Objectives

1. Map the distribution of the PMFB peatland ecosystems, and estimate the size of their above- and below-ground carbon stocks. This objective can be broken down into four steps.
    1.1. Map the distribution of different peatland ecosystem types in the PMFB using remote sensing approaches combined with extensive field validation.
    1.2. Estimate the total peatland carbon store in the PMFB using a combination of remote sensing and extensive field sampling, including both the above- and below-ground components.

    1.3. Quantify the relative contributions to the total peatland carbon stock and the carbon densities of the three main peatland ecosystem types (open peatlands, palm swamps and pole forests).
    1.4. Quantify the uncertainty associated with this estimate of total peatland carbon stock and identify the parameters which are most responsible for this uncertainty.
2. Investigate spatial patterns of floristic composition and diversity in PMFB peatland ecosystems. This objective can be broken down into five steps.
    2.1. Determine the alpha diversity of the two primary types of forested peatland ecosystems (palm swamps and pole forests) and the three non-peatland forest types (*terra firme forests,* seasonally flooded forests, white sand forests).
    2.2. Determine the beta diversity within and among peatland ecosystems (palm swamps and pole forests) and non-peatland forest types (*terra firme forests*, seasonally flooded forests, white sand forests).
    2.3. Determine whether classifications of peatland ecosystems based on their structure and assumed hydroperiod are also reflected in their floristic composition, using new floristic inventory data.
    2.4. Identify the species which are most abundant in peatland ecosystems and ascertain which of these species are shared with surrounding non-peatland ecosystems.
    2.5. Investigate whether the patterns of composition and diversity can provide new perspectives into the importance of the different ecological processes involved in community assembly.
3. Investigate patterns of floristic composition through time in peatland ecosystems. This objective can be broken down into five steps.
    3.1. Determine whether peatlands develop differently in different areas of the PMFB using pollen data from eight cores distributed evenly across two sites.
    3.2. Determine whether the changes in modern vegetation observed in space can be explained as chronosequences resulting from successional processes occurring through time.

3.3. Determine whether there are consistencies in pollen compositional patterns through time across eight different cores from two sites.

3.4. Investigate whether there is a link between past floristic dynamics and current floristic alpha diversity.

3.5. Investigate the utility of using low pollen counts for identifying ecological processes through time by employing novel multivariate statistical approaches.

1.7 Thesis approach

A final more general aim of this thesis is to utilise a novel interdisciplinary approach, incorporating aspects of remote sensing, community ecology and palaeoecology. Individually, these approaches allow patterns occurring through time or space to be described, but integrating these disciplines affords an increased understanding into the processes that govern these spatial and temporal patterns.

Remote sensing techniques have been used in this thesis in order to map the distribution of peatland carbon. This not only provides valuable estimates of landscape scale carbon storage, but also provides an understanding of the landscape scale controls on the distribution of peatland tree communities. Combining this mapping with detailed floristic analysis allows us to understand the landscape scale controls on plant diversity and composition. Palaeoecology provides a method for testing the importance of the historical processes that may determine the spatial patterns of floristic composition and diversity.

2. The distribution and amount of carbon in the largest peatland complex in Amazonia

2.1 Abstract

Peatlands in Amazonian Peru are known to store large quantities of carbon, but there is high uncertainty in the spatial extent and total carbon stocks of these ecosystems. Here, I use a multi-sensor (Landsat, ALOS PALSAR and SRTM) remote sensing approach, together with field data including 24 forest census plots and 218 peat thickness measurements, to map the distribution of peatland vegetation types and calculate the combined above- and below-ground carbon stock of peatland ecosystems in the Pastaza-Marañon Foreland Basin in Peru. I find that peatlands cover 35,600 ± 1,088 km^2 and contain 3.14 (95% CI; 0.44–8.15) Pg C. Variation in peat thickness and bulk density are the most important sources of uncertainty in these values. One particular ecosystem type, peatland pole forest, is found to be the most carbon-dense ecosystem yet identified in Amazonia (1392 ± 696 Mg C ha^{-1}). This novel application of combined optical and radar remote sensing alongside above- and below-ground carbon inventories is recommended for developing regional carbon estimates for tropical peatlands globally. Finally, I suggest that Amazonian peatlands should be a priority for research and conservation before the developing regional infrastructure causes an acceleration in the exploitation and degradation of these ecosystems.

2.2 Introduction

The large carbon stocks of Amazonian forests have been recognised for many years (Dixon *et al.* 1994), and estimates of total Amazonian above-ground biomass (AGB) for *terra firme* (dry land) forest, based on forest census data and remote sensing range from 58 to 134 Pg C (Olson *et al.* 1983; Fearnside 1997; Malhi *et al.* 2006b; Saatchi *et al.* 2007; Saatchi *et al.* 2011; Baccini *et al.* 2012; Mitchard *et al.* 2014). However, there is another significant store of carbon in Amazonia which has not, to date, been incorporated into regional or global carbon budgets: the carbon stored in peatlands. Recent work on the Pastaza-Marañón Foreland Basin (PMFB) in northwest Peru has revealed the presence of extensive and deep accumulations of peat that contain 2–20 Pg C in below-ground stocks (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012). Such values are significant in the context of both national (e.g. 6.9 Pg C held in AGB in Peru (Asner *et al.* 2014a; Asner *et al.* 2014b)) and regional carbon budgets. Hence it is important that the uncertainties in these estimates are reduced.

The PMFB in northwest Peru contains the most extensive peatlands yet discovered in Amazonia (Lähteenoja *et al.* 2012). It is a subsiding foreland basin of c.100,000 km^2 formed during the Cenozoic uplift of the Andes (Dumont *et al.* 1990; Rasanen *et al.* 1990; Dumont *et al.* 1991; Rasanen *et al.* 1992), and possibly still actively subsiding today (Dumont & Garcia 1991). High rainfall, frequent flooding and low lying topography provide the waterlogged and anoxic conditions required for peat formation which, in this geological setting, have enabled significant thicknesses (up to 7.5 m) of peat to accumulate (Lähteenoja *et al.* 2009a; Lähteenoja & Page 2011; Lähteenoja *et al.* 2012). Much smaller peatlands have also been reported from southern Peru (294 km^2, 0.027 Pg C (Householder *et al.* 2012)), central Amazonia (area and carbon stocks unknown (Lähteenoja *et al.* 2013)), and north of the Amazon Basin in the Orinoco delta (7000 km^2, 0.049 Pg C (Vegas-Vilarrubia *et al.* 2010)). In contrast with the better-known but highly degraded and at-risk peatlands of SE Asia (Miettinen *et al.* 2012), those of the PMFB remain largely intact and the threat of destruction from direct human impacts is comparatively low. Climate models suggest that by the end of the 21st century, the western Amazon, unlike SE Asia, is not likely to become significantly drier, though it is predicted to warm significantly (Li *et al.* 2007; Malhi *et al.* 2008). Increasing wet season precipitation over the last 20 years supports this prediction (Gloor *et al.* 2013), although evidence for decreased dry season river discharge over the same time period could suggest enhanced seasonality rather than any change in annual precipitation (Espinoza Villar *et al.* 2009). Therefore, improving carbon storage estimates for the PMFB peatlands is important as they face an uncertain future, which could enhance or diminish this carbon stock depending on climatic and land use change.

Uncertainties in the existing estimate of the amount of carbon stored in the PMFB peatlands derive from a number of factors. The geographical extent and remoteness of the PMFB mean that a relatively small proportion of the peatlands have been mapped in the field, and variability in peat thickness and carbon density at local scales mean that extrapolations from a small number of field observations introduce large uncertainties. In addition, although most of the peatlands are forested, little attempt has previously been made to estimate the above-ground component of the carbon stock using ground data (Guzmán Castillo 2007; Valderrama 2013), which may be valuable for validating recent remote sensing estimates of above-ground carbon stocks that include the PMFB (Asner *et al.* 2014b).

A remote sensing approach is useful for mapping peatland area as it provides detailed information at a regional scale, and is especially promising in the PMFB because the peatlands have been found to be floristically, structurally and topographically distinct from *terra firme* (Lähteenoja & Page 2011; Valderrama 2013). These features are not only distinctive on the ground, but also in satellite data. Landsat products are effective at describing the surface reflectance properties of vegetation and have previously been used to distinguish between peatlands and *terra firme* in this region and elsewhere (Lähteenoja *et al.* 2012). L-band SAR (Synthetic Aperture Radar) products, such as ALOS PALSAR, are able to penetrate the canopy and are effective in characterising forest structure (Imhoff 1995; Castel *et al.* 2002) and biomass in *terra firme* and peatland forests (Mitchard *et al.* 2009; Morel *et al.* 2011; Englhart *et al.* 2012). Additionally, SAR responds to soil moisture and can therefore distinguish between inundated and non-inundated areas (Hess *et al.* 1990). SRTM (Shuttle Radar Topography Mission) data provide an estimate of elevation and are useful for identifying large-scale topographical boundaries within tropical forests (Higgins *et al.* 2011; Higgins *et al.* 2012). The most effective approaches to mapping vegetation and estimating AGB identified so far combine data from multiple sensors, such as those described above, in a single analysis (Walker *et al.* 2010b; Englhart *et al.* 2012; Lehmann *et al.* 2012; Mitchard *et al.* 2012; Reiche *et al.* 2013).

Remote sensing data are not only useful for delineating peatland area but may also be useful for constraining the properties of peat (thickness, bulk density and carbon concentration) that account for much uncertainty in estimating carbon stocks. In the PMFB, peat has been found beneath palm swamp forest, ‘pole’ forests (low stature forest with many thin-stemmed trees), and almost entirely herbaceous ‘open’ communities (Lähteenoja & Page 2011). These different peatland vegetation types are associated with different peat properties and, therefore, differing quantities of below-ground carbon, as has been observed elsewhere in tropical peatlands (Phillips *et al.* 1997; Page *et al.* 1999). If peatland vegetation types can be identified by remote sensing and the amount of below-ground carbon is associated with vegetation type, as has been shown for northern peatlands (Chimner 2004), then detailed vegetation mapping has the potential to better constrain regional carbon estimates.

In addition to the use of data from multiple sensors and using vegetation type as a constraint on peat properties, my approach differs from previous work in the region (Lähteenoja *et al.* 2012) in the following ways:

- Remote sensing classifications have been performed on a single image which spans the entire region, rather than two Landsat scenes individually which can introduce errors in area estimates;
- The number of training points is approximately twice as large as in previous studies, providing more data for the remote sensing classification;
- The number of measurements of peat thickness, bulk density and carbon concentration has also been doubled, providing more representative mean values;
- The contribution of above-ground biomass has been included, utilising recently published species-specific allometric equations for palms (Goodman *et al.* 2013), which are a dominant component of peatland forests.

We thus incorporate vegetation and soil data with a number of suitable remote sensing products (Landsat, ALOS PALSAR and SRTM) to answer the following questions:

1. What is the total area and carbon stock of the peatlands of the PMFB?

2. How large are the above-ground biomass and peat elements of the carbon stock of the peatlands of the PMFB, and how do these vary spatially?

3. What are the relative contributions of the different peatland ecosystem types (pole forests, palm swamps and open peatlands) to the total carbon stock of the PMFB?

4. How accurate are these estimates of peatland area and carbon storage likely to be, and where does the uncertainty lie?

2.3 Methods

2.3.1 Study area and field data

The study area is the PMFB, located in Loreto, northeast Peru (Figure 2.1). Four categories of field data were used (Appendix 2.1): (1) 218 ground reference points, used for remote sensing classification; (2) 24 forest census plots, used to estimate quantities of above-ground carbon; (3) 218 peat-thickness measurement points, used to determine quantities of below-ground carbon; and (4) 33 peat cores, from which C content and dry bulk density were measured. The equal number of ground reference points and peat thickness measurements is coincidental: only 115 of the measurements occur at the same place. Some of these sites were selected as they have been identified as peatlands in previous studies (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012). Other sites were selected based on examination of Landsat data and chosen to provide a representative sample of the range of ecosystem types known to harbour peat.

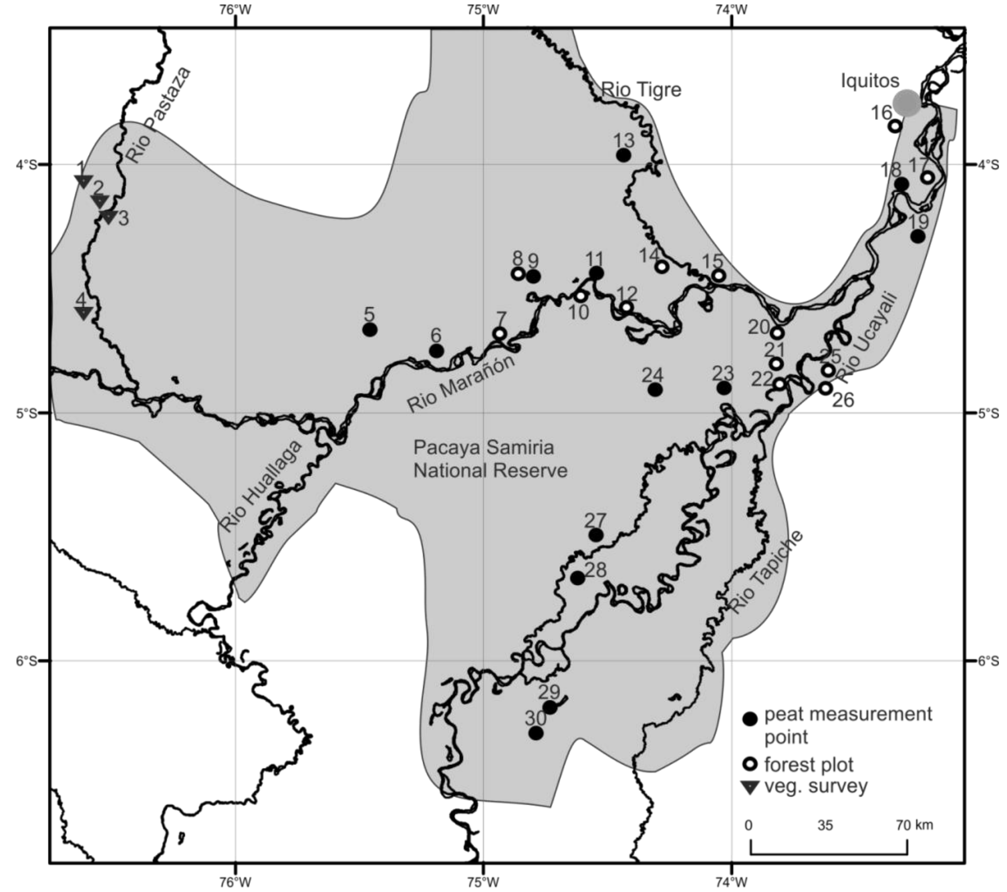

Figure 2.1 The location of 30 clusters of study sites within the PMFB (shaded area). Filled dots represent clusters of peat measurement points; ringed dots represent individual or clusters of 0.5 ha forest census plots; and triangles represent vegetation surveys where peat thickness was not measured (data from (Josse et al. 2007)). The boundary of the PMFB has been delineated using SRTM elevation data and is based on an elevation drop from c.140 to c.120 m above sea level. Numbers correspond to the site names provided in Appendix 2.1.

2.3.2 Ground reference data

Ground reference points consisted of forest census plots, peat measurement points and, in some instances, high resolution satellite imagery acquired from Google Earth (table 2.1). Ground reference points for the peatland classes consisted almost entirely of census plots or peat measurement points. However, where available, high spatial resolution (Geoeye-1 or Worldview-2) images freely available on Google Earth were used to supplement the training data, as at high resolution both palm swamps and open treeless areas could be identified. Additionally five vegetation surveys from the Rio Pastaza were used as ground truth points. These consisted of 30 x 30 m vegetation census plots where all trees >10 cm diameter at 1.3 m were identified (Josse *et al.* 2007). *Terra firme*/occasionally flooded forest, seasonally flooded forest, river and lakes, and urban/river beach ground reference points were assigned by using published data of location and habitat type (Nebel *et al.* 2001; Honorio Coronado *et al.* 2009;

Baraloto *et al.* 2011), and examination of Landsat and Google Earth imagery, as these classes are more easily identifiable. Where forest plots or peat depth measurements were spatially clustered (along a transect for example), then the entire cluster was treated as a single ground truth point. Ground reference points were assigned randomly to either the test or training datasets.

Table 2.1 Summary details indicating the quantity and source of ground reference points in each land cover class.

Land cover class	Forest census plot	Peat measurement point	High resolution satellite imagery	Landsat satellite data	TOTAL
Pole forest	11	6	–	–	17
Palm swamp	19	15	3	–	37
Open peatland	–	8	6	–	14
Seasonally flooded forest	8	11	–	–	19
Terra firme forest	5	–	–	46	51
River beach/ urban area	–	–	–	47	47
Open water	–	–	–	33	33
TOTAL					218

White sand forests

There are a number of areas known to harbour large patches of white sand forest in the region close to the PMFB, particularly on the Rio Nanay (Fine *et al.* 2010). These white sand forests are low in stature and elevation and bear some floristic similarity to peatland pole forest; these similarities caused them to be incorrectly classified as pole forest (i.e. a peat-forming vegetation formation). Therefore, as these patches have been well described and are known not to harbour significant peat deposits, they were masked out of the classification in order to prevent the estimated area of pole forest from being inflated. Other white sand forests, for example in the Allpahuayo-Mishana national reserve and close to the town of Jenaro Herrera, were not similarly confused as they occur at higher elevations.

2.3.2 Satellite imagery

All remote sensing image processing and analysis was conducted in ENVI 5.1 (Exelis VIS). Three data products were used: Landsat Thematic Mapper data from the Landsat 5 satellite (six scenes using bands 4, 5 and 7), Advanced Land Observing Satellite (ALOS)/Phased array Type L-band SAR (PALSAR) (25 scenes using HH and HV polarisations) and Shuttle Radar Topography Mission (SRTM) (Jarvis *et al.* 2008). Details of individual scenes can be found in appendix 2.2.

Satellite image pre-processing

Landsat

Six Landsat 5 TM orthorectified images were acquired from the USGS Earth Explorer (http://earthexplorer.usgs.gov/). Following radiometric calibration, all images were processed to remove the across-path radiometric gradient reported by (Toivonen *et al.* 2006) in a similar manner to (Higgins *et al.* 2012). This gradient causes a linear east to west brightness gradient which prevents seamless mosaicking of images. The gradient was removed in three stages. Firstly the gradient was quantified by extracting pixel values from across the scene in the same relatively homogeneous vegetation type, in this case *terra firme* forest. Secondly, linear regressions were performed on column number against extracted pixel value. R^2 values from these regressions ranged from 0.1 to 0.4 and were based on values from more than 400,000 pixels, and residuals were plotted against fitted values to ensure the trends were linear. Finally, the regression equation was used to create a correction factor which was applied to the original image. Following this detrending process the six-scene seamless mosaic was produced for bands 4, 5 and 7, as these bands have previously been found to be most effective in distinguishing the peatland vegetation types in this area (Lähteenoja & Page 2011).

PALSAR

ALOS PALSAR data was downloaded as 25 post-processed scenes in the FBD (Fine Beam Dual) mode in both the horizontal transmit horizontal receive (HH) and the horizontal transmit vertical receive (HV) polarisation modes with a mid-scene mean incidence angle of 34.3°. ALOS PALSAR data was downloaded from the freely available 50 m resolution 2010 dataset from JAXA (http://www.eorc.jaxa.jp /ALOS/en/index.htm). All 25 scenes were combined as one seamless mosaic. This mosaic was then converted from digital number (DN) values to back scatter (σ0) using the equation: $\sigma^0 = 10 \, . \, log_{10} \, \langle DN^2 \rangle - 83$, following (Shimada *et al.* 2009). Three ALOS PALSAR bands were used in the analysis, HH, HV and a ratio of HH/HV. The ratio was used as it has been shown to be less dependent on topographic variation than the HH and HV bands alone, and therefore provides more direct structural information (De Grandi *et al.* 2011).

SRTM

SRTM digital elevation model (DEM) data were downloaded as four fully processed mosaicked 5 deg x 5 deg tiles at 90 m resolution from CGIAR-CSI (Jarvis *et al.* 2008). These four tiles were then mosaicked together to create a single seamless DEM. No further processing was required.

Final mosaic

The final seven-band image stack consisting of Landsat bands 4, 5 and 7, PALSAR bands HH, HV and HH/HV and an SRTM band was then created (Figure 2.2). The pixel size of all layers was increased to 90 m using a pixel aggregate method, and the PALSAR and SRTM layers were warped to the Landsat layers using observable common features such as river confluences, islands and lakes with a Root Mean Square Error (RMSE) <1 Landsat pixel (30 m) in all cases. Mosaics of the three remote sensing data types can be seen in Figure 2.2.

2.3.3 Image classifications

A supervised classification method was used whereby a number of ‘known pixels’, assigned to predefined classes, were used to train a classifier for all pixels in the image. These known pixels correspond to ground reference points of a known location and class. In this study these classes are land cover or vegetation types corresponding to three peat-forming (pole forest, palm swamp and open peatlands) and four non peat-forming categories (*terra firme*/occasionally flooded forest, seasonally flooded forest, open water, and urban areas/river beaches). 218 ground reference points were used: half of these were used as known pixels to perform the classifications, henceforth referred to as ‘training data’. The remaining ground reference points (referred to as ‘test data’) were used to test the accuracy of the classifications by quantifying how closely the predefined classes of these known pixels correspond to the classes they have been assigned by the classification.

Three classifications were undertaken, firstly using Landsat data alone, secondly using Landsat and PALSAR data, and finally using Landsat, PALSAR and SRTM data. The accuracy of each classification was assessed and the most accurate classification was used to provide the area estimates that I used to generate carbon stock estimates. The support vector machine (SVM) classifier in ENVI was used for all classifications because this approach has been found to produce accurate results with limited field data (Mountrakis *et al.* 2011). In this instance it was also more accurate than either the maximum likelihood or ENVI standard neural network classifiers. The default ENVI SVM classifier was used with the radial basis function (RBF) kernel type. The SVM classifier is a binary classifier but a multiclass classification is achieved by implementing a pairwise classification strategy.

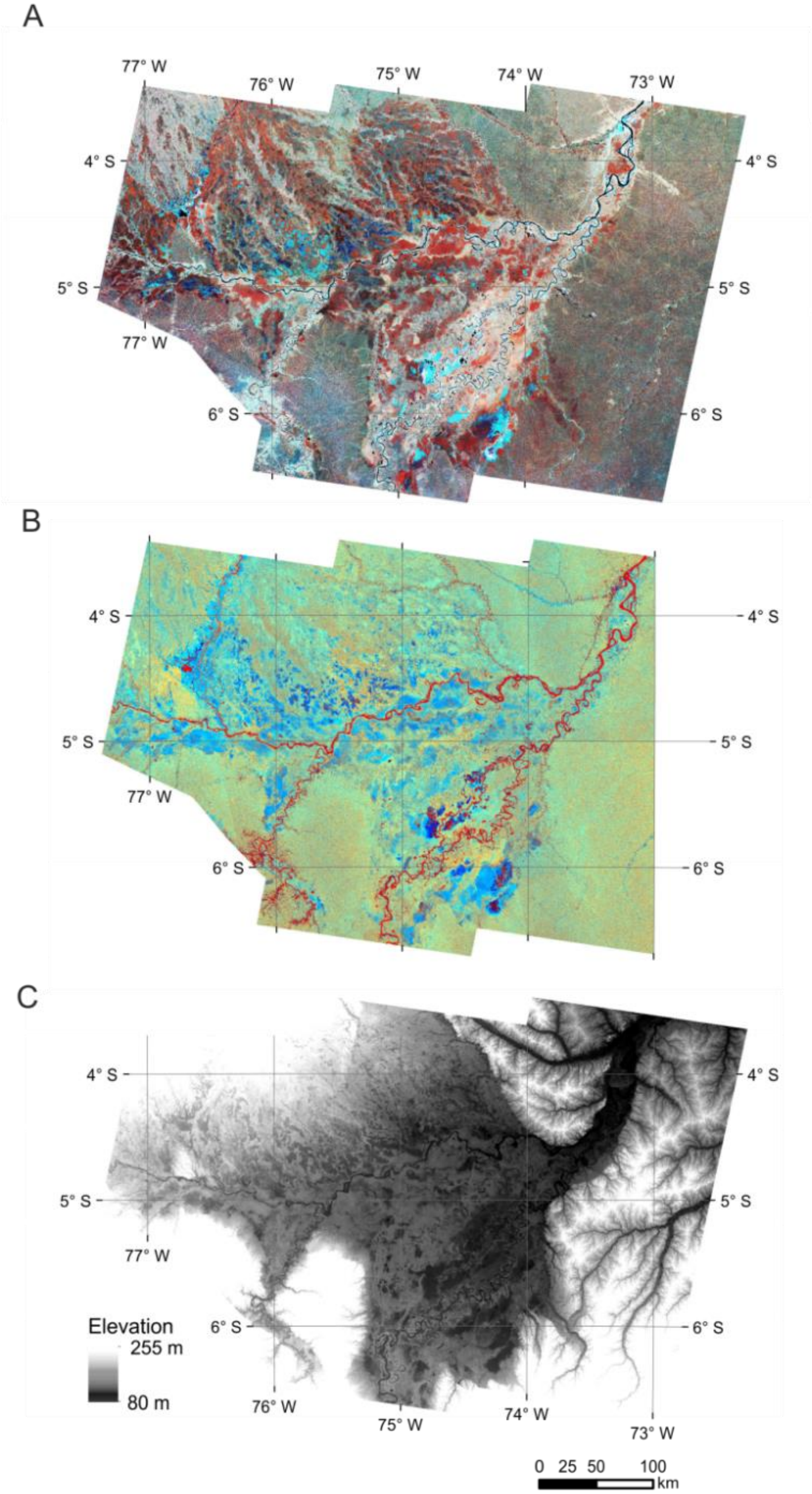

Figure 2.2 Remote sensing data mosaics. Panel A is an RGB composite Landsat image with bands 4, 5, and 7 assigned to red, green and blue, respectively. Panel B is an RGB composite of the PALSAR data, with HH, HV and HH/HV bands assigned to red, green and blue. Panel C is the SRTM data showing estimated metres above sea level.

2.3.4 Above-ground carbon measurements

Twenty-four 0.5 ha forest census plots were established following the RAINFOR (Amazon Forest Inventory Network) protocol (Phillips *et al.* 2009). Diameters of all trees with dbh (diameter at breast height, 1.3 m) ≥10 cm were recorded and each tree was identified to species (c. 70% of individuals) or genus level (c. 30% of individuals) by comparison with specimens held in herbariums Herrerense (HH) and Amazonense (AMAZ). Stem height of palms was measured using a clinometer or a laser range finder. The plots were established in five field seasons in 2008, 2009, 2010, 2012 and 2013. Biomass of dicot trees was estimated using the pan-tropical three-parameter (dbh, wood density and E) equation of (Chave *et al.* 2014). Species-specific wood density values were obtained from a local wetland dataset where available (Valderrama 2013), and the global wood density database otherwise (Chave *et al.* 2009; Zanne *et al.* 2009). These sources accounted for more than 95% of calculations in all plots. When species-specific wood density values were not available then a genus-level, or family level mean were used, and if no family-level values were available then the mean plot wood density was used, following (Baker *et al.* 2004b). Palm biomass was estimated using species-specific allometric equations (Goodman *et al.* 2013), which require stem or total height as the only parameter. Above-ground carbon was assumed to be 50% of above ground biomass.

2.3.5 Below-ground carbon measurements

Three measurements are required to determine quantities of below-ground carbon: peat thickness, dry bulk density and carbon concentration. Peat thickness was measured at each peat measurement point using a Russian-type corer (Jowsey 1966), peat thickness measurements were taken from both the edges and centre of the peatlands, though the number of measurements made varied between sites. Stratigraphic units were visually assessed in the field and assigned to peat, ‘clayey peat’, or ‘mud’ (deposits dominated by minerogenic sediments) following (Lähteenoja *et al.* 2012). Deposits assigned as ‘mud’ were excluded from all further analysis and were not included in peat thickness measurements. Thirteen peat cores from different vegetation types were analysed as part of this study. Dry bulk density (dry weight (g) / volume (cm^3)) was calculated on 100 cm^3 samples taken every 50 cm from the peat core and dried at

80°C for 24 hours or until a constant weight was reached. Carbon concentration was primarily determined using previously published data from 30 cores (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012), where carbon concentration was measured every 50 cm down-core. Additionally, ten further cores were used in which carbon concentration was determined in four samples from 5, 10, 20 and 30 depth. All carbon concentration estimates were made using an Elementar Vario Microcube.

2.3.6. Carbon stock calculations

The above- and below-ground peat carbon pool was calculated using the equation below, following (Page *et al.* 2011):

$$CP = \sum_{p=1}^{pv} \frac{D_p \, \rho_p \, C_p \, A_p}{10^{12}} + \frac{AGC_p \, A_p}{10^{12}} \qquad (1)$$

Where: *CP* is the total peatland carbon pool (Pg), *p* represents each peatland ecosystem type, pv represents the total number of peatland ecosystem types, D_p is peat thickness (m), ρ_p is dry bulk density (kg m^3), C_p is carbon concentration (expressed as the percentage mass of carbon in the dry peat), AGC_p is above-ground carbon (kg m^2), and A_p is area (m^2).

In order to generate mean values and confidence intervals for the carbon stock estimates for each peatland ecosystem type, a bootstrap resampling and randomized Monte Carlo method was used as the data are not normally distributed. Firstly, measured values for each variable of equation 1 were grouped into the three peatland ecosystem types providing a distribution of values for each variable in each ecosystem type, e.g. peat thickness in pole forest or bulk density in palm swamps. These distributions of values were then resampled with replacement 1000 times, generating a series of simulated bootstrapped distributions for each variable in each ecosystem type. A randomly selected, single value from each simulated distribution was then entered into equation 1. This process was repeated 10^7 times, to generate a distribution of simulated carbon stock values for each ecosystem type, from which the mean value and 95% confidence limits could be extracted.

Confidence intervals for peatland area were generated separately using the method described by (Olofsson *et al.* 2013), whereby the confusion matrix of the classification was used to estimate map classification error and 95% confidence intervals for the area of each peatland ecosystem type. These 95% confidence intervals were used to generate a simulated distribution of 1000 values of area for each peatland ecosystem type.

2.3.7 Sensitivity Analysis

To assess the importance of each input component (D_p, ρ_p, C_p, A_p and AGC_p, as defined in Equation 1) in determining the carbon stock output in each peatland ecosystem type, ranked partial correlation coefficients (RPCC's) were used. RPCC's assess the significance of the relationship between each input component and the carbon stock estimate, whilst controlling for variation in the other terms (Poulter *et al.* 2010). This was done by extracting 1000 simulated carbon stock values and the corresponding input values; RPCC's were then calculated for each input component in each peatland ecosystem type. All statistical analysis was performed in R (R Core Team 2012b).

2.4. Results

2.4.1. Carbon stock of the PMFB

The total peatland area of the PMFB is estimated to be 35,600 ± 1,088 km^2 (Table 2.2). Palm swamps account for the majority of the peatland area (78 ± 1.5%), with pole forests and open peatlands accounting for 11 ± 1.7% and 11 ± 0.3%, respectively (Table 2.2). Palm swamps have the greatest total carbon stock (2.3Pg C), followed by pole forests (0.5 Pg C) and open peatlands (0.3 Pg C), giving a total peatland carbon stock of 3.14 Pg C for the PMFB. However, pole forests store carbon at the greatest density (1391 ± 710 Mg C ha^{-1}). All three peatland ecosystem types store a greater amount of carbon per unit area than neighbouring *terra firme* forest (Figure 2.4).

Overall, approximately 90% of the carbon in these peatland ecosystems is stored below ground in peat, with the remaining 10% stored in AGB, though this ratio varies between peatland ecosystem types. Pole forests in this study are always located on thick peats (>0.9 m, mean 3.15 m) and have low above-ground biomass stocks due to their low stature and thin trunks. Palm swamps occur on both thin and, less typically, thick peats, and store large amounts of carbon in AGB, comparable to quantities of AGB found in *terra firme* forests (Figure 2.4).

Un-forested (open) peatlands were assumed to have negligible AGB with all carbon stored in peat, which was variable in thickness. Open peatlands had the lowest carbon density, as although their below-ground carbon density was approximately equivalent to that of palm swamps, the lack of appreciable AGB reduced their overall carbon stock (Figure 2.4).

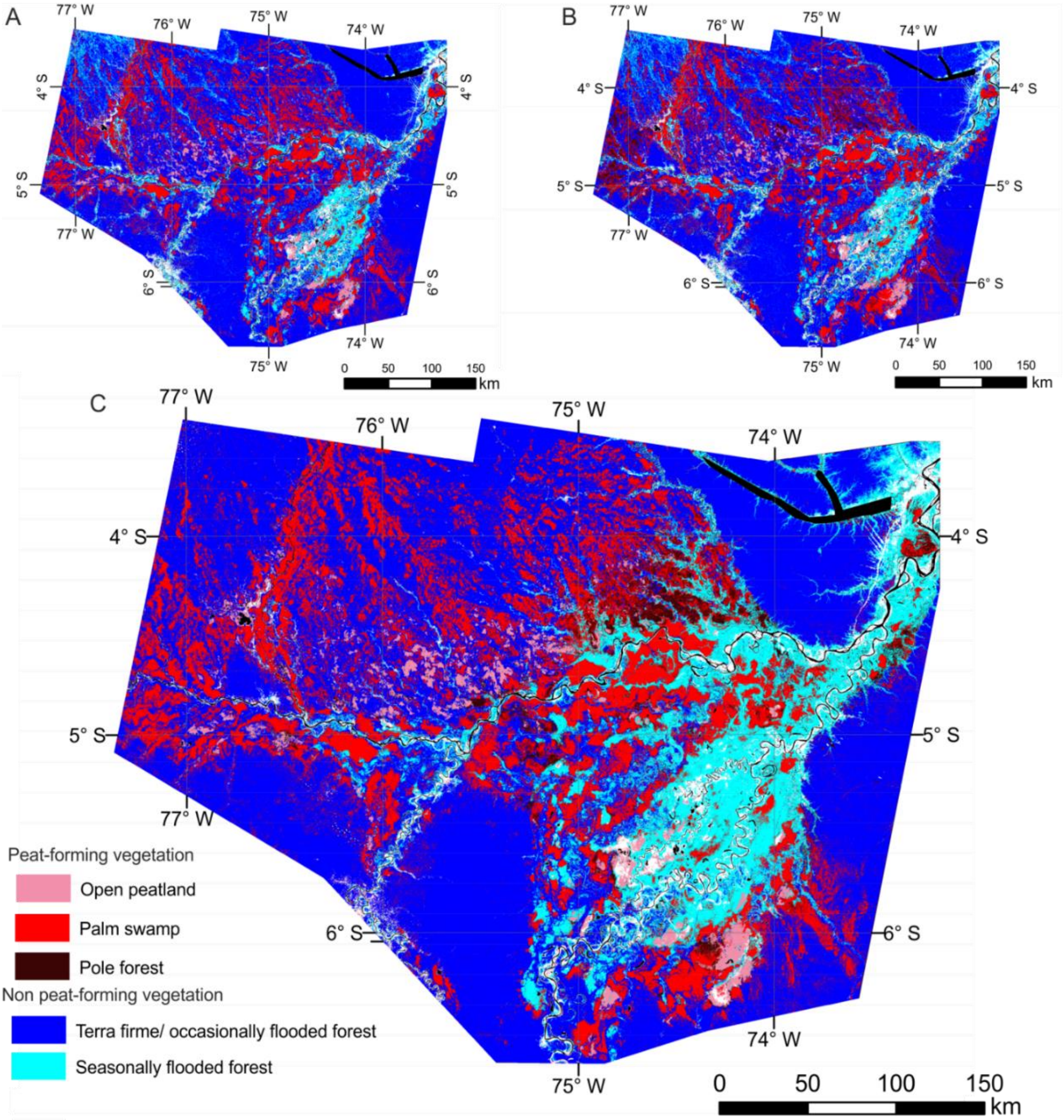

Figure 2.3 The three support vector machine supervised classifications of the study area, created from Landsat bands 4, 5 and 7 alone (panel A), Landsat bands 4, 5 and 7 and PALSAR bands HH, HV and HH/HV (panel B) and finally Landsat bands 4, 5 and 7, PALSAR bands HH, HV and HH/HV and an SRTM band (Panel C).

Table 2.2 Summary of above- and below-ground carbon stocks in different peatland ecosystem types within the PMFB and the mean, minimum and maximum values of the parameters used to calculate these figures and their corresponding 95% confidence intervals. AGC and BGC refer to above- and below-ground carbon stocks respectively. Confidence intervals for the carbon stock estimates are provided based on bootstrap resampling and randomized Monte Carlo method.

Peatland ecosystem type		Area (km^2)	Dry bulk density (g cm^3)	Peat thickness (cm)	C conc. (%)	Ash content (%)	AGC (Pg)	BGC (Pg)	AGB:BGB	Total C stock (Pg)	C density
Pole forest	Mean	3,686	0.084	315	50.5	6.9	0.030	0.494	0.06	0.524	1422
	95% CI	±810	±0.007	±26.8	±1.6	±1.1	0.009–0.074	0.110–1.131	0.13	0.138–1.174	374–3185
	Min	–	0.01	90	23.2	0.5	–	–			
	Max	–	0.239	660	59.1	25.0	–	–			
	n		143	80	125	113					
Palm swamp	Mean	27,732	0.099	173	44.0	10	0.263	2.073		2.336	842
	95% CI	±1101	±0.009	±23.4	±2.7	±3.1	0.138–0.355	0.012–5.738		0.268–5.997	97–2162
	Min	–	0.028	0	24.0	1.3	–	–			
	Max	–	0.181	540	55.6	29.8	–	–			
	n		44	105	61	25					

Open peatland	Mean	4,181	0.051	265	48.5	8	–	0.277		0.277	663
	95% CI	±222	±0.016	±37.8	±2.8	±2.5				0.034–0.974	81–2329
	Min	–	0.012	50	27.7	3.5	–	–			
	Max	–	0.183	450	56.1	24.3	–	–			
	n		31	38	33	20					
TOTAL		**35,600**					**0.293**	**2.844**		**3.137**	
	95% CI									**0.440–8.145**	

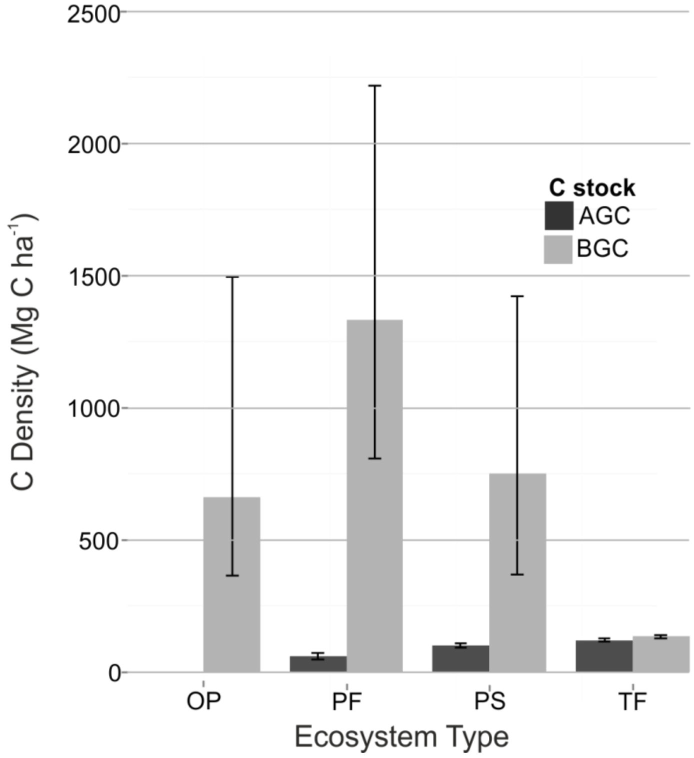

Figure 2.4 Above- and below- ground carbon density of the three peatland ecosystem types: open peatlands (OP), palm swamps (PS), pole forests (PF) and mean values for Amazonian *terra firme* forests (TF). The negligible AGC of open peatlands is assumed to be zero. *Terra firme* above-ground values are taken from (Baker *et al.* 2004b) and below-ground values from (Malhi *et al.* 2009). Error bars represent standard errors.

2.4.2 Distribution of peatland ecosystem types

Peatlands in this region are not randomly distributed across the landscape but instead appear to be largely confined to the low-lying areas of the PMFB (Figure 2.3). Whilst individual pixels in upland areas may have spectral and/or structural similarities to peatland vegetation, they can be assumed to be part of the upland forest mosaic in the form of tree fall gaps, heavily degraded forest, small isolated swamps in topographic depressions, or patches of white sand forest. Some of these areas may contain shallow peat deposits, but their inclusion in the classification would lead to increased confusion between *terra firme* forest and peatlands and potentially overestimations of peatland area. Furthermore, the different peatland ecosystem types show a strong spatial pattern across the PMFB (Figure 2.3). Pole forests are apparently restricted to the north-eastern part of the basin; palm swamps are most extensive in the Pacaya-Samiria National Reserve and bordering the Rio Pastaza (see Figures 2.1 and 2.3), and open peatlands are most common in the northwest and far south of the region (Figure 2.3).

2.4.3 Performance of remote sensing classification

The classification performed well when tested against an independent dataset (Table 2.3 and Figure 2.5), with a mean, minimum and maximum user's accuracy (the proportion of the classified area that corresponds to the correct class based on ground reference points) of 91%, 79% and 100%, and an overall kappa coefficient (coefficient of agreement accounting for agreement occurring by chance) of 0.94. The most accurately mapped vegetation class was *terra firme* forest; pole forest was the least accurately mapped. The inclusion of the three different satellite products, including optical (Landsat) and radar (ALOS PALSAR and SRTM) data, improved the accuracy of the classification for most classes apart from flooded forests (Figure 2.5) with mean user's accuracy, producer's accuracy (the proportion of ground reference pixels that have been correctly classified) and kappa coefficients all increasing with the addition of each product (Table 2.4).

Table 2.3 Confusion Matrix for the final SVM classification using Landsat, PALSAR and SRTM data showing the number of pixels per class in both the training data set (used to generate the classification) and test data set (used to assess the accuracy of the classification), how data from these two independent datasets correspond and where errors of omission and commission are found. Additionally the total number of ground reference points (GRPs) for each class and the percentage accuracy for each training and test class are shown. Abbreviations refer to land cover classes; Palm swamps (PS), open peatlands (OP), pole forest (PF), seasonally flooded forest (FF), *Terra firme*/occasionally flooded forest (TF), urban areas and river beaches (UB) and open water rivers and lakes (RL).

	PS-test	OP-test	PF-test	FF-test	TF-test	UB-test	RL-test	Total	Total GRPs	Accuracy (%)
PS-train	538	0	41	0	103	0	0	682	37	78.9
OP-train	0	425	0	0	0	27	0	452	12	94.0
PF-train	10	0	88	2	10	0	0	110	17	80.0
FF-train	12	1	9	149	2	13	0	186	19	80.1
TF-train	2	0	0	0	1881	3	0	1886	53	99.7
UB-train	0	20	0	0	0	1238	0	1258	47	98.4
RL-train	0	0	0	0	0	0	1042	1042	33	100
Total	562	446	138	151	1996	1281	1042	5616	218	
Accuracy (%)	95.7	95.3	63.8	98.7	94.2	96.6	100			

Landsat data were generally effective at distinguishing land cover classes, and successfully identified some of the areas of peatlands. However, the Landsat classification was not able to differentiate between pole forest and palm swamp, or between pole forest and *terra firme* forests (Fig 2.5). This was improved by the addition of ALOS PALSAR data, which can identify the structural differences between the forest types because the backscatter signal of pole forest (many small trees) is very different to that of both *terra firme* forest (fewer but larger trees) and palm swamp forest (many palm species with no lateral growth). Finally, the use of SRTM data further improved the classification by constraining it to areas of suitable low-lying topography within the PMFB (Figure 2.5 and Table 2.3).

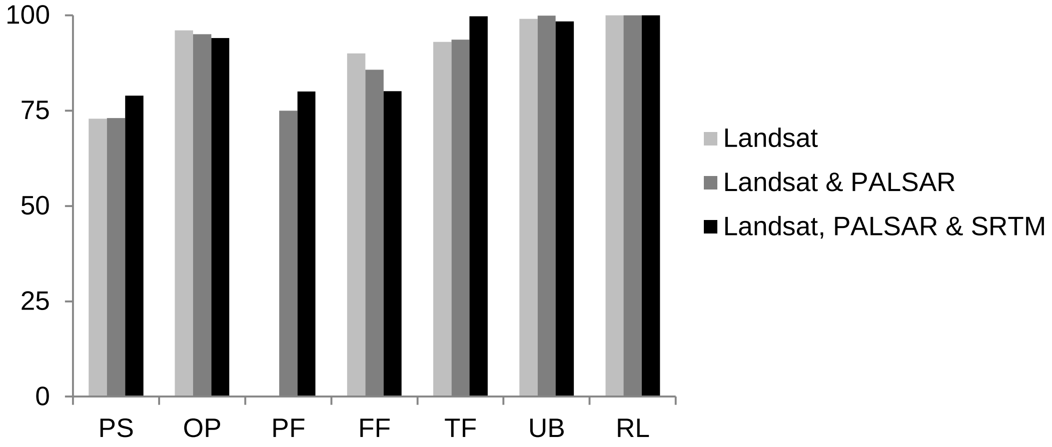

Figure 2.5 The proportion of the classified area that corresponds to the correct class based on ground reference point (user's accuracy) assessment for three SVM classifications using only Landsat (light grey), Landsat and PALSAR (dark grey) and Landsat, PALSAR and SRTM (black).

Table 2.4 Mean user's and producer's accuracy and kappa coefficients for the three SVM classifications, using Landsat, PALSAR and SRTM data.

Classification	**User's accuracy (%)**	**Producer's accuracy (%)**	**Kappa coefficient**
Landsat data only	75	80	0.90
Landsat and PALSAR data	89	83	0.92
Landsat, PALSAR and SRTM data	91	92	0.94

2.5. Discussion

2.5.1. Carbon stock of the peatlands of the PMFB

This analysis confirms the importance of the peatlands of the PMFB as a substantial store of carbon (best estimate 3.14 Pg C), and the most carbon-dense landscape in Amazonia, storing 892 ± 535 Mg C ha^{-1}. Of the three peatland vegetation types, pole forest is the most carbon-dense with 1391 ± 710 Mg C ha^{-1}. Compared with typical *terra firme* forests which store 63-190 Mg C ha^{-1} in AGB (Baker *et al.* 2004b; Malhi *et al.* 2006b) and a similar amount (132 Mg C ha^{-1}) below ground (Quesada *et al.* 2011), this study therefore suggests that peatland pole forests are, by a large margin, the most carbon-dense forest type in Amazonia.

My best estimate of the total PMFB peatland carbon stock of 3.14 Pg C, including below-ground carbon, is nearly 50% of a recent estimate of above-ground carbon for the whole of Peru (6.9 Pg C (Asner *et al.* 2014b)), whilst only occupying 3% of the area of Peruvian forest (Saatchi *et al.* 2007). It is therefore apparent that these peatlands account for a very large proportion of carbon stocks at regional and national levels and therefore need to be included in total carbon storage estimates. Where another study (Saatchi *et al.* 2011), estimated below-ground biomass stocks for Amazonia, a simple positive relationship between AGB and BGB was assumed. In the PMFB the reverse of this relationship is generally true, illustrating that carbon stocks in peatlands cannot be estimated accurately with more general methods developed for pantropical carbon stock estimates.

AGB typically contributes 10% to the overall carbon stock of these peatland ecosystems; however, this varies between peatland ecosystem types. Unsurprisingly, low-stature pole forest has low AGB (61.8 ± 9.8 Mg ha^{-1}). Previous topographical and geochemical studies have indicated that pole forest occurs on domed, ombrotrophic (i.e. entirely rain-fed) peatlands (Lähteenoja & Page 2011). The consequently nutrient-poor, acidic conditions exclude many species and presumably also lead to low net primary productivity and, as a result, lower AGB compared to upland forests. Similar structural characteristics are seen in the nutrient-poor white sand forests of Amazonia (Anderson 1981; Fine *et al.* 2010) and on Southeast Asian ombrotrophic peatlands (Anderson 1983; Page *et al.* 1999). Palm swamps, in contrast, have an above-ground carbon density (100.9 ± 7.7 Mg ha^{-1}) that is broadly comparable with surrounding *terra firme* forest (c. 120 Mg C ha^{-1} (Baker *et al.* 2004b)). The high AGB of the dominant palm species, *Mauritia flexuosa*, contributes substantially to the high above-ground carbon density of the palm swamps. *M. flexuosa* regularly grows to heights greater than 30 m, and due to the lack of lateral growth in the canopy, can achieve high stem densities (>150 individuals ha^{-1}). Moreover, the use of allometric equations that have not specifically been developed for palms underestimates the biomass of tall, adult *Mauritia (Goodman et al. 2013).*

2.5.2 Sources of uncertainty

The uncertainty associated with this estimate of the total PMFB peatland carbon stock remains substantial (0.4–8.1 Pg C), but significantly lower than previous published estimates (1.7-19.0 Pg C (Lähteenoja *et al.* 2012)). There is uncertainty associated with each component of the carbon stock calculation and the magnitude of uncertainty within each component varies with vegetation type. Overall, the source of greatest uncertainty is variation in peat thickness and bulk density (Table 2.5). In palm swamps, peat thickness provided the greatest uncertainty due to large variation in peat thickness within and between sites, while in the pole forests, which consistently grow on thick peat, bulk density was the most important source of uncertainty. Systematically increasing these measurements across all peatland ecosystem types and in all areas across the basin would provide more reliable estimates. However, the substantial variation in peat thickness and bulk density occurring both within and between sites suggests that a high degree of uncertainty will likely persist regardless of sampling effort because of the complexity and dynamism of the PMFB landscape. My analysis indicates relatively little uncertainty associated with the estimated peatland area (Table 2.5). Although this is encouraging, there is an assumption within these uncertainty estimates that the training and testing ground reference points provide complete coverage of the study area, which is not the case. More ground reference points in data-deficient areas are needed to test the classification further. Root biomass is another source of uncertainty in my analysis: although fine roots form part of the peat matrix and are incorporated in my BGC estimates, coarse root biomass is not included in my analysis.

Further work on coarse root volume and biomass is required in these ecosystems, to account accurately for this uncertainty.

Table 2.5 The relative importance of each input component in determining carbon stock for each peatland ecosystem type. Importance is defined on the basis of partial ranked correlation coefficients between each input variable and the final output (carbon stock).

Peatland ecosystem type	Component of carbon stock calculation	Partial rank correlation coefficient (Spearman's ρ)
Pole forest	Peat depth	0.88
	Peatland area	0.25
	Dry bulk density	0.89
	Carbon concentration	0.56
	Above-ground biomass	0.17
Palm swamps	Peat depth	0.94
	Peatland area	0.11
	Dry bulk density	0.81
	Carbon concentration	0.56
	Above-ground biomass	0.38
Open peatlands	Peat depth	0.88
	Peatland area	0.04
	Dry bulk density	0.92
	Carbon concentration	0.49

One surprising finding is that my carbon stock estimate is c. 50% of the previous best estimate of 6.232 Pg (Lähteenoja *et al.* 2012), even with the addition of the AGB component. The disparity between these estimates is partly due to the difference in estimates of total peatland area: this more thorough approach yields an area of 35,600 ± 1088 km^2, which is 8258 km^2 smaller than the previous estimate of 43,858 km^2. However, this decreased area only accounts for a decrease of 1.17 Pg C, which equates to approximately 38% of the disparity in C stock estimates. The increased number of peat thickness and bulk density measurements reduced the carbon stock estimate slightly, reducing mean peat thickness from 2.48 to 2.39 m and bulk density from 0.083 to 0.079 g cm^{-3}, although it is encouraging that increasing the number of sites and measurements did not cause large changes in mean peat depth and dry bulk density. The process of constraining peatland carbon stock estimations by three vegetation types rather than averaging across all individual sites also contributed to reducing this estimate of overall carbon stock. The thickest peat deposits under pole forest account for a small proportion of the total peatland area while palm swamps, although more extensive, store less carbon per unit area.

2.5.3 The role of multiple remote sensing products

I have shown that combining Landsat, ALOS PALSAR and SRTM products is more effective in distinguishing different ecosystem types in my study area than using any one product alone. In particular, including PALSAR and SRTM datasets in this analysis improved our ability to distinguish between the swamp classes. I recommend the use of this data fusion approach in the future, though I stress that spatial uncertainties remain in the map, particularly to the west of the study area where there are currently few ground reference points. The bootstrap analysis I performed allowed these uncertainties to be propagated through to my carbon estimates.

2.5.4 Distribution of peatland ecosystem types

A key finding of this study is the strong spatial pattern of the different peatland ecosystem types. Pole forests are largely limited to the north-eastern areas and are underlain by the thickest, oldest and probably most ombrotrophic peat deposits (Lähteenoja & Page 2011; Lähteenoja *et al.* 2012). The correspondence between thick peat and pole forest may be the result of long term geomorphological stability which has allowed peat to accumulate above the maximum flood level, leading to ombrotrophic conditions, low nutrient status and vegetation succession to pole forest. This explanation is supported by geological evidence that this north-eastern area has experienced decreasing frequency of river avulsions and increased stability since the isolation of the Rio Tigre from the Rio Pastaza c.8000 years BP (Bernal *et al.* 2011). The build-up of peat above the maximum flood level during the course of its development is supported by geochemical evidence which records a transition from high- to low-nutrient status through the peat profile (Lähteenoja & Page 2011), consistent with models of fen to bog transitions in peatlands at high latitudes (Hughes & Barber 2004). Palm swamps, by contrast, are typically found close to large and geomorphologically dynamic rivers (Rasanen *et al.* 1992), and minerogenic intrusions in the peats formed under this vegetation provide evidence of frequent flooding (Lähteenoja & Page 2011). I suggest that frequent fluvial influence has maintained higher nutrient input throughout their development, up to the present day, and that in these geomorphologically dynamic settings there has not been sufficient time for ombrotrophic conditions to develop. Open peatlands are found primarily close to large and dynamic rivers (Dumont & Garcia 1991), and while their depth and nutrient status vary (Lähteenoja *et al.* 2009a; Lähteenoja & Page 2011), radiocarbon dating from the two deepest sites shows they are significantly younger than pole forests (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012). I suggest that open peatlands may represent an early successional community in the development of peatland ecosystems.

Work in progress on the vegetation history of these peatlands will help to test these hypotheses about potential landscape controls on the distribution and development of the different peatland vegetation types. A further vegetation type that is known to harbour peat is seasonally flooded forest (Lähteenoja *et al.* 2009b). This peatland ecosystem type was excluded from this analysis because it is uncommon and poorly known (only two such sites, locally known as *tahuampa*, have been confirmed to hold peat). Further fieldwork is required to quantify its contribution to the carbon stock.

2.5.5 Contribution of PMFB to the tropical peatland carbon pool

In terms of tropical peatlands globally, the peatlands of the PMFB account for 6.5% of their area and 3.5% of their carbon stocks (Page *et al.* 2011). Whilst these figures are small in comparison to the deeper and more extensive peatlands of Southeast Asia, the conservation importance of Peruvian peatlands should not be dismissed. Southeast Asian peatlands have experienced decades of destruction, leading to a 50% loss of intact peat swamp forest (Miettinen *et al.* 2012), and large carbon emissions (Page *et al.* 2002; Hooijer *et al.* 2010). At current rates of destruction they would be lost entirely by 2030 (Miettinen *et al.* 2012). Peruvian peatlands, on the other hand, remain almost entirely intact, though they face an increasing range of threats including degradation by large-scale cutting of palms for fruit, hydrocarbon extraction, illegal logging, oil palm plantation expansion, and direct disturbance by proposed rail and road links from the city of Iquitos to the rest of Peru, as well as the knock-on consequences of improved access (Finer & Orta-Martínez 2010; Gutiérrez-Vélez *et al.* 2011; Finer *et al.* 2014). I therefore suggest that the peatlands of the PMFB should be a priority for carbon-focussed conservation strategies, because they constitute a large carbon stock, and there is an opportunity to protect these areas before infrastructure develops sufficiently for them to be degraded and exploited.

Accurate carbon stock information for tropical peatlands is required to inform initiatives such as REDD+ (Reducing Emissions from Deforestation and Degradation) (Gibbs *et al.* 2007; Murdiyarso *et al.* 2013). To my knowledge this is the first study in tropical peatlands to estimate both above- and below-ground components of the carbon pool at a regional scale. Estimates of below-ground carbon stocks elsewhere in tropical peatlands have been based on a small number of individual peatlands (Jaenicke *et al.* 2008; Householder *et al.* 2012), or on historical, continental or national level inventories, which have little empirical basis and are difficult to verify (Anderson 1983; Bord na Móna 1984; Brown *et al.* 1993). AGB estimates have been developed to assess the efficacy of remote sensing products and have used limited ground data (Ballhorn *et al.* 2011; Ballhorn *et al.* 2012; Kronseder *et al.* 2012). I suggest that the method applied here, using extensive above- and below-ground field data alongside multiple remote sensing products, is the most effective way of generating the kind of regional and national carbon stock inventories required by initiatives such as REDD+.

2.5.6 Conclusions

This investigation provides the most accurate estimates to date of the carbon stock of an area that is the largest peatland complex in the Neotropics, and confirms the status of the PMFB as the most carbon-dense landscape in Amazonia. The novel approach of combining optical and radar remote sensing with above- and below-ground carbon inventories is shown to increase the accuracy of regional carbon stock estimates and is recommended for developing regional carbon estimates for tropical peatlands globally. The PMFB remains almost entirely intact, but threats to its persistence are increasing. If Amazonian peatlands are to continue to act as a carbon store and avoid the fate of their counterparts in Southeast Asian, then they must be a conservation and research priority.

3 Floristic composition and diversity of lowland peatland ecosystems in Northern Peru

3.1 Abstract

The extensive peatland ecosystems of northern Peru are the most carbon dense ecosystems in Amazonia. However, despite their importance as a carbon stock, their floristic composition remains largely undescribed. Understanding patterns of diversity in these environmentally extreme ecosystems is important for quantifying β-diversity across the region which contains some of the world's most diverse forests, and for understanding determinants of diversity more generally in tropical forests. Here I explore patterns of tree diversity and composition in two peatland ecosystem types – palm swamps and pole forests – using 26 forest census plots. I place these results in a regional context by making comparisons with secondary datasets representing the three major ecosystem types of western Amazonia: *terra firme* forests (29 plots), white sand forests (23 plots) and seasonally inundated forests (11 plots).

I find that peatland ecosystems have extremely low (within-plot) α-diversity. In particular, pole forests have perhaps the lowest levels of diversity recorded in Amazonia with an estimated 20 species per 500 stems and a Fisher's α of 4.6. Despite substantial variation within both peatland ecosystem types (high β-diversity), they are compositionally different from each other as well as from other ecosystems in the region. No species are endemic to these peatlands based on this sample; instead, many generalist species, as well as specialists from other ecosystem types, particularly white sand and floodplain forests, dominate the peatlands. I suggest that historical geomorphological dynamism, alongside environmental filtering and limited dispersal, is responsible for structuring patterns of composition and diversity in these ecosystems. Amazonian peatland ecosystems play an important role in maintaining regional β-diversity and have shed light on diversity patterns and community assembly mechanisms. This biological value should be incorporated alongside their carbon storage capacity to add to their status as a conservation priority.

3.2 Introduction

The forests of West Amazonia are floristically remarkable as they are among the most diverse (local scale alpha-diversity) communities on Earth (Gentry 1988b; Valencia *et al.* 1994; Ter Steege *et al.* 2003). Additionally, West Amazonian forests harbour communities with numerous endemic species (e.g. white sand forest) (Fine *et al.* 2010) and exhibit high species turnover over small spatial scales (Gentry 1988a; Tuomisto *et al.* 1995; Tuomisto *et al.* 2003). Previous studies of floristic composition in this region, have been largely limited to non-inundated (*terra firme*) forests, although seasonally flooded forests have been included in some analyses (Nebel *et al.* 2001; Fortunel *et al.* 2014). Recently, extensive peatland ecosystems in the Pastaza Marañon foreland basin (PMFB) have been described in terms of their substantial below-ground carbon stocks (Lähteenoja *et al.* 2012; Draper *et al.* 2014). The PMFB at 120,000 km^2, is the largest area of contiguous wetland in Amazonia, and yet the floristic composition and diversity of the peatlands remains largely undescribed, representing a substantial omission in our understanding of this landscape.

Examination of satellite data, field observations and geochemical data suggest that the PMFB holds a diverse range of wetland ecosystem types, many of them peat-forming (Kalliola *et al.* 1991a; Irion & Kalliola 2009; Lähteenoja & Page 2011; Draper *et al.* 2014). Some of these ecosystem types (e.g. palm swamps and open herbaceous ecosystems) fit into existing wetland classifications (Prance 1979; Encarnación 1985; López Parodi & Freitas 1990; Kalliola *et al.* 1991a; Junk *et al.* 2011). Others (e.g. pole forests) have been observed previously (García Villacorta *et al.* 2011), but their floristic composition remains largely undescribed, making it impossible to place these into existing wetland classifications. Indeed, it remains to be shown quantitatively that these ecosystem types, which are largely based on forest structure, qualitative assessment of apparent hydroperiod and ad hoc floristic observations, represent discrete floristic assemblages. The peatlands of the PMFB are distributed across two designated RAMSAR wetlands of international importance, namely the Pastaza fan (site number 1174) and the Pacaya Samiria national reserve (site number 546) (Ramsar 2015). Quantifying the contribution the peatlands make to regional β-diversity is a research priority, which has implications for further developing effective protected areas, and understanding the mechanisms that drive community assembly in this region.

In addition to the high floristic and structural variation that may occur within peatlands, remote sensing and field observations also suggest that there are structural and compositional similarities between peatland and *terra firme* vegetation that have not previously been appreciated. Peatland pole forests, for example, appear to share structural properties (short and thin stems) with white sand forests as well as a number of white sand specialist tree species (Lähteenoja *et al.* 2009a; Roucoux *et al.* 2013; Draper *et al.* 2014; Kelly *et al.* 2014). If this compositional similarity is found extensively in peatland forests, it would have implications for conservation, as peatlands could be providing previously unappreciated migratory corridors, as well as a greater total area of suitable habitat for white sand specialist plant and animal species. This is important as white sand forests harbour a number of endemic and endangered tree and bird species and are an established conservation priority (Alonso *et al.* 2013), whilst peatlands, as yet are not.

Although the vegetation of Amazonian peatlands is almost entirely undescribed, swamps more generally (which may or may not be peat forming) have received greater attention. For example, in a recent study Pitman *et al.* (2014) reviewed the literature regarding the tree communities of Amazonian swamps and summarised three general findings: (1) swamps are dominated by one or more species of arboreal palm, most commonly *Mauritia flexuosa* (Kahn & Mejia 1990; Endress *et al.* 2013; Pitman *et al.* 2014); (2) swamps are less diverse at local scales (low α-diversity) than neighbouring *terra firme* forests (Richards 1969; Prance 1979; Dumont *et al.* 1990; Pitman *et al.* 2014); (3) there is high variability in composition among sites (high β-diversity) and through time (Roucoux *et al.* 2013). Pitman *et al* (2014) also demonstrated the importance of surrounding upland vegetation in determining the composition of patches of swamp forests, showing that > 80% species found in swamps were also found in upland plots, and that < 10% of species were restricted to swamps. However, these sites are predominantly small patches of forest within upland forest; larger patches may show different patterns, as patch size has been suggested to be an important determinant of diversity in tropical forests (ter Steege *et al.* 2000)

Currently the only detailed floristic work in tropical peatlands comes from Southeast Asia, where there are large areas of peat swamp forest (Anderson 1963, 1983). Although they are still poorly understood, Southeast Asian peatlands, like Amazonian swamps, are less floristically diverse than most upland forests, apart from white sand 'heath forest', with which they have comparable levels of diversity (Posa *et al.* 2011). Southeast Asian peatlands have been reported to harbour numerous specialist and apparently endemic taxa, although like swamp forests and white sand forests in Amazonia, most tree species that occur in these areas are also found in neighbouring upland forests (Fine *et al.* 2010; Posa *et al.* 2011; Pitman *et al.* 2014).

This study is the first to describe in detail the floristic composition of Amazonian peatland forests. Based on equivalent ecosystems in Southeast Asia, we may expect to find a distinctive and diverse flora with numerous specialists. Such discoveries would enhance the conservation status of the peatlands, which thus far has been based on their large below-ground carbon stocks (Draper *et al.* 2014). Furthermore, this study provides a unique dataset that represents large areas of the major ecosystems types found in West Amazonian lowlands, and spans perhaps the most important environmental gradients of fertility and inundation. Importantly, the study has been conducted at a scale suitable for revealing the processes that determine diversity patterns (Ricklefs 2008).

Specifically the questions I address are:

1. How floristically diverse are peatland forests, and how does their diversity compare with surrounding upland and seasonally inundated forest types?
2. How similar, in terms of floristic composition, are peatland forest plots to one another and to surrounding upland and seasonally inundated forest types?
3. Do these similarities and differences in floristic composition reflect previous classifications based on forest structure and environmental conditions?

   Which species are most abundant in peatland forests, and how many of these species are shared with surrounding upland and seasonally inundated forest types?

3.3 Materials and Methods

3.3.1 Forest inventories

Three different floristic data sets were used to describe the floristic composition of the different vegetation types in the region. Data for peatland forests and seasonally flooded forests are presented for the first time here, whilst data for white sand forests and *terra firme* forests come from published datasets. Inventory protocol and plot size varied between datasets. Plot sizes and sampling protocols were selected in order to best represent the floristic composition of adult trees in a given vegetation type. As the forest structure varies then so must sampling design in order to capture equivalent information. For example, white sand forests and pole forests consist of far smaller trees than *terra firme* forests; if inventories were limited to trees > 10 cm dbh then the majority of individuals would be excluded from the census. Plots within each inventory were assigned to the different ecosystem types based on substrate character, forest structure and observed hydroperiod (Table 3.1).

Table 3.1 Environmental characteristics of different ecosystem types.

Ecosystem type	**Forest structure**	**Substrate character**	**Observed hydroperiod**
Pole forest	Low canopy thin trees	Peat present	Water table at surface, no flooding
Palm swamp	Dominated by arboreal palms, open canopy	Peat present	Water table at surface, some flooding
Terra firme forest	High canopy large trees	mineral clay sediment	No evidence of flooding
Seasonally flooded forest	High canopy large trees	mineral clay sediment	Strong evidence of flooding
White sand forest	low canopy thin trees	white sand	No evidence of flooding

Peatland forest inventories were conducted between 2008 and 2012. A total of 26 plots were established across 11 peatland locations across the PMFB, northeast Peru (Figure 3.1). Of these plots, 16 were established by me as part of this PhD project, the remaining plots had been established previously and are published in Honorio Coronado *et al.* (2015). Clusters of plots were present at a number of locations, the maximum number of plots in any given locations was five, and plots were located at least 500 m from the next closest plot. Of these plots 23 were 0.5 ha in area and were established based on a modified version of the RAINFOR protocol (Phillips *et al.* 2009), whereby all trees with a diameter at breast height (dbh) > 10 cm were measured and identified. As the peatland forests often contain many trees that are small in stature, the protocol was modified to include a 4 x 100 m transect in which all trees with a dbh > 2 cm were measured and identified. Additionally, three 1 ha plots following the same protocol were established.

Seasonally flooded forest plot data came from the published dataset of Honorio Coronado *et al.* (2015). These plots were 0.5 ha and based on a modified version of the RAINFOR protocol (Phillips *et al.* 2009), whereby all trees with a diameter at breast height (dbh) > 10 cm were measured and identified.

White sand forest data came from a number of data sources. Data from 16 white sand forest plots came from the published dataset of Fine *et al* (2010). 13 of these plots consist of 0.1 ha forest plots in *varillal* type forests (defined by a canopy height 10-20 m [García Villacorta *et al.* 2003]), where all trees > 5 cm dbh were identified and specimens collected. A further three 0.025 ha plots were established in extremely stunted *chamizal* type forest (defined by a canopy lower than 5 m [García Villacorta *et al.* 2003; Encarnación 1985]) . Due to the small size classes found in these *chamizal* forests, all trees > 2.5 cm dbh were identified and specimens were collected. These plots were augmented with a further four 0.1 ha plots, in which all stems > 2 cm dbh were included. Finally, three 1 ha forest plots from the RAINFOR network where all stems > 10 cm dbh were identified completed the white sand forest dataset.

The *terra firme* plot data consisted of 29, one ha published plots from the RAINFOR network (Peacock *et al.* 2007; Pitman *et al.* 2008; Honorio Coronado *et al.* 2009). These plots are located across northern Peru on upland, well drained soils. All trees > 10 cm dbh were identified and herbarium samples were collected where necessary. Details and coordinates of all plots are given in Appendix 3.1.

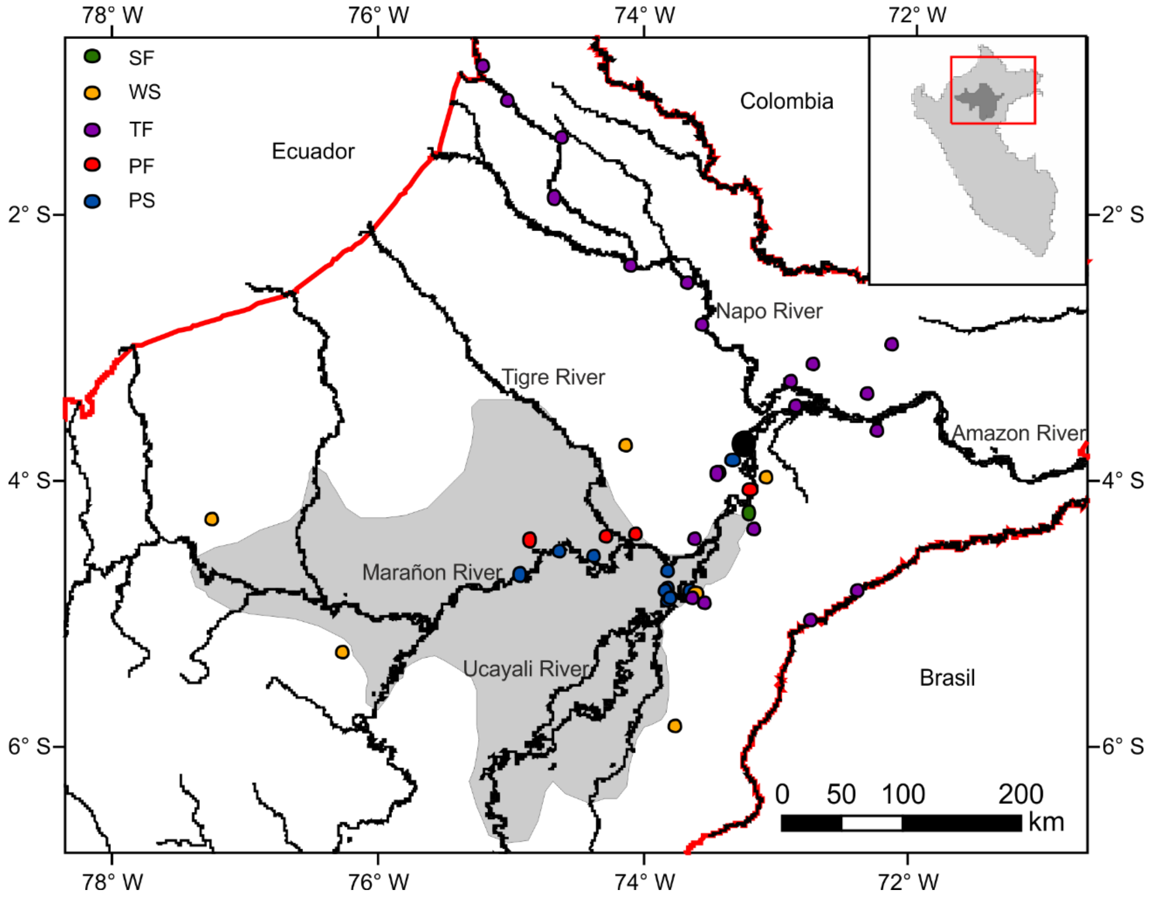

Figure 3.1 Location map showing all plots, the location of the PMFB (shaded area) within Peru (red boundary). Different colours and corresponding codes represent different ecosystem types, seasonally flooded forest (SF); white sand forest (WS); *terra firme* forest (TF); pole forest (PF); palm swamp (PS). Many locations contain more than one plot. Full details of all plots can be found in Appendix T1. River and country boundary was downloaded from (DIVA GIS 2014).

3.3.2. Taxonomic standardisation

Voucher specimens for all species encountered were collected, and collections were standardised within but not between datasets, the collections presented here for the first time from peatland and seasonally flooded forest were standardised and compared with specimens at the herbarium Amazonense (AMAZ) in Iquitos. Morphospecies were consistently identified within but not amongst the different plot datasets, and therefore all morphospecies and individuals not identified to species level were grouped as unidentified morphospecies and excluded from the subsequent analysis. These exclusions led to an approximate 10% loss of taxa apart from in terra firme forests where it was closer to 30% (Table 3.2). These exclusions also led to a reduced number of species within each plot and are likely to increase similarity among plots, particularly in *terra firme* forest, as there are many unidentified individuals within these highly diverse plots (Table 3.2). However, patterns of species diversity (Fisher's alpha) and community similarity (Bray-Curtis index) are robust, and have been shown to persist following removal of unidentified morphospecies in a dataset with a similar level of morphospecies (Pos *et al.* 2014).

Table 3.2. Summary information for the plot dataset across five ecosystem types showing the number, size and area of plots in each ecosystem type as well as the total number of stems and species recorded.

	Pole forest	**Palm swamp**	***Terra firme***	**Seasonally flooded**	**White sand**
No. plots	11	15	29	11	23
Plot size (ha)	0.5	0.5	1	0.5	1 and 0.1
Minimum diameter	2 cm	2 cm	10 cm	10 cm	2 cm
Total area of plots (ha)	5.5	7.5	29	5.5	5.275
Total stems	8048	4880	8180	2078	6577
Total unidentified stems	1487	361	2686	194	316
Total identified species	84	258	568	167	283
Total unidentified morphospecies	11	13	259	14	30
Stem density (stems ha^{-1})	1462	607	307	423	1321

3.3.3 Community diversity analysis

In order to standardise across these different plot sizes, rarefaction curves for each forest community type were extrapolated following the multinomial model method of Colwell *et al.* (2012), where the number of species in a chosen number of individuals is estimated by examining (by resampling without replacement) the form of the relationship between the number of individuals and the number of species. Extrapolated rarefaction curves were generated using *estimate-S* (Colwell 2013). A standard number of 500 stems was used to estimate diversity across all forest ecosystem types as this number of stems provided a good representation of diversity at the local scale (α-diversity); the rarefaction curve for all ecosystem types was approaching its asymptote but the sample size was small enough not to encompass a substantial element of β-diversity. Diversity was also estimated using two of the most widely used metrics, Fisher's alpha and Shannon index (Rosenzweig 1995; Magurran 2013), alongside estimated species richness. These two metrics reflect slightly different qualities of diversity, with Shannon index better representing the evenness quality of diversity (Gotelli & Chao 2013). Estimated Fisher's alpha and Shannon entropy were based on the same 500 individuals and were also calculated using *estimate-S*.

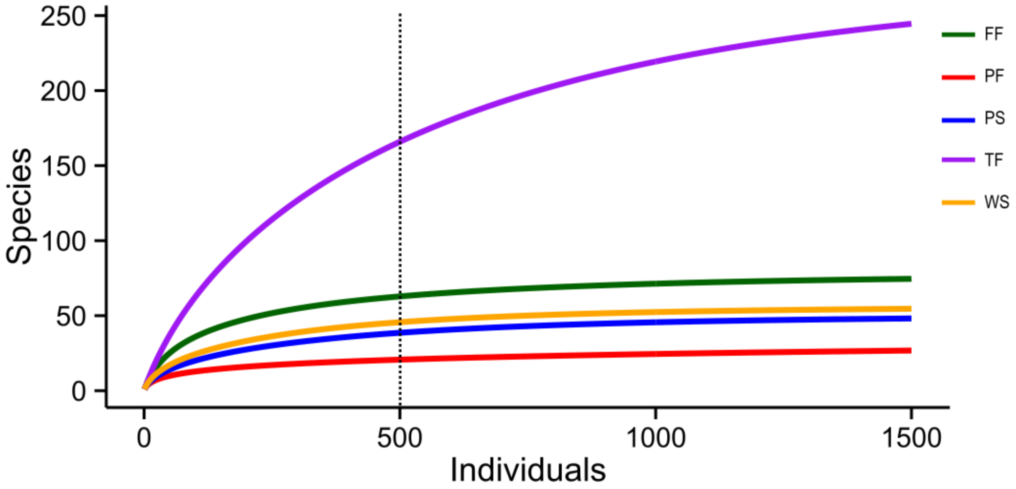

Figure 3.2 Extrapolated rarefaction curves for the five ecosystem types. Coloured dots represent the different ecosystem types: pole forests (red); palm swamps (blue); white sand (gold); seasonally flooded forest (green) and terra firme forest (purple). Dashed line shows the sample size used to calculate diversity indexes. Dots represent estimated number of individuals in a given plot.

3.3.4 Community similarity analysis

In order to compare floristic composition between plots of different sizes and with different sampling protocols it was necessary to standardise stem numbers across the plot dataset. To achieve this, the number of individuals per plot was reduced to the minimum number of individuals found in any plot, 73. This was done by randomly selecting (without replacement) 73 individuals from each plot. This method is likely to artificially increase the β-diversity across ecosystem types, particularly among those plots with high diversity because such small samples are likely to exclude many species (Cardoso *et al.* 2009; Tuomisto 2010b). *Terra firme* forests were most affected by this procedure as these large plots typically contain the largest number (500-700) of individuals and the greatest species richness.

Once the plots had been standardised to have the same number of stems, ecological distance matrices were constructed using the Hellinger and Chao distance metrics (Chao *et al.*

2005; Legendre & Legendre 2012a). The Hellinger distance was chosen as the dataset contained plots taken from a wide range of environmental conditions, resulting in many “double zeros”, whereby many species are absent from both the plots being compared. The Hellinger distance is an asymmetrical distance coefficient and provides a distance measure based only on the species that are present (Legendre & Legendre 2012a; Legendre & De Cáceres 2013). The Chao distance was also used as the plot data had been substantially rarefied in some instances; the Chao distance provides an estimate of community similarity whilst accounting for unseen shared species (Chao *et al.* 2005). The distance matrices were constructed in the *vegan* package of R (Oksanen *et al.* 2013), and were used to create non-metric multidimensional scaling (NMDS) ordinations in order to visualise the similarities and differences between plots within and amongst ecosystem types.

3.3.5 Geographic distance and community similarity

In order to test whether my conclusions concerning the floristic similarity of the different ecosystem types were affected by the distances among plots, a distance decay approach was also used to analyse patterns of community composition. Specifically, a negative binomial generalised linear model (GLM) with a log link function was used to model the importance of geographic distance in determining ecological similarity within ecosystem types (Millar *et al.* 2011). Here ecological similarity was calculated using the inverse Hellinger distance which was standardised to give values ranging from zero (completely dissimilar) to one (identical). In order to generate 95% confidence intervals, a modified bootstrap resampling procedure was adopted. This procedure consists of repeatedly performing the GLM outlined above with a randomly selected subset of sites 1000 times. To remove the problem of comparing the same site with itself (i.e. with a similarity of one and a distance of zero) in the bootstrap procedure, all analysis was completed on only the bottom triangle of the similarity and distance matrices following Millar *et al*. (2011).

3.3.6 Null Models

A non-parametric permutational multivariate analysis of variance (PERMANOVA) was conducted in order to test the significance of the variation in species composition among ecosystem types, following Anderson (2001). In order to assess the probability that the dissimilarity between plots within and among ecosystem types are more similar or more different than expected by chance, a Raup-Crick null model permutation approach was used following (Chase *et al.* 2011). This method compares the observed shared species between pairs of plots with a distribution of randomly drawn species for each plot, based on 1000 bootstrapped resamples. The product of this method is a pairwise community dissimilarity metric ranging from -1 to 1 that describes how similar the observed shared species between two plots are to what would be expected if species were drawn at random. Metric values approaching -1 suggest that communities are more similar than expected by chance, values approaching 0 suggest that communities are as similar as would be expected by chance, and values approaching 1 are more dissimilar than would be expected by chance. All data manipulations and diversity analyses apart from species richness extrapolations were conducted in the R statistical environment (R Core Team 2012).

3.3.7 Criteria for defining ecological guilds

All species found in peatland plots were split into ecological guilds based on their occurrence in different ecosystem types following similar definitions to Pitman *et al* (2014). ‘Generalists’ were defined as species that occurred in the relevant peatland vegetation type and were common (occurred in more than 50% of plots) in two or more ecosystem types. ‘Spill-over’ species were defined as species that occurred in the relevant peatland ecosystem type and were also common in one non-peatland vegetation type. ‘Specialists’ are those species that are common in one peatland ecosystem type but were entirely absent from non-peatland ecosystems. Taxa with fewer than five individuals across all plots were considered too rare for their distribution to be characterised in this way.

3.4. Results

3.4.1 Species richness and diversity

The two peatland ecosystem types show very different patterns of species richness and diversity compared with other ecosystem types. Pole forest was found to be substantially less species rich and less diverse than any other ecosystem type (Figure 3.3). For example, pole forest plots contained as few as six species or morphospecies with dbh > 10 cm in a 0.5 ha plot, and were estimated to hold approximately 20 species per 500 stems (Figure 3.3). Palm swamps were also found to low levels of diversity with an estimated 38 species per 500 stems (Figure 3.3). *Terra firme* plots were always the most diverse and species rich forest ecosystem type, with an estimated 166 species per 500 stems (figure 3.3).

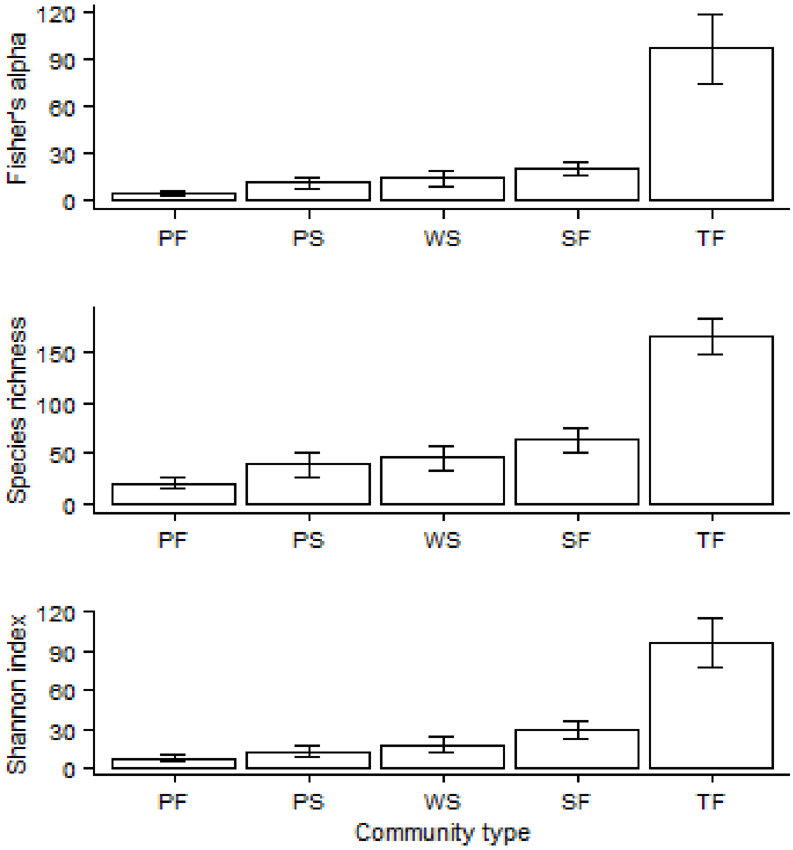

Figure 3.3. Estimated species richness (panel A) and species diversity as estimated by the Fisher's α (panel B) and the Shannon index (panel C) for the five forest types: Pole forest (PF), palm swamp (PS), white sand forest (WS), seasonally flooded forest (SF) and *terra firme* forest (TF). Estimated richness and diversity were calculated for 500 extrapolated individuals. Error bars are 95% confidence intervals in panel A and standard deviations in panel B & C.

3.4.2 Floristic similarity within ecosystem types

The ecological dissimilarity within peatland ecosystems is slightly lower than in the other ecosystem types (Figures 3.5 and 3.5), although the larger error bars in peatlands demonstrate that floristic similarity is more variable among plots within peatland ecosystems (Figure 3.5). This pattern is consistent between different ecological distance metrics (Hellinger and Chao), therefore only the Hellinger has been used in subsequent analyses and discussion. When floristic similarity within ecosystem type is compared with a null model using the Raup-Crick method, mean Raup-Crick distance values ranged from 0.16 to 0.30, suggesting that within ecosystem types, sites are slightly less similar to one another in terms of floristic composition than would be expected by chance (Table 3.3).

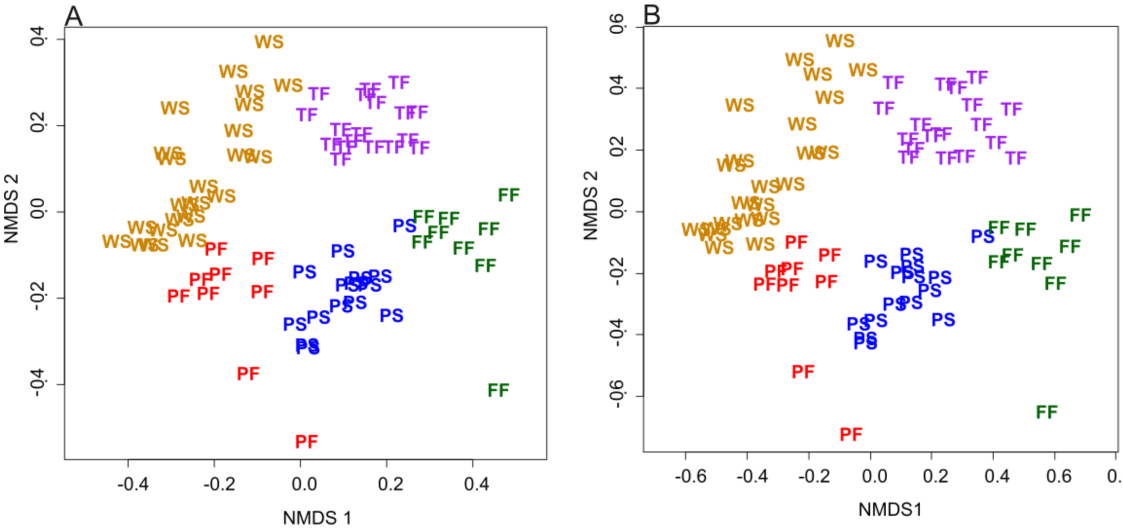

Figure 3.4 NMDS ordinations showing the similarity of all 81 forest plots within and between forest community types. Panel A is an NMDS ordination using the Chao distance, Panel B is an NMDS ordination using the Hellinger distance. Labels and colours correspond to forest community types: Pole forest (PF, red); palm swamp (PS, blue); seasonally flooded forest (FF, green); terra firme (TF, purple); white sand forests (WS, orange).

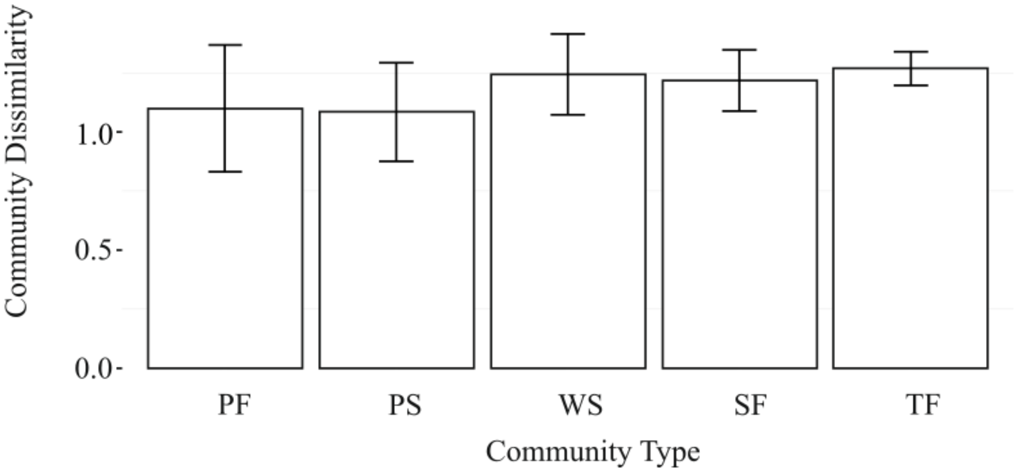

Figure 3.5 Community dissimilarity within forest community types using the Hellinger distance. The five forest community types are: Pole forest (PF); palm swamp (PS); white sand forest (WS); seasonally flooded forest (FF) and *terra firme* forest (TF). Error bars show standard deviation. Maximum possible dissimilarity = $\sqrt{2}$. (≈1.414)

3.4.3 Floristic similarity and geographic distance

Overall floristic similarity declines with distance, but the importance of distance varies among vegetation types. Floristic similarity decreases with distance more strongly in peatland forests and seasonally flooded forests than in upland ecosystems (Figure 3.6). Consistent with figure 3.5, overall similarity is high in peatland ecosystems than in the other ecosystem types. However, floristic similarity within peatland ecosystem types is far more variable than is found within upland plots, particularly within pole forests, indicated by the large confidence intervals in Figure 3.6. This variability in floristic similarity in peatlands seems to be independent of distance, as high variability is found between plots that are located both close and far from one another (Figure 3.6).

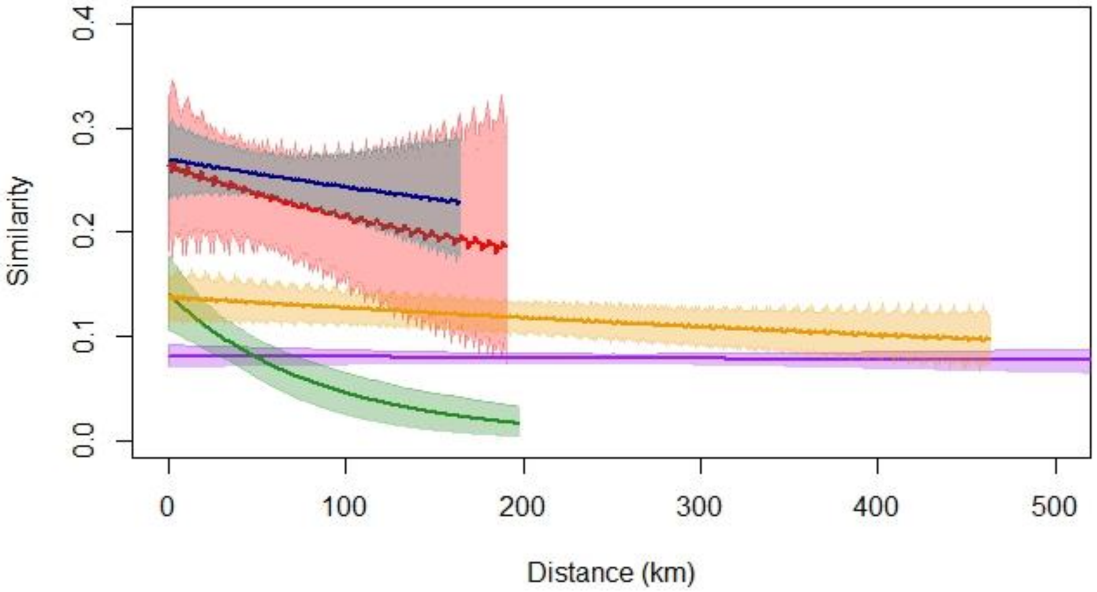

Figure 3.6 Floristic similarity (inverse Hellinger distance) between pairs of plots, within ecosystem types, as a function of geographical distance between the plots. Solid lines show the mean similarity from the GLM models and shaded areas show the 95% confidence interval. Colours represent different ecosystem types: red (pole forest), blue (palm swamp), purple (*terra firme* forest), green (seasonally flooded forest) and orange (white sand forest).

3.4.4 Floristic similarity amongst ecosystem types

The five ecosystem types are found to be clearly distinct from one another in terms of their floristic composition when plotted in the NMDS ordination (Figure 3.4). The mean ecological dissimilarity between plots of different ecosystem types is always higher than the mean dissimilarity within ecosystem types (Table 3.3). This result is further supported by the PERMANOVA test, which suggests that the floristic differences between the different ecosystem types are highly significant (P=<0.001).

Table 3.3. Mean forest community dissimilarity as measured by the Hellinger distance using a subset of 73 individuals from each of the 74 forest plots. Higher numbers indicate greater dissimilarity with $\sqrt{2}$ (≈1.414) being the maximum possible dissimilarity.

	PF	PS	SF	WS	TF
PF	1.10	1.30	1.41	1.29	1.40
PS	–	1.08	1.36	1.39	1.38
SF	–	–	1.22	1.41	1.38
WS	–	–	–	1.24	1.39
TF	–	–	–	–	1.27

Results from the Raup-Crick null model provides further support for the significance of the floristic differences amongst ecosystem types. Overall the dissimilarity between the different ecosystem types is positive and most values approach one, suggesting that dissimilarity between ecosystem types is far greater than would be expected by chance (Table 3.4). There is, however, substantial variation among different community types. For example, pole forests are found to be marginally more similar to white sand forests than to palm swamp forests, whilst palm swamps are more similar to pole forest, then seasonally flooded forests (Table 3.4). The Raup-Crick analysis suggests however, that the compositional differences between pole forests and palm swamps are closer to what would be expected by chance than the differences between pole forests and white sand forests (Table 3.4).

Table 3.4 Mean Raup-Crick community dissimilarity. The given value indicates the degree to which the similarity between community types is more similar, equally similar, or less similar, than would be expected by chance. The observed similarity was tested against 1000 random permutations of a null model. Values approaching zero indicate levels of similarity expected by random chance, and values approaching 1 indicate greater dissimilarity than expected by random chance.

	PF	PS	SF	WS	TF
PF	0.16	0.38	0.90	0.50	0.90
PS	–	0.21	0.86	0.83	0.56
SF	–	–	0.30	0.86	0.91
WS	–	–	–	0.26	0.96
TF	–	–	–	–	0.17

3.4.5. Associations between peatlands and uplands

Few pole forest or palm swamp species emerge as strict specialists (nine and 14 species respectively) (Figure 3.7, appendix 3.2). From this list a further seven species (three pole forest species and four palm swamp species) could be removed as their presence has been previously confirmed in upland and or seasonally flooded forests in this region (Vasquez Martinez 1997). Therefore just six pole forest species and ten palm swamp species are strict specialists. The majority of species that are found in both peatland forest types could be considered either generalists (common in two or more ecosystem types) or spill-over species (common in one other ecosystem type) (Figure 3.7). In pole forests spill-over species predominantly came from white sand forests (Figure 3.7).Within palm swamps the most important source of spill-over species was seasonally flooded forests.

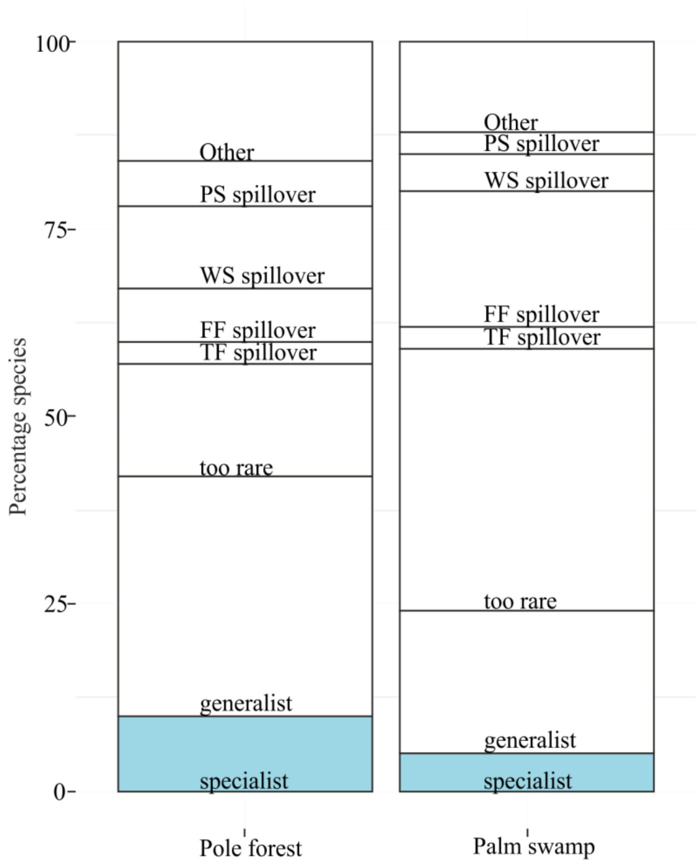

Figure 3.7 Percentage of species in the two peat forming ecosystem types (pole forests and palm swamps) belonging to specific ecological guilds defined above. Species that do not qualify for any ecological guild have grouped under 'other'.

Table 3.5 The ten most abundant taxa found in pole forest peatlands, the total number of individuals in all ten 0.5 ha plots, and the total number of plots in which the taxa occur.

Species	Number of individuals	Number of plots	Ecological guild
Pachira brevipes	2294	7	WS spill-over
Cybianthus cf. reticulatus	1343	4	PF and PS specialist
Tabebuia insignis var. monophylla	839	8	PF and PS specialist
Platycarpum sp.	456	7	PF specialist
Macrolobium multijugum	406	2	PF and PS specialist
Hevea guianensis	330	8	generalist
Mauritiella armata	248	3	generalist
Pagamea guianensis	214	4	WS spill-over
Mauritia flexuosa	201	7	PF and PS specialist
Calophyllum brasiliense	146	3	generalist

Table 3.6 The ten most abundant taxa found in palm swamp peatlands, the total number of individuals in all 15 plots, and the total number of plots in which the taxa occur.

Species	Number of individuals	Number of plots	Ecological guild
Mauritia flexuosa	1379	14	PF and PS specialist
Tabebuia insignis var. monophylla	461	4	PF and PS specialist
Mauritiella armata	362	7	generalist
Tovomita cf. krukovii	173	2	PS specialist
Virola pavonis	157	11	generalist
Euterpe precatoria	150	10	generalist
Elaeis oleifera	113	2	Palm swamp specialist
Symphonia globulifera	102	12	*terra firme* spill-over
Socratea exorrhiza	84	7	*terra firme* spill-over
Cybianthus cf. reticulatus	75	2	PF and PS specialist

3.5. Discussion

3.5.1. Diversity of peatland forests

Overall, the α-diversity of the peatlands is low compared with *terra firme* forests; this finding is consistent with numerous records from Amazonian swamps (which may or may not be peat-forming; (Dumont *et al.* 1990; Kahn & Mejia 1990; Pitman *et al.* 2014). The pole forests are, however, much less diverse than the palm swamps and to my knowledge the least diverse ecosystem yet recorded in Amazonia with an estimated Fisher's α of 4.5 (ter Steege *et al.* 2000). This result is particularly striking as it contrasts so strongly with the record for the highest α-diversity of trees (283 species) which was recorded in a single hectare *terra firme* plot within 250 km of the least diverse pole forest plot (Gentry 1988b). Why are these ecosystems so species-poor? Patterns of local diversity are a result of the contribution of regional diversity (limited by environmental filters and dispersal limitation) and local processes such as competitive exclusion and predatory removal (Figure 3.8; (Ricklefs 2004; ter Steege 2009). Assessing the relative importance of these processes, which operate at multiple spatial and temporal scales, is very difficult and may often be impossible (Ricklefs 2004; Weiher *et al.* 2011). Although I do not have a sufficient range of environmental, phylogenetic and ecological data to quantify and separate the importance of each of these processes, the patterns and context of my observations do provide novel insights into the reasons for the presence of low diversity in some tropical forest ecosystems.

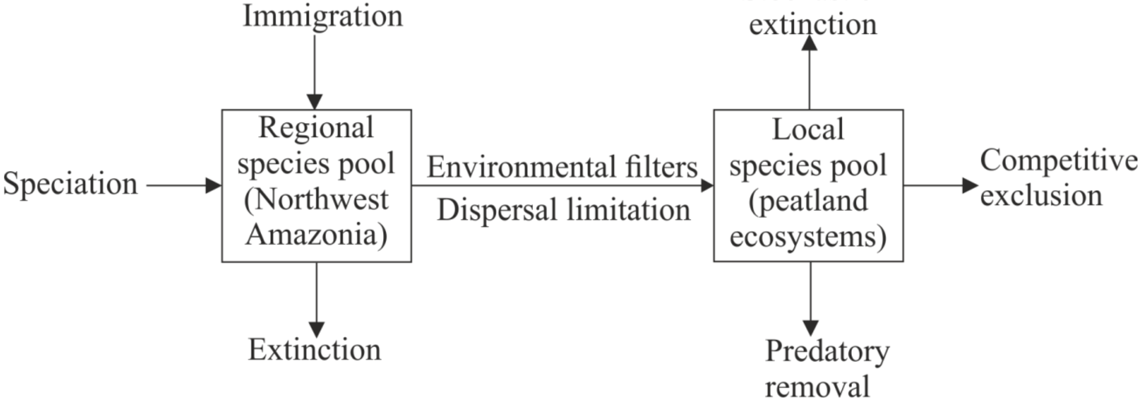

Figure 3.8 Conceptual model of the processes that determine the assembly of local species communities in study region (adapted from ter Steege (2009)).

For example, a previous explanation for the low diversity found in swamps and other edaphically extreme areas is that the low diversity results from their small area and isolated nature, which leads to enhanced dispersal limitation, and increased vulnerability to stochastic extinctions (ter Steege *et al.* 2000; Stropp *et al.* 2009; ter Steege 2009). This hypothesis is consistent with both neutral theory (Hubbell 2001) and area-diversity theory (Rosenzweig 1995). To some extent my results are consistent with this area-based hypothesis, because the palm swamps occupy a much greater area (27,732 km^2) than the less diverse pole forests (3,686 km^2), as well as occurring in larger, more continuous patches (Draper *et al.* 2014). However, the white sand forests also occupy only a small total area in isolated patches (Fine *et al.* 2010). If species diversity was largely attributable to habitat area, then much greater diversity would be expected in the palm swamps than in the white sand forests. Furthermore, far smaller patches of swamp forest in western Amazonia have been shown to have much greater levels of diversity than was found in this study (e.g. up to 164 species ha^{-1}; (Cornejo Valverde & Janovec 2006). These findings suggest that the diversity of swamp forests does not always increase with patch size, and in fact the opposite seems to be the case in this instance. One possible explanation for this is that small swamp patches surrounded by *terra firme* have many species that can potentially disperse into the swamp, although strong environmental filters may prevent a stable population from forming. Larger swamp areas effectively form their own buffer area, as only *terra firme* species with well-dispersed seeds can reach the swamp interior.

Another possible explanation for these results is that the low diversity observed in the peatlands is a direct result of strong environmental filters preventing species from the regional species pool from occurring in the local peatland species pool. The environmental filters which have been found to be most important across peatlands are substrate fertility, pH, and waterlogging (Page *et al.* 1999; Wheeler & Proctor 2000; Økland *et al.* 2001). Pole forests are known to be very nutrient poor as rain water and atmospheric dust are the only inputs of nutrients into the ecosystem (ombrotrophic), whilst also maintaining a low pH and a surface water table (Lähteenoja *et al.* 2009a; Lähteenoja & Page 2011). However, both palm swamps and white sand forests share a number of these environmental filters.

In terms of fertility, whilst palm swamps often have much higher nutrient content than pole forests due to fluvial nutrient input, white sand forests have exceptionally nutrient-poor soils, broadly comparable with peatland pole forests in terms of concentration of exchangeable cations (Janzen 1974; Kalliola & Flores Paitan 1998; Fine *et al.* 2005; Quesada *et al.* 2010; Lähteenoja & Page 2011; Quesada *et al.* 2011). Therefore, whilst the low diversity in pole forests compared to palm swamps, *terra firme* and flooded forests may be explained by the much lower fertility of pole forests, the disparity between pole forest and white sand forest diversity requires a different explanation. Similarly, measured pH values from pole forests (3.5-4.5) are comparable to those of white sand forests (4.4 ± 0.2) and palm swamps (4.4-6.1) (Anderson 1981; Lähteenoja *et al.* 2009a; Lähteenoja & Page 2011). Finally, palm swamp forests appear to experience equivalent levels of water logging to pole forests, but may also be exposed to the added stress of regular extended inundation. Together these results suggest that whilst the cumulative effect of environmental filters are likely to reduce diversity in peatlands, environmental filters alone cannot fully account for the extremely low diversity observed in pole forests.

A final possible explanation for the low diversity of pole forests, is that the peatlands are species-poor because they are naturally dynamic ecosystems and present day habitats are relatively recent features on the landscape. The process of peat accumulation changes the nature of the environmental filters through time as the peat surface rises above flooding levels and away from underlying parent material and fluvial mineral inputs (Charman 2002). Within this context, peatlands may be analogous to an early successional system where species turnover is fast but diversity at any one point in space or time is relatively low (White *et al.* 2006). For example, pollen analysis has shown that peatlands in this region have undergone vegetation change through their development (Roucoux *et al.* 2013). Currently, the oldest known peatlands are about 8000 years old (Lähteenoja *et al.* 2012), which contrasts markedly with the age of white sand forest soils. Diversity may therefore not have had enough time to accumulate in these ecosystems.

Data from Southeast Asia provide a useful comparison for understanding these patterns, because both pole forest and white sand forest are also extensive in this region. Interestingly, Southeast Asian peatlands, particularly pole forests, are much more diverse than those of the PMFB, with 65-80 species recorded in a series of 0.16 ha plots (Poesie *et al.* 2010; Posa *et al.* 2011), in contrast to the 7-35 species identified in the 10 0.5 ha plots in this study. Additionally, the floristic diversity seen in Southeast Asian pole forest is similar to that found in white sand 'heath forest' in the same region (Posa *et al.* 2011). This provides further support that the strong environmental filters present in the Peruvian pole forests, cannot alone account for the extremely low levels of diversity described.

Southeast Asian peatlands differ from those of the PMFB, in that they occupy a much greater area e.g. approx. 207,000 km^2 in Indonesia (Page *et al.* 2011). Southeast Asian peatlands have also appear to have been a feature on the landscape for a much greater time than peatlands in the PMFB. Radiocarbon dating from a number of studies suggests that peatlands in Southeast Asia have been developing since at least 26,000 cal. yr BP, (Anshari *et al.* 2001; Page *et al.* 2004; Morley 2013; Dommain *et al.* 2014). This contrasts to the peatlands in this study which began to accumulate 2000 – 7,000 cal. yr BP (Lähteenoja *et al.* 2012). Therefore, I suggest that alongside environmental filters, the most important factors in determining low diversity in the PMFB peatlands are their small size and their relatively recent presence on the landscape. It will be important to test the importance of ecosystem duration in determining diversity using palaeoecological methods.

3.5.4 β-diversity amongst peatlands and surrounding uplands

This study has shown that the peatland forests of the PMFB have a distinct floristic composition when compared to the other inundated and non-inundated ecosystem types that are encountered across the landscape. Overall, these floristic differences correspond to the previously used classification of peatland ecosystem types based on forest structure and environment (Draper *et al.* 2014). The significance of these compositional differences indicates that there are strong deterministic mechanisms underlying the patterns seen in figure 3.4. This is supported by the results from the Raup Crick null models which also suggest that the differences between peatlands and other ecosystem types are greater than expected by chance (Table 3.4). As has been found previously in swamp and *terra firme* forests (Pitman *et al.* 1999; Phillips *et al.* 2003; Pitman *et al.* 2014), very few species found to occur in peatlands are obligate specialists; instead differences between ecosystem types are driven by habitat associations.

Palm swamps were found to be most similar to seasonally flooded forests, whilst pole forests were found to be most similar to white sand forests (Table 3.3 and Figure 3.4). In fact, a number of species that had previously been considered white sand endemics are common or even dominant in pole forests, such as *Pachira brevipes* (Table 3.5) (Fine *et al.* 2010).This is likely to be because pole forests and white sand forests share a common environmental filter (Keddy 1992) in extremely low fertility (Kalliola & Flores Paitan 1998; Quesada *et al.* 2010). Similarly, the primary environmental filters operating in palm swamps and seasonally flooded forests are inundation and waterlogging. This is further supported by the analysis of ecological guilds which shows that pole forests contain many spill-over taxa from white sands, and palm swamp contain many spill-over taxa from seasonally flooded forests (Figure 3.7). It is difficult, though, to separate the environmental filters from possible dispersal limitation, as palm swamp forests are often found close to seasonally inundated forests and pole forests are most common in the north-east of the PMFB close to the extensive white sands found on the Nañay river (Fine *et al.* 2010; Draper *et al.* 2014).

3.5.3 β- diversity within peatland ecosystems

There is a now large body of work that has examined variation in floristic composition in tropical forests through space, and the potential drivers of that variation. Typically, these studies have examined the importance of dispersal limitation and environmental variation in determining floristic composition, and have found evidence for both, although environmental parameters often explain more of the variation (Phillips *et al.* 2003; Tuomisto *et al.* 2003; Jones *et al.* 2006; Kristiansen *et al.* 2012; Baldeck *et al.* 2013; Guèze *et al.* 2013). In this study we do not have consistent environmental data across all of these plots to test this association within peatland ecosystems. However, it seems clear that environmental variation accounts for some of the floristic variation seen in the peatlands of PMFB, as peatlands occur over such strong environmental gradients.

The β-diversity within peatland ecosystems is slightly lower and far more variable than that found among upland *terra firme* (Table 3.3 and Figure 3.6). Together with the exceptionally low α-diversity recorded, these patterns suggest that for a given peatland plot we can predict with some confidence that few species are likely to be encountered, and that the species encountered will come from a limited list. However, we can have little confidence about predicting exactly which species from that list will be present or how abundant those species will be. This pattern is particularly striking in the field as the high turnover in composition and abundance can occur over very short distances. For example, in one pole forest plot *Pachira brevipes* accounts for 527 stems and ~70 % of individuals, while in another pole forest plot < 1 km away *Pachira brevipes* is entirely absent. Similarly high turnover has been found in white sand habitats (Fine *et al.* 2010), and may be a product of strong fertility gradients occurring over relatively short distances. Further geochemical analysis is required to determine if significant environmental gradients occur within ecosystem types, and if such environmental gradients can explain these sharp patterns of floristic turnover.

The significant decrease in community similarity with increasing distance between peatland plots (Figure 3.6), particularly pole forest plots, is assumed to primarily reflect dispersal limitation in peatlands, rather than some unstudied gradient such as environmental variation. This is because whilst there are strong environmental gradients within the peatlands, these gradients do not appear to vary systematically across the basin within ecosystem types (Lähteenoja & Page 2011). The apparently high dispersal limitation in peatlands contrasts with other ecosystem types, *terra firme* forests in particular appear to experience little dispersal limitation over large (up to 500km) distances, an observation consistent with other studies on this region (Condit *et al.* 2002). The apparent importance of dispersal limitation in peatlands is somewhat unexpected, as they are distributed more closely and continuously than, for example, white sand forests, which have a more patchy distribution over a much greater area. One explanation for this is that whilst white sand forests have been a feature of the landscape for millions of years, the peatlands included in this analysis have been present for only 2000-7000 years (Lähteenoja *et al.* 2012). Hence, species able to grow in white sand habitats have had much longer to migrate to suitable habitat than species able to grow in peatlands.

As mentioned previously, peatlands are unusual in that they constantly modify their own environment as leaf litter, roots and other organic matter accumulate as peat (Charman 2002). As peat has been found to accumulate rapidly in the PMFB (typically >1 mm year^{-1}), this process, alongside changes to hydroperiod as a result of fluvial dynamics, can result in profound edaphic changes over centennial timescales. In contrast, *terra firme* environments may be edaphically relatively homogenous for many thousands of years. The autogenic process of peat accumulation can therefore result in successional patterns as the changing edaphic properties give a selective advantage to different sets of species over time. Pollen records have shown that peatlands in this region have undergone changes in vegetation composition through their development (Roucoux *et al.* 2013). These interdependent peat development–vegetation succession temporal patterns are likely to be spatially variable across peatland sites and therefore are likely to contribute to the high levels of observed β-diversity. Elsewhere in tropical peatlands, high β-diversity across sites has been interpreted as a chronosequence of successional communities resulting from peat accumulation (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997; Page *et al.* 1999).

3.5.2 Endemism in peatlands

It is remarkable that there are no clear candidates for peatland endemic species. Peatlands are known to present a distinct combination of environmental filters compared with upland forests. It would be expected that this distinct environment would lead to parapatric speciation as species evolve to specialise in this habitat, as has been shown comprehensively for white sand forests in both plant and bird communities (Fine *et al.* 2004; Fine *et al.* 2005; Fine *et al.* 2006; Fine & Kembel 2011; Alonso *et al.* 2013; Fine *et al.* 2014). Therefore, the lack of endemism that is observed in the PMFB peatlands is curious, and suggests that there has been little evolutionary opportunity for speciation.

There are a number of possible reasons why the peatland environment has not provided sufficient evolutionary pressure for peatland specialization to occur. One possibility is that the dual environmental filters of extreme waterlogging and low nutrient availability may be particularly difficult to adapt to, which could lead to especially low speciation rates. The apparently high number of endemic species reported in Southeast Asian peatlands would suggest that this is unlikely (Posa *et al.* 2011). Although other sources have questioned the number of endemic species in Southeast Asian peat swamp forests (Anderson 1963).

Alternatively, it may be that peatlands are a relatively recent or transient feature of the landscape of the PMFB. Wetland swamp habitats have been a feature on the landscape since the early Miocene, although their permanence in the landscape remains largely unknown (Hoorn 1994; Hoorn *et al.* 2009; Hoorn *et al.* 2010b). Peatlands can be exceptionally sensitive to climate change, in particular to changes to precipitation and the flood regime (Fenner & Freeman 2011). For example, climatic changes during the Quaternary are one possible cause of the transient nature of peatlands. Although Western Amazonia probably only experienced modest drying during glacial periods (Cheng *et al.* 2013), even slightly reduced rainfall may have been sufficient to cause peatlands to disappear from the landscape for long periods, as decomposition rates are so high in the tropics (Dommain *et al.* 2014). This loss of habitat would result in increased extinction rates, especially in pole forests since they appear to occur on ombrotrophic peat domes making them especially sensitive to reduced precipitation. If peatlands have been transient features on the landscape, then there also may have insufficient time for speciation to occur.

One species variety that is amongst the most common in both peatland forest types and which appears to be a peatland specialist is *Tabebuia insignis var. monophylla*. Interestingly, this variety is also abundant in peat swamps in Guyana and Venezuela but apparently has not yet been recorded in other ecosystems or areas (Gentry 1992a; Steege *et al.* 1993; White *et al.* 2002; Van Andel 2003; Vegas-Vilarnibia *et al.* 2006). This disjunct geographical distribution suggests that either *T. insignis var. monophylla* is able to disperse over exceptionally large distances, or that peatlands have previously been better connected and more extensive across

Amazonia. Alternatively, there may be many small peatlands distributed across Amazonia, which also contain *T. insignis var. monophylla*, but are yet to be inventoried. Of these three explanations the second appears the most likely, as although this species is wind dispersed, cross continental dispersal seems improbable. As this group was of particular interest to A.H. Gentry, perhaps the most prolific Neotropical botanist of all time, it seems unlikely that it has a far more widespread occurrence across the Amazon (Gentry 1992a).

3.5.5 Conservation importance of peatland forests

Whilst these peatland ecosystems may lack the alpha diversity of *terra firme* and endemism of white sand forests, they make a substantial contribution to the regional β-diversity. This contribution to regional β-diversity, provides a strong rationale for conservation, quite apart from their value as a carbon store and potential sink. It should be noted that in this study I discussed only tree diversity, and it may well be that peatlands harbour a wider range of shrubs or herbaceous taxa. For example, a diverse range of Vanilla orchid species appear to occur in peatlands elsewhere in Peru (Householder *et al.* 2010). The peatlands also harbour a number of economically important species. *Mauritia flexuosa* in particular is one of the most important crop plants in this region, providing a valuable resource for local communities (Manzi & Coomes 2009; Horn *et al.* 2012; Endress *et al.* 2013; Gilmore *et al.* 2013). Additionally, as the peatlands have been confirmed to harbour a number of white sand specialist species (including several previously described as endemics) in high abundance, they appear to provide a previously unaccounted-for link between isolated patches of white sand forests. Therefore, conserving peatlands may be an important step in conserving white sand endemic species that have been identified as a conservation priority (Alonso *et al.* 2013).

3.5.6 Conclusions

The largest peatland complex in Amazonia can be considered a diversity anomaly due to its extremely low α-diversity, high β-diversity, dominance of a minority of species and lack of endemic species. Whilst habitat area and soil fertility are important drivers of diversity, my results indicate that a complex interplay of mechanisms operating on different timescales are responsible for the spatial patterns seen in peatland ecosystems. In particular, ecological dynamism over centennial timescales may contribute to the low α-diversity and high β-diversity that is observed, whilst the lack of endemic taxa found may be a result of environmental instability over longer, millennial timescales.

4 A palynological approach to understanding floristic patterns in time and space in West Amazonian peatlands

4.1 Abstract

The peatland ecosystems of the Pastaza Marañon foreland basin in Northern Peru harbour some of the least diverse and most spatially variable tree communities found in Amazonia. Explaining these striking patterns of diversity has proved difficult when only present day processes are considered. Here I use palaeoecological data to understand the role of historical processes in determining current patterns of composition and diversity in Amazonian peatland communities using an innovative multidisciplinary approach. Combining pollen data from eight peat cores and floristic data from eight forest census plots distributed across two sites, I show that the most species-poor ecosystems are a relatively recent feature on the landscape. This finding suggests that ecosystem age may be a key determinant of their low diversity. Both autogenic (internal biotic) processes and allogenic (external environmental) factors can be significant determinants of floristic change through time. These results demonstrate the importance of often-ignored historical processes in the assembly of tropical forest communities.

4.2 Introduction

Extensive peatland ecosystems have recently been discovered in the Pastaza Marañon Foreland Basin (PMFB) in North-western Amazonia, and have become a focus for research due primarily to the large stocks of carbon that they harbour (Lähteenoja *et al.* 2009b; Lähteenoja *et al.* 2012; Draper *et al.* 2014). Peat has been shown to occur under a range of different ecosystem types which exhibit some of the most unusual floristic patterns found in Amazonia, including strikingly low levels of (within site) α-diversity and exceptionally variable levels of (among sites) β-diversity (Chapter 3) (Lähteenoja & Page 2011; Draper *et al.* 2014). In contrast, neighbouring *terra firme* forests hold the global record for α-diversity (Gentry 1988b) and have consistent high levels of β-diversity over wide spatial scales (Chapter 3). Explaining the processes that lead to these floristic patterns will not only allow us to understand how these ecosystems have developed, but also has the potential to inform our understanding more generally of the processes that underlie the assembly of Amazonian tree communities.

Spatial variation in the composition of tropical tree communities has principally been explained by ecologists as a result of two factors: firstly, by environmental gradients (and their associated biotic interactions) determining where species are able to survive (Phillips *et al.* 2003; Tuomisto *et al.* 2003; Fine *et al.* 2004; Kristiansen *et al.* 2012), and secondly by a combination of dispersal limitation and stochastic demography (Hubbell 2001; Condit *et al.* 2002). Whilst these studies provide valuable insight, they have included little role for historical processes. Where historical processes have been integrated, the focus has been on processes operating over evolutionary timescales, i.e. how speciation and extinction influence current patterns of composition (Dexter *et al.* 2012; Baker *et al.* 2014). Ecological processes operating over centennial timescales, have been largely overlooked, and present a missing link in our understanding of community assembly in the tropics (Rull 2012; Jackson & Blois 2015).

The importance of ecological processes operating over centennial timescales is particularly relevant in peatland ecosystems, where spatial variation in floristic composition has been interpreted as representing chronosequences of successional communities (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997; Page *et al.* 1999). Here succession is defined as an orderly, directional and therefore predictable pattern of vegetation development through time, that results from the modification of the physical environment by the community (Odum 1969). A chronosequence is defined as a series of successional communities distributed through space, and where gradients in space reflect gradients in time (Walker *et al.* 2010a). Peatlands experience succession because the accumulation of organic material as peat (an autogenic process) changes the physical and chemical environment (e.g. hydrology, nutrient availability) experienced by plants (Rydin & Jeglum 2013). However, testing apparent chronosequences in tropical peatlands with palaeoecological data has rarely been undertaken (but see Phillips 1997 and Morley 1981), and never in Amazonia. The interpretation of floristic variation as a chronosequence based purely on spatial patterns has often been proved to be false once palaeoecological records become available (Johnson & Miyanishi 2008). Within Amazonia, assumed chronosequences have previously been used to explain patterns of floristic variation in swamps based on descriptions of modern communities alone (Kalliola *et al.* 1991a; Kalliola *et al.* 1991b). In this study, the importance of historical processes, including succession, in determining spatial patterns of floristic composition is investigated using palaeoecological data and a novel multivariate statistical approach.

One aim of this paper is to test the extent to which the high beta diversity encountered in peatlands of the PMFB is attributable to succession, since this has important implications for understanding community assembly in this region, particularly if the pattern of succession is consistent across a range of sites. Different peatland ecosystem types, and the vegetation communities they hold, are known to be identifiable over large spatial scales in satellite imagery (Draper *et al.* 2014). If these ecosystem types occur along a consistent successional trajectory, new insights could be gained into ecosystem development at a landscape scale. Additionally, if succession was found to be important this could help explain the extremely low patterns of alpha diversity observed. The relationship between alpha diversity and ecosystem age is especially poorly understood, and their interaction with space even less so (Rosenzweig 1995; Adler & Lauenroth 2003; Adler *et al.* 2005; White *et al.* 2010). However, alpha diversity may be expected to be low in ecologically young communities, particularly in some of these peatlands ecosystems which often exist as small isolated fragments where barriers to dispersal may be prevalent (Adler *et al.* 2005; Adler & Levine 2007).

An alternative and equally plausible explanation is that the spatial variation in composition is attributable to variation in the physical environment that is not mediated by community dynamics (i.e. they do not represent biological succession in the sense of Odum [1969]). In the PMFB, perhaps the two most important abiotic factors are topography and water chemistry, which together determine the nutrient input and duration of anoxia in any given peatland (Räsänen *et al.* 1987; Rasanen *et al.* 1992; Kalliola *et al.* 1993). The high beta diversity among sites may be a response to differing levels of fluvial nutrient input, independent of peat accumulation. Vegetation patterns arising from this abiotic model would be less predictable and more stochastic through both time and space.

These two hypotheses, i.e. that spatial floristic patterns are primarily driven by successional processes (which are community mediated and, to a large extent, directional and predictable) or by allogenic environmental change (which may be less predictable) are not mutually exclusive. Instead, it is perhaps more likely that in some sites there is greater influence of abiotic factors, particularly fluvial dynamics, whilst vegetation change at more geomorphologically stable sites may be driven more or less entirely by autogenic succession. The relative importance of either successional or abiotic processes may be reflected in pollen data. If succession is an important process then pollen composition should be strongly related to the age and depth of the sample, and the pattern of change through time should be consistent between cores. Alternatively, if abiotic factors such as fluvial dynamics are important, changes in pollen composition may show little pattern with depth and age, and instead there may be strong differences among cores.

The PMFB contains a number of environmental gradients which are a result of the complex geomorphology of the basin. At the most fundamental level, the basin can be divided into two distinct geomorphological units (Rasanen *et al.* 1992). The first is the Pastaza fan which is located to the north of the Marañon River. This alluvial fan-like depositional feature underlies the Holocene peat deposits, and is characterised by a number of relatively straight rivers which run almost parallel from the northwest to the southeast and which are separated by small inter-fluvial ridges. The second is a highly dynamic area of fluvial aggradation to the south of the Marañon, which is dominated by strongly meandering rivers that flood annually (Rasanen 1991; Rasanen *et al.* 1992). In order to address how geomorphology may influence peatland development, this study examines the palaeoecology of two sites, one site in each geomorphological unit.

A further aim of this study is to explore some methodological aspects of pollen analysis, particularly the required number of pollen grains counted per sample to provide ecologically meaningful information. Pollen analysis can be a laborious, time-consuming process, and the number of grains that must be counted in order to provide a representative sample is a recurrent but rarely quantified issue (Birks & Birks 1980; Keen et al. 2014). Typically, 300–500 pollen grains are used to characterise a sample, and this sample size is employed across biomes and continents even though species richness varies by several orders of magnitude from the poles to the tropics. These count limits were developed in temperate/boreal ecosystems, as samples of this size provide both a statistically robust estimate of the proportion each taxon within the whole pollen assemblage (Birks & Birks 1980).

Due to the diversity of tropical forests, it not possible to gain a statistically meaningful sample of rare taxa using a sample of 300-500 pollen grains (Colinvaux *et al.* 1999). However, this does not mean that low pollen counts are not useful in tropical ecosystems. Using multivariate statistics, the modern pollen assemblages of different neotropical community types have been shown to be distinguishable using samples of 200 grains (Bush 1991). Counting fewer pollen grains per sample allows more samples to be counted given limited resources and time. Tropical forest neo-ecologists face a similar issue in determining the number of trees that need to be identified to provide a representative sample of a given forest. A range of sample sizes have been employed, from 50 ha plots containing >200,000 trees, to very small 0.1 ha plots with a perhaps 100 individuals (Gentry 1988a; Wills *et al.* 2006). These different approaches allow for different insights, large plots providing great detail whilst many replicated small plots provide information at large spatial scales. Palaeoecological studies, however, have typically had more rigid methodologies, which have produced information-rich descriptions of single or a small number of sites but often little or no spatial replication. Therefore, in this study I assess the efficacy of using spatially replicated pollen counts to answer novel questions linking temporal and spatial processes, accepting the necessary trade-off between number of samples and number of grains counted per sample.

A recent effort to tackle this problem using a statistical subsampling method has shown that, where diversity is low, a main sum of 300 may be more than necessary, whereas in diverse ecosystems more grains may be required to accurately characterise the vegetation, e.g. in tropical forest communities (Keen *et al.* 2014). However, an alternative method that is perhaps more informative, relatively simple and statically robust is rarefaction analysis (Birks & Line 1992). Rarefaction analysis examines the relationship between the number of individuals in a sample (in this case, the number of pollen grains) and the number of taxa in the sample (in this case, pollen morphotypes). Rarefaction analyses can now be extrapolated beyond the maximum number of individuals in a sample (Colwell *et al.* 2012; Colwell 2013), allowing assessment of how increased counting would improve estimates of pollen richness. For example, if we count a sample of 300 pollen grains and encounter 30 pollen taxa, extrapolated rarefaction analysis can be used to ask how many pollen types would be encountered if we only counted 100 grains or if we counted 500 grains.

4.2.1 Research questions

In this chapter I use pollen data from eight peat cores alongside vegetation data from the same eight locations distributed across two sites located in different geomorphological units to address a number of themes related to peatland ecosystem development. Firstly, I investigate patterns of floristic change through time and use multivariate statistical approaches to test whether these patterns can be attributed to specific autogenic or allogenic processes. I then investigate the role of these temporal processes in determining current spatial patterns of composition and diversity. Finally, I address the methodological issue of pollen sample size and the utility of using low pollen counts in multivariate statistical frameworks. The primary research questions of this study are as follows.

1. Can floristic changes through time in Amazonian peatlands be attributed to autogenic succession or are allogenic factors more important determinants?
2. Can the abrupt vegetation changes seen through space in two Amazonian peatlands be interpreted as chronosequences of successional communities?
3. Do peatlands located in seemingly distinct geomorphological units develop following different pathways?
4. What role do long-term processes over centennial timescales have in determining α-diversity?
5. How useful are low pollen counts and can they be used to identify ecological processes when analysed in quantitative multivariate framework?

4.3 Site Descriptions

This study was conducted at two sites in Northern Peru, within the Pastaza Marañon Foreland Basin (PMFB). The first site was located close to the village of Veinte de Enero on the Yanayacu River, within the confines of the Pacaya Samiria National Reserve (Figure 4.1). The second was located close to the Airico River, which is a tributary of the Chambira; the closest village is Ollanta, from which the site takes its name (Figure 1). These sites were selected based on the examination of Landsat and ALOS PALSAR satellite data, and were chosen based on the criteria that: (a) they probably harboured peat deposits, based on their inferred floristic composition, (b) they provided examples of the main peatland types we currently know about (i.e. palm swamps, pole forests and open peatlands) over a manageable distance (<5 km), and (c) they represented the two major geomorphological units (the Pastaza Fan and the Ucamara Depression) discussed above.

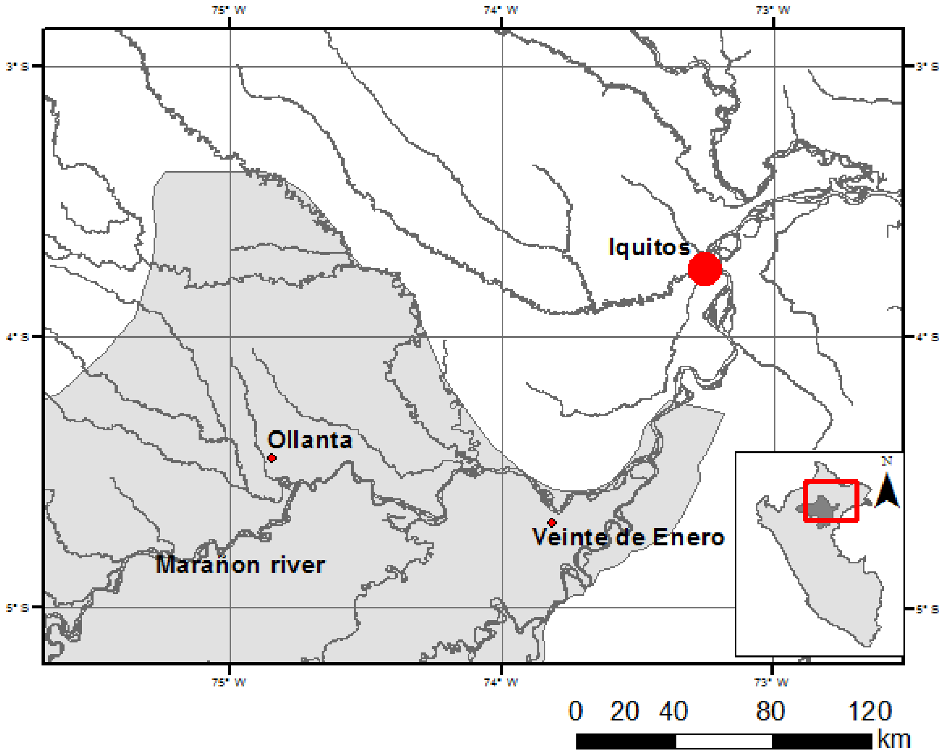

Figure 4.1. Map showing location of the sites in relation to the PMFB (grey) and Peru (see inset map).

The Veinte de Enero site appears to be an open peatland surrounded by palm swamp and showed evidence of concentric zonation within these two ecosystem classes (Draper et al. 2014 and Figure 4.2*)*. It was also deemed to be broadly representative of the peatlands in the Ucamara Depression. The Ollanta site appears to contain pole forest vegetation and was deemed to be representative of this peatland ecosystem type, and also of the older and less dynamic Pastaza fan geomorphological unit found to the north of the Marañon River (Rasanen et al. 1992).

4.4 Methods

4.4.1 Site surveys

In order to characterise the peatland across each site a 3.5 km transect was established perpendicular to the edge of the peatland towards the centre as identified in satellite imagery (Figure 4.2). At 100 m intervals the thickness of the peat was established using a Russian-type peat corer (Jowsey 1966), and the base of the peat was determined as the point at which continuous minerogenic sediment started to be recovered. At the same points the depth of the water table was measured and the maximum flooding depth was estimated by measuring the height of the flood mark on trees above the ground. Additionally, the height of the canopy was estimated by measuring the height of the ten tallest trees within a 20 m radius of the sample point using a laser rangefinder. Finally, one of three ecosystem types (pole forest, palm swamp or open peatland) was prescribed based on the floristic and structural similarity to the four floristic plots at each site.

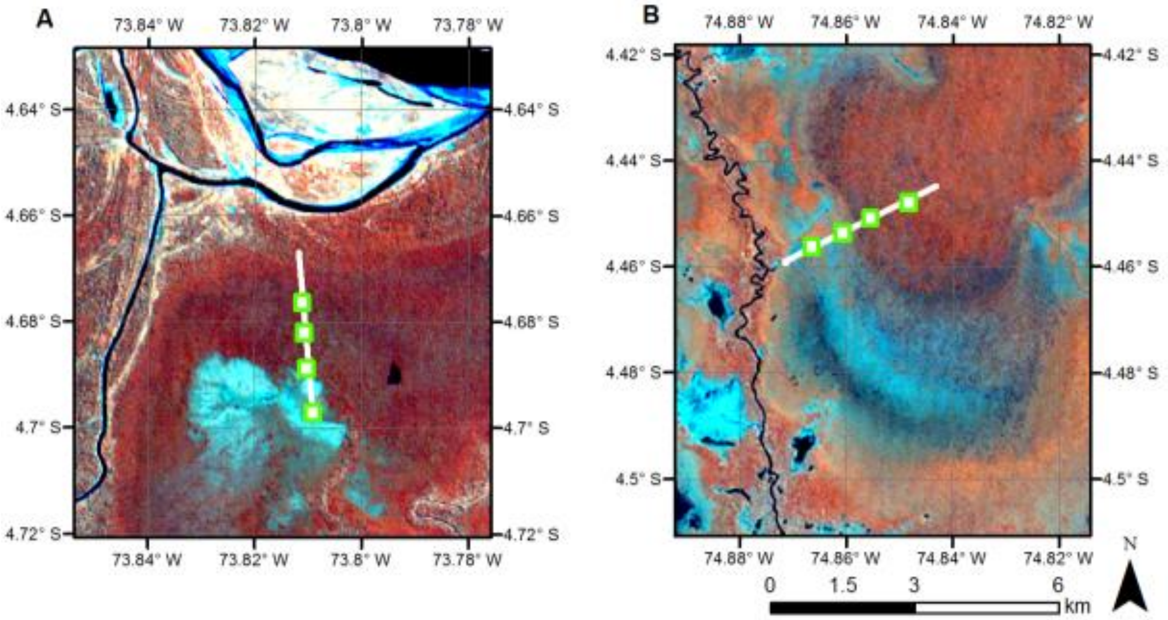

Figure 4.2 Landsat satellite imagery of the two sites where bands four, five and seven have been assigned to red, green and blue respectively. Broadly speaking, in this region shades of pale blue indicate open peatlands, dark red shades indicate palm swamps and brown/orange shades indicate pole forests (chapter 1). The site transects have been marked with white lines; plot and core location are marked with green boxes.

4.4.2 Forest census data

In order to characterise the vegetation in terms of composition and diversity at the present day, the transect crossing each site was divided into the major vegetation zones differentiated on the basis of forest structure and composition. Approximately in the centre of each vegetation zone a 0.5 ha forest plot was established. The forest plots were established following a modified RAINFOR protocol (Phillips et al. 2009), whereby all trees with a diameter greater than 10 cm at 1.3 m above ground level (dbh) were measured, given an individually numbered tag, and identified to the highest possible taxonomic resolution. In addition to these measurements of large trees, a 4 x 100 m subplot was established in each plot, within which all trees and shrubs with a dbh between 2 and 10 cm were measured and identified. A final subplot of 1 x 100 m was used to identify herbaceous taxa. This protocol is the same as in Chapters 2–4. Botanical samples were taken for all species identified in the plots, and field identifications were confirmed or corrected following comparisons with herbarium specimens at the Herbario Amazonense in Iquitos.

4.4.3 Core retrieval

In order to obtain palaeoecological records, peat cores were recovered from the centre of each forest census plot using a manually operated Russian-type peat corer (Jowsey 1966). Cores were sub-sampled in the field at 16 cm intervals, and samples were double bagged and transported to Iquitos and subsequently to the UK where they were stored under licence at 4°C. The cores from Veinte de Enero were recovered in July 2012 and the cores from Ollanta in August 2013. Pollen surface samples were also taken from the centre of each of the census plots.

4.4.4 Pollen analysis

1 cm^3 subsamples were taken at intervals of between 0.32 and 0.16 m intervals through each of the cores. Pollen samples were prepared for analysis following Berglund and Ralska-Jasiewiczowa (1986). A known concentration of 'exotic' *Lycopodium clavatum* spores was added to act as a marker in order to determine the concentration of pollen grains in each sample (Stockmarr 1971). Samples were mounted in silicone oil and examined at x630 magnification and at x1000 for critical determinations. Samples from the central cores from both sites (OLL 1 and VEN 1) were counted up to a main sum total of at least 300 grains. Samples from the other six cores were counted until a main sum of at least 100 grains was reached. The main sum did not include Pteridophyte spores or damaged pollen grains that could not be identified. Pteridophyte spores were excluded because, where they did occur, they were often found in exceedingly high concentrations. If these spores were included in the main count it would have led to the exclusion of the majority of tree taxa in many samples, which would have meant a substantial loss of ecological information.

4.4.5 Pollen sample size

In order to assess the efficacy of using low pollen counts to describe peatland pollen communities, rarefaction analysis was undertaken. The core in which the greatest number of pollen types were found (OLL 1) was chosen for this analysis, as this core is likely to be least well represented by small pollen counts due its high diversity. Samples in this core had been counted to a minimum of 300 grains. Rarefaction curves were generated for each sample and extrapolated up to 500 grains, in order to assess how increased counting would affect estimates of pollen taxa diversity. All samples were bootstrap resampled 500 times in order to generate these rarefaction curves. All rarefaction analysis was performed using the *EstimateS* programme (Colwell 2013).

4.4.6 Pollen taxonomy

Pollen identifications were based on pollen reference collections at the University of Leeds, published pollen floras (Roubik & Moreno 1991; Colinvaux et al. 1999), the Neotropical pollen database (Bush & Weng 2007), and relevant published descriptions (Weber et al. 1999; Burn & Mayle 2008). All pollen morphotypes were identified to the lowest possible taxonomic level, and details of all pollen types can be found in Appendix 4.1. Pollen types were deemed to be ecologically insignificant if the taxonomic level to which they could be identified offered little ecological information. For example, pollen assigned to Rubiaceae undifferentiated could represent a range of lifeforms (herbs, lianas, shrubs or large trees) and a range of habitat types (Gentry 1994) and therefore provides little information. Summary pollen diagrams were constructed for each core using PSIMPOLL (Bennett 2008). Pollen taxa that offered some ecological information but cannot be associated with a specific forest community type have been presented individually in the pollen diagrams.

4.4.7 Statistical analysis

Multivariate analysis was used to identify patterns in pollen composition within and amongst cores and sites. Non-metric multidimensional scaling (NMDS) ordinations were constructed using abundance data for all identified pollen morphotypes. Due to the high number of zeros within the sample by morphotype matrix, the data were first transformed into a Hellinger distance matrix (Legendre & Legendre 2012a; Legendre & De Cáceres 2013). Ordination analysis was undertaken on the two sites separately and together. Site scores were then extracted and plotted against sample depth.

Additionally, a novel multivariate modelling technique was used to test the significance of the relationship between pollen composition and the explanatory variables of sample depth, sample age, core and site. This approach provides an opportunity to explore the role of autogenic and allogenic processes in determining vegetation development patterns. If succession is an important process in determining patterns of development within each site, then a significant relationship between pollen composition and sample depth or sample age would be expected across cores. Additionally, there would be little interaction between sample depth and core because an increase in peat depth would be expected to have a predictable effect on floristic composition. Alternatively, if allogenic processes are important, then sample age and sample depth would be poor predictors of pollen composition and there would be significant differences between cores and a strong interaction effect between core and sample depth. If the successional pathway was consistent between sites then significant relationships would be expected between pollen composition and sample depth and age across all cores from both sites. Additionally, there would be no significant interaction between sample depth and site.

To complete these tests, a multiple generalised linear model (many GLM) framework in the R package MVABUND was used (Wang et al. 2012). This procedure involves firstly fitting individual GLMs to abundance data for each pollen morphotype using a common set of explanatory variables (sample depth, sample age, site and core). Next, generalised estimating equations were used to model the community level response (i.e all pollen morphotypes) to the set of explanatory variables (Warton 2011). Finally, a bootstrap resampling anova function was used to test the significance of sample depth, sample age, core and site in determining pollen composition. As expected, the pollen morphotype abundance data had a strong mean variance relationship, i.e. as mean abundance of each taxon increases so does its variance (Figure 4.3, panel A), and therefore a negative binomial distribution was used to model the pollen abundance data. This distribution was found to be suitable as shown in the residuals versus fitted plot (Figure 4.3, panel B*).* All statistical analysis was conducted in the R statistical environment (R Core Team 2012a).

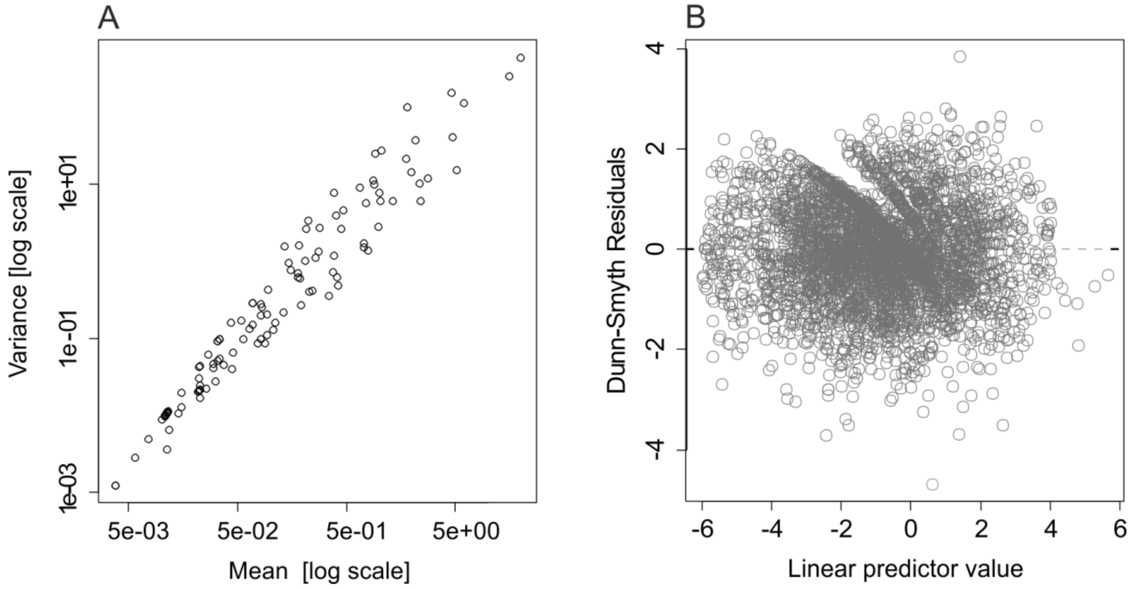

Figure 4.3 Model suitability tests for the MVABUND modelling framework for pollen morphotype abundance data for all taxa across all sites. Suitability of the negative binomial GLM is confirmed by a strong mean variance relationship (panel A) and no obvious pattern in the residual vs. fitted values plot (panel B).

4.4.8 Age models

Fourteen radiocarbon dates were obtained across the two sites, from four samples at equally spaced depths from the central cores of both sites (OLL-C1 and VEN-C1), and from the base of the remaining cores. All radiocarbon dates consisted of bulk peat samples, which were sieved to remove root material that could contaminate the samples prior to analysis. Samples were treated with acid-base-acid digestions prior to analysis in order to remove carbonates and humic acids, and dated by AMS at the NERC radiocarbon facility, East Kilbride. The dates were calibrated using the R package clam v2.2 (Blaauw 2010) and the INTCAL13 calibration curve (Reimer et al. 2013).

4.5 Results

4.5.1 Site survey

At the Veinte de Enero site peat depth increased from the margin towards the centre of the peatland for the first 1500 m, at which point the peat was a fairly uniform three metres in thickness, until the 2700 m point where peat thickness decreased to 2.2 m before increasing again to a maximum depth of 3.6 m (Figure 4.4). Canopy height at this site decreased from the margins towards the centre and the vegetation changed from seasonally flooded forest, through palm swamp, to a small area of pole forest, and finally to an open peatland. The water table was within a few cm of the surface across the site. Basal radiocarbon dates from across the site suggest that peat first began to accumulate in the centre of the peatland and most recently towards the peatland margin (Figure 4.4). However, the similar dates from cores VEN 3 and VEN 4 suggest that peat initiated at similar times across much of the marginal area of the site.

The Ollanta site shows quite different patterns to the Veinte de Enero site in a number of ways. Firstly, canopy height increased towards the centre and the vegetation along the entire transect was composed of pole forest although its composition varied substantially. Peat depth initially increased from the edge of the site towards the centre, from < 1 m to 4 m, although the peat soon became shallow again, suggesting that there is a slightly deeper area, possibly a channel, towards the edge of the peatland. The peat depth again increased towards the centre of the peatland for the remaining 2 km of the transect. Unlike Veinte de Enero, the oldest basal date was not found in the centre of the site but towards the peatland margin, in the small but deeper area, where peat began to form some 4000 years before the next closest sample along the transect (Figure 4.4). The centre of the site, in fact, began to accumulate peat most recently, whilst the two middle cores have similar basal dates suggesting that peat initiation was more or less synchronous over this part of the site (Figure 4.4).

The Ollanta site also appears to be different to Veinte de Enero in terms of the degree to which it is flooded by the nearby river. Clear flood marks could be seen on trees at the Ollanta site; these marks were 3 m high at the edge of the site and gradually decreased in height towards the centre until they were no longer visible at approximately 2000 metres (Figure 4.4). This suggests that the site may be domed with the centre of the peatland at least 3 m higher than the edge. Furthermore, as peat thickness close to the site margin is broadly equivalent to the central part of the site, the underlying topography must also be higher in the middle than at the edge.

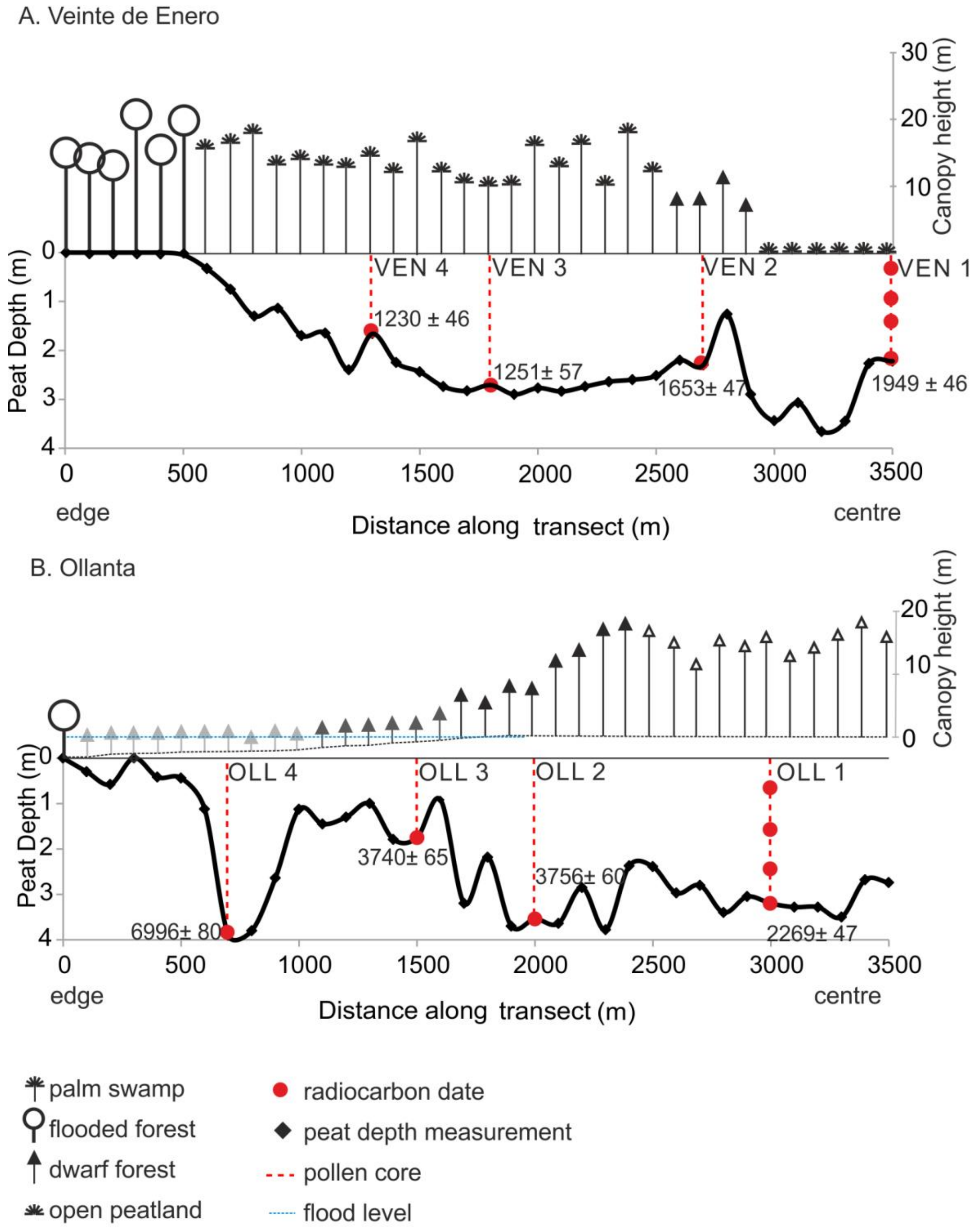

Figure 4.4. Site schematics for the Veinte de Enero site (panel A) and the Ollanta site (panel B). Schematics show a diagrammatic cross section of the transects at each site, giving the peat thickness and canopy height of the vegetation across the transect. Different shades of grey for the pole forest at the Ollanta site indicate the different types of pole forests as defined by the vegetation structure and composition. Pollen core depths presented here do not reflect the exact depths of these cores, but instead provide a visual representation of core locations. Separate cores were taken for pollen analysis and radiocarbon dating. Precise depths of pollen samples and radiocarbon dates are presented in the pollen diagrams.

4.5.2 Forest plot analysis

Vegetation communities differed not only between the two study sites but also within each site, as had been predicted based on analysis of satellite imagery. The edge of the Veinte de Enero site was marked by a transition from a tall seasonally inundated forest into a mixed palm swamp dominated by the large arboreal palm *Mauritia flexuosa*. This was evident in Veinte de Enero plot four, in which *M. flexuosa* accounted for 75% of stems ≥10 cm dbh (Table 4.1). Another arboreal palm, *Mauritiella armata*, became increasingly dominant towards the centre of the peatland, and was the most abundant species in Plot 3. The next vegetation zone represented by Plot 2 was marked by a decrease in these two large palm species and an increase in small trees and shrubs, particularly those belonging to Clusiaceae and Myrtaceae (Table 4.1). The final vegetation zone found in the centre of this peatland was an open and almost entirely herbaceous community), a few small individuals of *Tabebuia insignis* were recorded along with a number of *Ilex sp.* and *Mauritiella armata* saplings on the two subplot transects (4 x 100 m) that made up Plot 1 (no full plot was established as there were no trees with a dbh ≥ 10 cm). The dominant taxa in this zone were herbaceous species, particularly grasses (Poaceae) and sedges (Cyperaceae).

The Ollanta site was found to have a different but equally striking vegetation transition, both structurally and floristically, despite all vegetation communities along the transect being broadly classified as pole forest on the basis of their structure (Chapter 2). The first vegetation zone at the peatland margin was a low stature pole forest, dominated by species associated with seasonal inundation such as *Macrolobium multijugum* and *Symmeria paniculata* as found in Ollanta Plot 4 (Table 4.2). This was followed by an extremely low stature (3 m canopy) dense forest, which was almost entirely dominated by *Tabebuia insignis* and *Cybianthus cf. reticulatus*. These two species together accounted for more than 80 % of the stems in Plot 2. Other taxa of importance in this zone, particularly in stems ≥ 10 cm dbh, were the palm *Mauritiella armata* and the swamp specialist *Lueheopsis hoehnei*. As the transect continued towards the centre of the peatland out of the seasonally flooded zone, *Pachira brevipes*, previously considered to be a white sand specialist became increasingly dominant. In plot two

P. brevipes formed a monodominant stand and accounted for over 75% of stems. Another important transition at this stage was the palm *Mauritia flexuosa* increasing in abundance and effectively replacing *Mauritiella armata*. The community (represented by Plot 1) in the centre of the Ollanta site was a relatively tall and diverse pole forest, comparable with other peatland pole forests in the region (Chapter 3). *Pachira brevipes* remained abundant, but was now augmented with *Platycarpum sp.1*, a large canopy tree belonging to the Rubiaceae (Table 4.2).

4.5.4 Relationship between pollen and vegetation composition

At both sites the current vegetation assemblages are reflected in the pollen composition of core top samples, and different peatland ecosystems types can be distinguished based on the pollen composition. However, the relationship between pollen and vegetation composition is complex. In some instances a minority of key indicator taxa provide much of the ecological information. For example, in the top samples of cores OLL 1 and OLL 2, the presence of *Pachira brevipes*, a pole forest specialist (Chapter 3), is a strong indicator of pole forest as both this species and its conspicuous pollen are found in no other ecosystem. Similarly, the presence of *Symmeria paniculata* pollen in the top sample of core OLL 4 clearly represents a seasonally flooded ecosystem (Gentry 1994). In other pollen assemblages the concentration of common anemophilous taxa are more useful descriptors. For example, in core VEN 1 there are few key indicator taxa and, instead, an open peatland is represented by high concentrations of grass and sedge pollen alongside substantial amounts of the anemophilous tree genus *Cecropia*. Likewise, palm swamp ecosystems in cores top samples of VEN 3 and VEN 4 are represented by high concentrations of *Mauritia* type and *Ilex* pollen.

Table 4.1. The ten most abundant species of tree in two size classes in the four forest census plots at Veinte de Enero. Taxa in bold are those which are identified in the pollen record.

Veinte de Enero P1

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1				**Bignoniaceae**	***Tabebuia insignis***	19
2				**Euphorbiaceae**	***Alchornea*** *discolor*	5
3				**Aquifoliaceae**	***Ilex*** *cf. inundata*	5
4				**Arecaceae**	***Mauritiella*** *armata*	3
5				Arecaceae	*Montrichardia*	
6				**Poaceae**	*Pariana*	
7				**Cyperaceae**	*Scleria*	

Veinte de Enero P2

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Arecaceae**	***Mauritia*** *flexuosa*	80	Clusiaceae	*Tovomita cf. krukovii*	161
2	**Bignoniaceae**	***Tabebuia insignis***	47	**Rubiaceae**	*indet*	26
3	**Aquifoliaceae**	***Ilex sp***	27	**Myrtaceae**	*Calyptranthes sp.1*	13
4	**Arecaceae**	***Mauritiella*** *armata*	21	**Myrtaceae**	*Blepharocalyx sp. 1*	11
5	**Annacardiaceae**	***Tapirira guianensis***	13	**Annacardiaceae**	***Tapirira guianensis***	9
6	Primulaceae	*Cybianthus cf. reticulatus*	10	**Euphorbiaceae**	***Alchornea*** *discolor*	8
7	**Clusiaceae**	***Symphonia globulifera***	3	Clusiaceae	*Garcinia sp.1*	4
8	**Urticaceae**	***Cecropia*** *latiloba*	2	Annonaceae	*Guatteria sp.1*	3
9	**Euphorbiaceae**	***Alchornea*** *discolor*	2	Lauraceae	*Ocotea sp.1*	3
10	**Malvaceae**	***Lueheopsis*** *hoehnei*	2	**Apocynaceae**	***Malouetia*** *tamaquarina*	2

Veinte de Enero P3

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Arecaceae**	***Mauritiella*** *armata*	141	**Bignoniaceae**	***Tabebuia insignis***	43
2	**Arecaceae**	***Mauritia*** *flexuosa*	126	**Aquifoliaceae**	***Ilex*** *cf. inundata*	19
3	**Bignoniaceae**	***Tabebuia insignis***	17	**Euphorbiaceae**	***Alchornea*** *discolor*	7
4	**Aquifoliaceae**	***Ilex cf. inundata***	13	**Arecaceae**	***Mauritiella*** *armata*	4
5	**Euphorbiaceae**	***Alchornea*** *discolor*	3	Clusiaceae	*Clusia hammeliana*	4
6	**Urticaceae**	***Cecropia*** *latiloba*	2	Araliaceae	*Dendropanax indet*	2
7	Primulaceae	*Cybianthus cf. reticulatus*	2	Lauraceae	*Ocotea indet*	2
8	**Moraceae**	***Ficus americana***	1	**Clusiaceae**	***Symphonia globulifera***	1
9				**Annacardiaceae**	***Tapirira guianensis***	3
10				Primulaceae	*Cybianthus cf. reticulatus*	1

Veinte de Enero P4

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Arecaceae**	***Mauritia*** *flexuosa*	179	**Bignoniaceae**	***Tabebuia insignis***	58
2	**Bignoniaceae**	***Tabebuia insignis***	26	**Clusiaceae**	***Symphonia globulifera***	12
3	**Aquifoliaceae**	***Ilex*** *cf. inundata*	14	**Euphorbiaceae**	***Alchornea*** *discolor*	10
4	**Arecaceae**	***Mauritiella*** *armata*	13	Clusiaceae	*Tovomita cf. krukovii*	7
5	**Arecaceae**	***Euterpe precatoria***	11	**Rubiaceae**	*Kutchubaea semisericea*	7
6	**Euphorbiaceae**	***Alchornea*** *discolor*	4	**Myrtaceae**	*Blepharocalyxindet*	3
7	**Annacardiaceae**	***Tapirira guianensis***	1	**Myristicaceae**	***Virola*** *pavonis*	3
8	**Moraceae**	***Ficus*** *americana*	1	**Sapotaceae**	***Pouteria*** *cuspidata*	3
9	**Fabaceae**	***Macrolobium*** *multijugum*	1	**Moraceae**	***Ficus*** *caballina*	3
10				**Myrtaceae**	*Eugenia stipitata*	2

Table 4.2. The ten most abundant tree species in two size classes in the four Ollanta forest census plots. Taxa in bold are those identified in the pollen record.

Ollanta P1

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Fabaceae**	***Macrolobium*** *sp. 1*	95	**Rubiaceae**	*Remijia pacimonica*	31
2	Annonaceae	*Oxandra mediocris*	75	Annonaceae	*Oxandra mediocris*	21
3	**Arecaceae**	***Mauritia*** *flexuosa*	65	**Rubiaceae**	*Ferdinandusa loretensis*	21
4	**Malvaceae**	***Pachira brevipes***	63	**Euphorbiaceae**	*Hevea guianensis*	19
5	**Rubiaceae**	*Platycarpum sp. 1*	62	**Bignoniaceae**	***Tabebuia insignis***	18
6	**Euphorbiaceae**	*Hevea guianensis*	49	Lauraceae	*Aniba hostmanniana*	16
7	**Rubiaceae**	*Remijia pacimonica*	23	Annonaceae	*Guateria decurrens*	15
8	Sapindaceae	*Matayba inelegans*	15	**Rubiaceae**	*Platycarpum sp. 1*	14
9	Annonaceae	*Guateria decurrens*	9	Annonaceae	*Pseudoxandra polyphleba*	13
10	**Aquifoliaceae**	***Ilex*** *vismiifolia*	9	Olacaceae	*Heisteria acuminata*	12

Ollanta P2

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Malvaceae**	***Pachira brevipes***	442	**Malvaceae**	***Pachira brevipes***	85
2	Primulaceae	*Cybianthus cf. reticulatus*	73	**Bignoniaceae**	***Tabebuia insignis***	42
3	**Arecaceae**	***Mauritia*** *flexuosa*	26	**Rubiaceae**	*Pagamea guianensis*	38
4	**Rubiaceae**	*Platycarpum sp.1*	21	**Euphorbiaceae**	*Hevea guianensis*	36
5	**Fabaceae**	***Macrolobium*** *sp. 1*	13	Annonaceae	*Oxandra mediocris*	10
6	**Rubiaceae**	*Pagamea guianensis*	7	Annonaceae	*Guateria decurrens*	9
7	Fabaceae	*Ormosia coccinia*	2	**Fabaceae**	***Macrolobium*** *sp. 1*	8
8	Fabaceae	*Vatairea sesbania*	1	Primulaceae	*Cybianthus cf. reticulatus*	7
9	**Moraceae**	***Ficus*** *americana*	1	Clusiaceae	*Tovomita sp.1*	3
10	Sapindaceae	*Matayba inelegans*	1	Sapindaceae	*Matayba inelegans*	3

Ollanta P3

		Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**	
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	**Arecaceae**	***Mauritiella armata***	51	Primulaceae	*Cybianthus cf. reticulatus*	739
2	**Malvaceae**	***Lueheopsis*** *hoehnei*	14	**Bignoniaceae**	***Tabebuia insignis***	707
3	Primulaceae	*Cybianthus cf. reticulatus*	7	**Rubiaceae**	*Pagamaea guianensis*	75
4	**Rubiaceae**	*Pagamea guianensis*	3	**Combretaceae**	*Buchenavia grandis*	4
5	**Bignoniaceae**	***Tabebuia insignis***	2	**Euphorbiaceae**	*Hevea guianensis*	38
6	**Euphorbiaceae**	*Hevea guianensis*	2	**Malvaceae**	***Lueheopsis*** *hoehnei*	20
7				Annonaceae	*Pseudoxandra polyphleba*	8
8				**Polygonaceae**	*Coccoloba sp*	7
9				**Aquifoliaceae**	***Ilex*** *vismiifolia*	6
10				Olacaceae	*Tetrastylidium sp*	6

Ollanta P4

	Stems ≥ 10 cm DBH			**Stems 2-10 cm DBH**		
Rank	**Family**	**Genus-species**	**No. of stems**	**Family**	**Genus-species**	**No. of stems**
1	Fabaceae	***Macrolobium*** *multijugum*	297	Primulaceae	*Cybianthus cf. reticulatus*	510
2	**Arecaceae**	***Mauritiella*** *armata*	188	**Fabaceae**	***Macrolobium*** *multijugum*	107
3	Sapotaceae	*Chrysophyllum sp1*	16	Sapotaceae	*Chrysophyllum sp1*	46
4	Primulaceae	*Cybianthus cf. reticulatus*	6	Lauraceae	*Aniba guianensis*	35
5	**Combretaceae**	*Buchenavia grandis*	3	**Polygonaceae**	***Symmeria paniculata***	15
6	**Moraceae**	***Ficus*** *americana*	3	**Rubiaceae**	*Chimarrhis hookeri*	13
7	**Aquifoliaceae**	***Ilex*** *vismiifolia*	3	Polygonaceae	*Coccoloba sp*	12
8	**Bignoniaceae**	***Tabebuia insignis***	1	Fabaceae	*Machaerium macrophyllum*	11
9	**Euphorbiaceae**	***Alchornea*** *discolor*	1	**Myrtaceae**	*Calyptranthes cf. multiflora*	9
10	Fabaceae	*Machearium cuspidatum*		**Combretaceae**	*Buchenavia Amazonia*	3

4.5.3 Age-depth models

Calibrated radiocarbon dates from the Veinte de Enero central core (VEN 1) are in broadly stratigraphic order (Figure 4.5, panel A). The two middle samples from this core were found to be similar in age. This suggests either a rapid rate of peat accumulation during this period, or that the upper sample at 95 cm has been contaminated with some modern root material despite careful sieving. Calibrated radiocarbon dates from the Ollanta site are more clearly in stratigraphic order (Figure 4.5, panel B), apart from the topmost sample which suggests that accumulation rates have been fast within the top 50 cm. Age-depth models were developed using linear interpolation. Mean peat accumulation rate at the two sites was similar, 1.29 mm yr-1 at the Veinte de Enero site and 1.27 mm yr-1 at the Ollanta site.

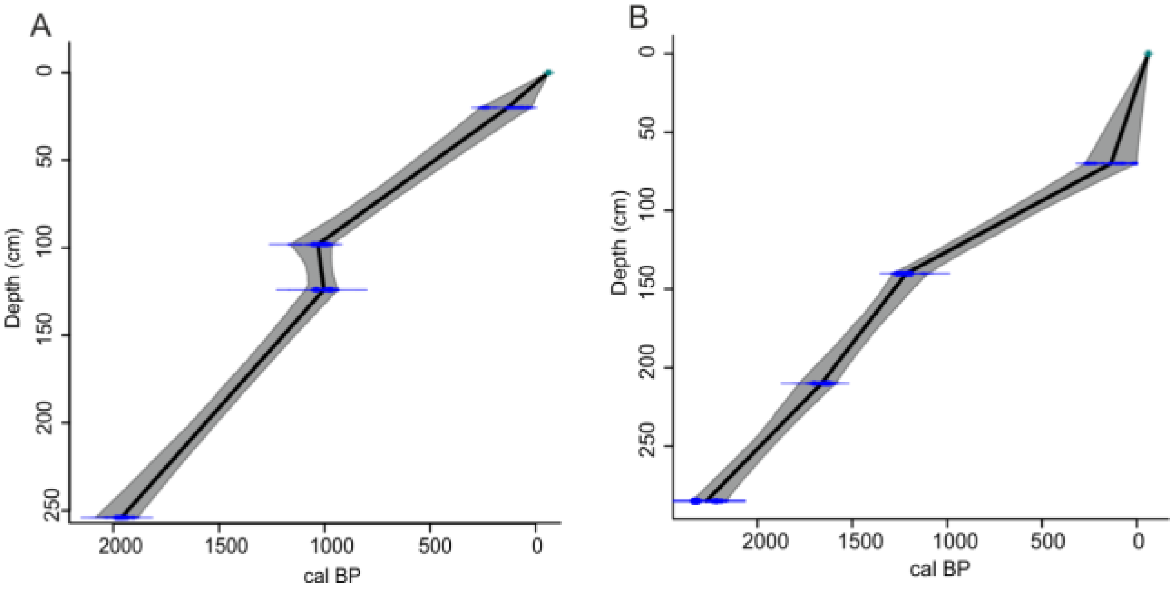

Figure 4.5 Age-depth models from the two central cores of Veinte de Enero (panel A) and Ollanta (panel B), The solid black line shows the interpolated statistically optimal model, the grey shaded area shows the 95% confidence interval and the probability distributions of each calibrated date based on the INTCAL13 calibration curve (Reimer et al. 2013) are shown in blue.

4.5.5 Pollen analysis

The four pollen diagrams from the Veinte de Enero site show a number of consistencies. One common feature is a high concentration of anemophilous *Cecropia* pollen at the base of the cores despite peat initiating at different times across the site (Figure 4.6 and Table 4.3). This indicates that either *Cecropia* trees were abundant at the site at peat initiation, perhaps reflecting some large scale disturbance such as river avulsion as *Cecropia* is a genera of pioneer species. Alternatively high concentrations of *Cecropia* may indicate that the site was open during the onset of peat formation, as *Cecropia* is anemophilous and occurs in high concentrations in lake samples when it is regionally abundant. Another consistency towards the base of the four cores is the occurrence of *Symmeria paniculata*, Myrtaceae and possible *Miconia* pollen (Figure 4.6 and Table 4.3), indicating that a flooded forest community followed the initial open phase. Moving up through these cores, the middle section is dominated by Poaceae and Cyperaceae pollen alongside typically herbaceous taxa including Compositae and *Begonia* (Figure 4.6 and Table 4.3). Together these taxa indicate that an open and predominantly herbaceous community was present at this site throughout much of its development. This community is found currently in the centre of the peatland, and the vegetation composition is well represented by the pollen (Table 4.1 and Figure 4.6).

In three of the cores (VEN 2, VEN 3 and VEN 4) there is also evidence of the development of aquatic conditions, inferred from the occurrence of *Pistia stratiotes* pollen. This common aquatic herb is found in lake and river environments as well as peat swamp forest (Atrium 2014). In core VEN 4 there is a particularly prominent peak in *Pistia* pollen, suggesting that there was an aquatic phase at this core site. The final major transition is from an open, herb-dominated ecosystem into a palm swamp (Figure 4.6 and Table 4.3). This transition appears to occur first in the cores towards the peatland margin, whilst in the centre of the peatland *Maurita/Mauritiella* pollen is a relatively recent arrival, this is reflected in the present day vegetation, which is predominately open but contains a few patches of *Mauritiella*.

The four Ollanta pollen diagrams show considerable variation across the site (Figure 4.7 and Table 4.4). Despite this variation, however, there are three consistent patterns occurring in the lower section of the cores across the site. Firstly, *Mauritia/Mauritiella* type pollen is found at the base of three of the four cores (Figure 4.7 and Table 4.4), suggesting that this site was already a palm swamp at the onset of peat formation as its pollen is not transported far (Rull 1998). Secondly, three of the cores (excluding the central core) show high concentrations of *Cecropia* pollen near the base, indicating either disturbance or increased canopy openness in the early phases of peat accumulation (Figure 4.7 and Table 4.4). Thirdly, this trend is followed by the characteristic flooded forest taxa *Symmeria paniculata*, Myrtaceae and Combretaceae.

At this point the diagrams diverge, and substantial differences can be seen across the site. The pollen in the core closest to the peatland boundary (OLL4) appears to switch repeatedly between an inundated forest, an open herbaceous peatland and more occasionally a palm swamp (Figure 4.7 and Table 4.4). The area of the site appears to have been an inundated forest for most of its development, and this is also reflected in the current vegetation at OLL 4. Although the site has been classified as a pole forest, it has strong elements of a black water flooded forest, including the presence of *Symmeria paniculata*, and species in the Combretaceae and Myrtaceae. Such flooding is likely to leave significant alluvial deposits, and the numerous layers of clay found in these outer cores provide further support for persistent flooding at the site margin.

The pollen diagrams from the two more central cores (OLL 1 and OLL 2) show that the taxa associated with flooded forests, *Symmeria paniculata* and Combretaceae, have been less abundant towards the centre of the site. Instead, *Mauritia /Mauritiella* have been abundant since peat initiation, although there has been greater variation in OLL 2. This suggests that this central area of the peatland has been a palm swamp for most of its development. There are also a number of other clear stages including a period dominated by first an unknown Malvaceae and then by a species belonging to *Pouteria*. Crucially, *Pachira brevipes*, the species which dominates the present pole forest flora, is a relatively recent addition to the site, being evident only in the top few samples (Figure 4.7). The unknown Rubiaceae that appears at the top of these two cores is assumed to be either the *Platycarpum sp.1* morphospecies, or *Remijia* *pacimonica*, both of which were observed in the forest census and are also key indicators of pole forest communities.

Core OLL 3 shares some similarities with Core OLL 4, such as reversals between palm swamp forest and seasonally flooded forest. However, it also has a number of differences. The high concentrations of *Cecropia* and grass pollen in the bottom half of the core suggest that there has been a relatively open canopy for much of the development at this core site. The abundance of *Mauritia/Mauritiella* and *Lueheopsis* pollen also suggest that this core site has frequently been a palm swamp. However, a similar palm swamp signal is obtained in the surface sample, and whilst the two most common trees over 10 cm dbh are *Mauritiella armata* and *Lueheopsis hoenhi*, over 80% of the stems are made up of thin stemmed small stature *Tabebuia insignis* and *Cybianthus cf. reticulatus*. *Tabebuia insignis* is poorly represented in the pollen signal and *Cybianthus cf. reticulatus* does not appear to have been recorded at all, perhaps because they are not flowering at this site. This suggests that whilst high concentration of *Mauritia* type pollen do indicate an abundance of *Mauritia* and or *Mauritiella*, this does not necessarily indicate a monodominant palm swamp.

There seem to be a few similarities between the two sites and numerous differences. One similarity across many of the cores is the high concentrations of *Cecropia* pollen at the base. This occurs to a much lesser extent at the Ollanta site and not at all in some cores (OLL 1). This pattern of high concentrations of *Cecropia* pollen at the core-base, suggests that either an open canopy or disturbance can be associated with peat initiation. Another cross-site consistency is the occurrence of floodplain taxa, particularly *Symmeria paniculata* near the base of the pollen records. The occurrence of this floodplain specialist suggests that inundation is also a shared characteristic across these two sites at the point of peat initiation. One of the key differences between the two sites is that whilst all four cores at Veinte de Enero have an extended herbaceous phase dominated by Poaceae and Cyperaceae, only OLL 4 shows any evidence of such a phase at Ollanta. Equally, the occurrence of *Mauritia* type pollen only occurs at the very top of the Veinte de Enero cores, whilst at Ollanta *Mauritia* type pollen is found throughout each of the cores. A final difference is that the key pole forest indicator *Pachira brevipes* is only found at the Ollanta site.

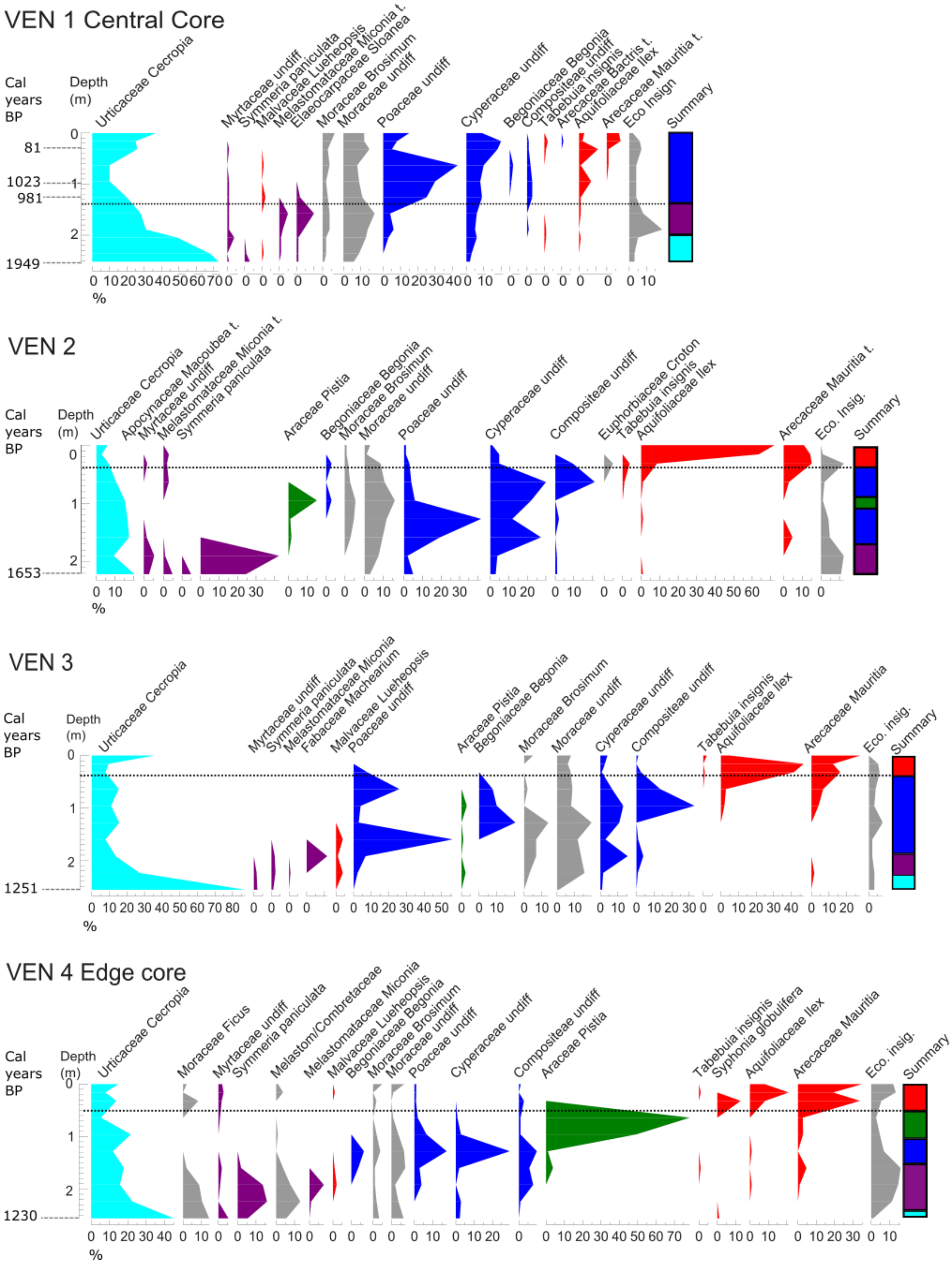

Figure 4.6 Veinte de Enero summary pollen diagrams. Shading represent taxa that can be associated with specific forest communities, palm swamp taxa (red), inundated forest taxa (purple), open herbaceous taxa (dark blue), pole forest (maroon). As *Cecropia* is predominantly interpreted as representing canopy openness it has been given unique shading (light blue). Taxa that are not considered to be ecologically significant have been shaded grey. Horizontal dotted line represents an estimate of where the current vegetation type began to establish.

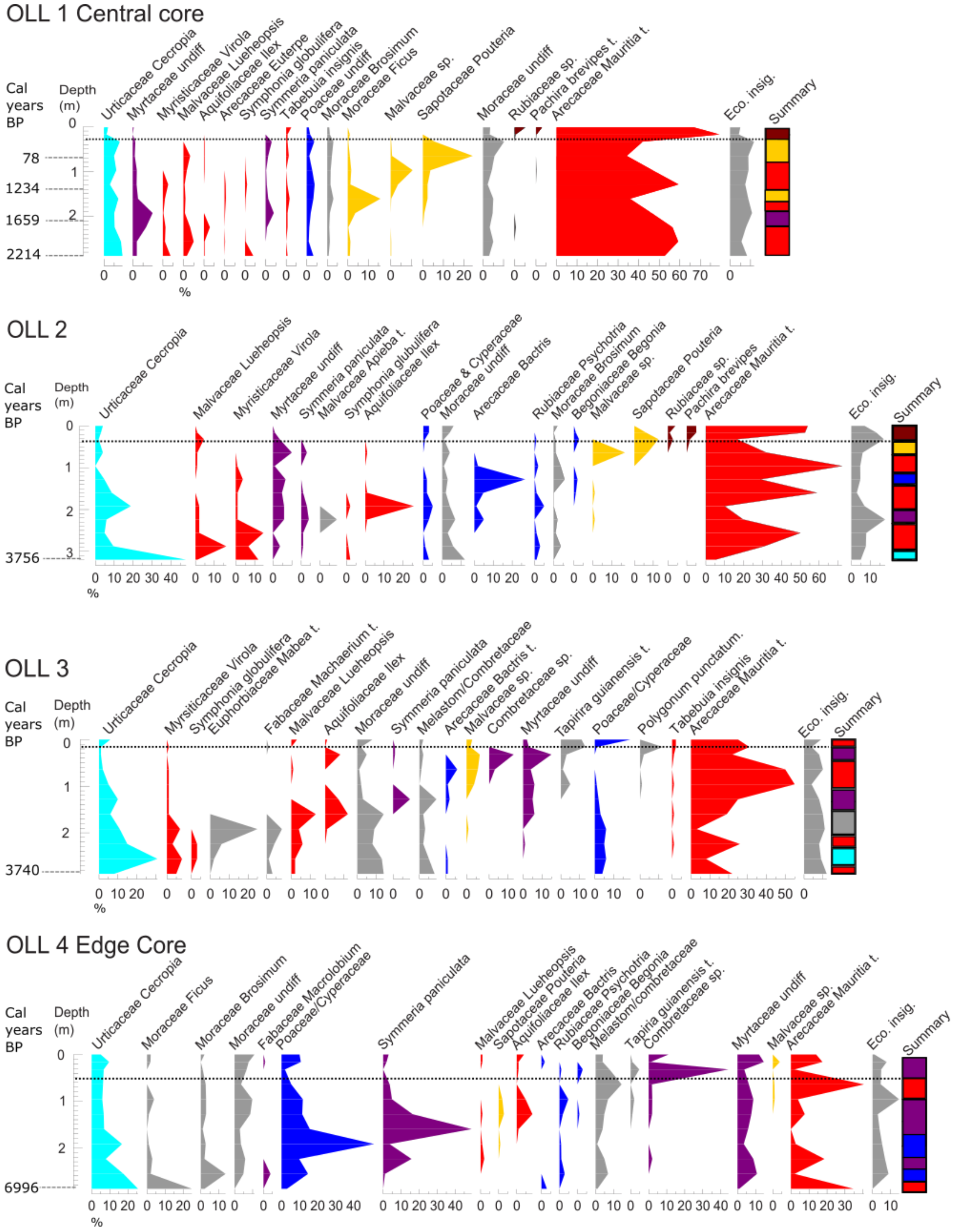

Figure 4.7 Ollanta summary pollen diagrams. Shading represents taxa that can be associated with specific forest communities, palm swamp taxa (red), inundated forest taxa (purple), open herbaceous taxa (dark blue), pole forest (maroon). As *Cecropia* is predominantly interpreted as canopy openness it has been given unique shading (light blue). Yellow shading has been assigned to an unknown sequence that appears to precede pole forest establishment. Taxa that are not considered to be ecologically significant have been shaded grey. Horizontal dotted line represents an estimate of where the current vegetation type began to establish.

Table 4.3 Summary descriptions of the interpreted main community types present in the four Veinte de Enero pollen cores. Top rows represent the present vegetation communities, bottom rows represent communities found at the base of the core. Horizontal rows do not represent equivalent time periods

VEN 1	**VEN 2**	**VEN 3**	**VEN 4**
Evidence of palm swamp taxa establishing, however present community remains open.	Establishment of palm swamp indicated by local presence of *Mauritia/ Mauritiella* and *Ilex*. Exceptionally high abundance of *Ilex* reflected in present community	Establishment of palm swamp indicated by local presence of *Mauritia/ Mauritiella* and *Ilex*.	Establishment of palm swamp indicated by local presence of *Mauritia/ Mauritiella* and *Ilex*.
Open, herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp. Low concentrations of *Pistia* present throughout	High concentration of aquatic taxon *Pistia* indicates an aquatic community was locally present.
Flooded forest, indicated by presence of *Symmeria paniculata*.	Presence of aquatic taxon *Pistia* indicates an aquatic community was locally present	Flooded forest, indicated by presence of *Symmeria paniculata*.	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.
Open community, high concentration of *Cecropia*, possible lake.	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.	Open community, high concentration of *Cecropia*, possible small lake.	Flooded forest, indicated by presence of *Symmeria paniculata*.
	Flooded forest, indicated by presence of *Symmeria paniculata*.		Open community, high concentration of *Cecropia*, possible small lake.

Table 4.4 Brief descriptions of the interpreted main community types present in the four Ollanta pollen cores. Top rows represent the present vegetation communities, bottom rows represent communities found at the base of the core. Horizontal rows do not represent equivalent time periods.

OLL 1	**OLL 2**	**OLL 3**	**OLL 4**
Establishment of pole forest community, indicated by *Pachira brevipes*.	Establishment of pole forest community, indicated by *Pachira brevipes*.	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*.	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae
A community that appear to precede pole forest, dominated by *Ficus* an unknown possibly Malvaceae taxon and a species in the genus *Pouteria*	A community that appear to precede pole forest, dominated by *Ficus* an unknown possibly Malvaceae taxon and a species in the genus *Pouteria*	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*
Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae
A community that precedes pole forest, dominated by *Ficus*, an unknown possibly Malvaceae taxon and a species in *Pouteria*	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.
Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	This phase cannot be attributed to a specific community type, but appears to be dominated by the genus *Mabea*.	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae
Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae	Flooded forest, indicated by presence of *Symmeria paniculata* and Myrtaceae	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Open herbaceous community, locally abundant Poaceae and Cyperaceae, possibly floating mat or fen swamp.
Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	Open community, high concentration of *Cecropia*, possible small lake.	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*
	Open community, high concentration of *Cecropia*, possible small lake.	Palm swamp community, indicated by local abundance of *Mauritia/ Mauritiella*	

4.5.6 Statistical analysis

NMDS biplots reveal some general compositional patterns in the pollen assemblages across the two sites (Figure 4.8). Firstly, in the Veinte de Enero biplot (Figure 4.8 panel A), taxa appear to be distributed along the most important axis of variation (axis one): flooded forest taxa cluster towards the far right of axis one, herbaceous taxa indicative of open communities cluster in the centre, and palm swamp taxa cluster towards the far left of axis one. A similar pattern can been seen in the Ollanta biplot (Figure 4.8 panel B). Again flooded forest taxa cluster towards the far right of axis one, open herbaceous taxa are found in the centre of axis one, palm swamp taxa are found towards the left of axis one and pole forest species are found at the far left of axis one.

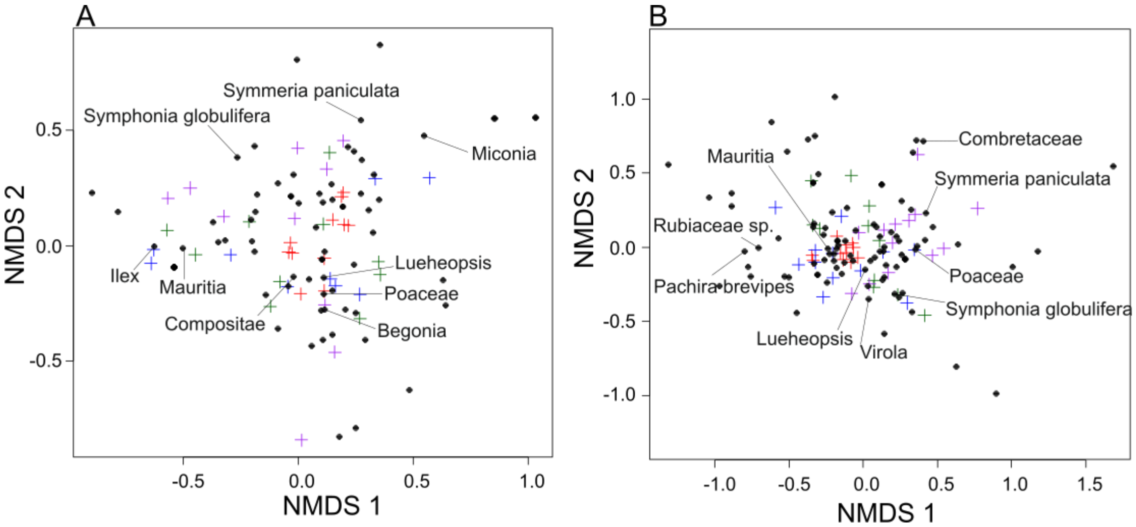

Figure 4.8. NMDS ordination biplots for the Veinte de Enero (Panel A) and Ollanta (Panel B) sites. Sample scores are shown with + symbols and different colours refer to differ cores, core one (site centre, blue), core two (red), core three (green) and core four (site margin, purple). Pollen morphotype scores are shown as black dots, and key taxa have been labelled for clarity.

There are no clear patterns in the site scores in these, rather congested, NMDS biplots, but patterns become evident when these site score are extracted and plotted against depth and age (Figures 4.9 and 4.10). In the individual site level analyses there are clear patterns, indicating similar changes in pollen composition with sample depth and sample age within sites (Figure 4.9 panels A-D and Figure 4.10 panels A-D). There is also clear variation between cores, and some cores are more variable than others; the four Ollanta cores in particular appear to be more variable than those from Veinte de Enero.

When the NMDS sample scores for all cores across both sites are plotted together against depth and age then there are again some clear patterns (Figures 4.9 E and 4.10 E). Firstly, the differences in pollen composition between the two sites are reflected in two distinct site clusters, indicating that the two sites have developed in different ways. Secondly, the limited overlap in pollen composition between the two sites appears to be restricted to the palm swamp communities found towards the base in the Ollanta cores, and towards the top in the Veinte de Enero cores. Core OLL 4 shares similarities with the Veinte de Enero cores throughout its development, presumably reflecting the open communities found in core OLL 4. Finally, although these figures strongly illustrate the differences in the vegetation development between the two sites, they also hint at some similarities. Both communities appear to follow similar trajectories of change through time, as the NMDS gives more weight to common species, reflecting broad scale patterns in the most abundant taxa: for example, the general increase in the concentration of *Mauritia/Mauritiella* towards the top of the cores, and the typically high concentration of *Cecropia* towards the base.

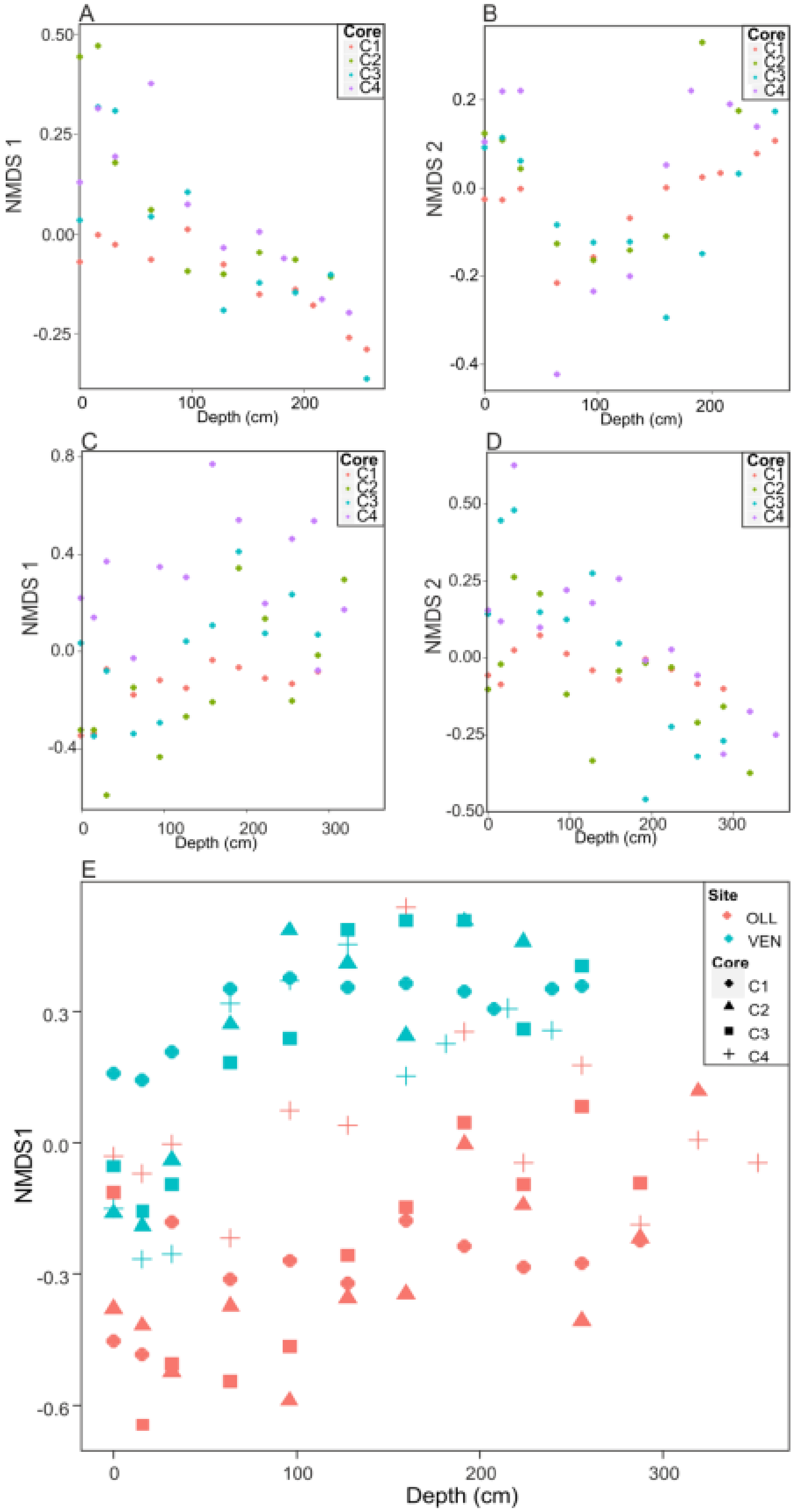

Figure 4.9 Pollen composition as represented by NMDS axis one and two scores plotted against depth for the two sites individually and together. Panels A and B show scores from the four Veinte de Enero cores, panels C and D the four Ollanta cores and panel E all eight cores together.

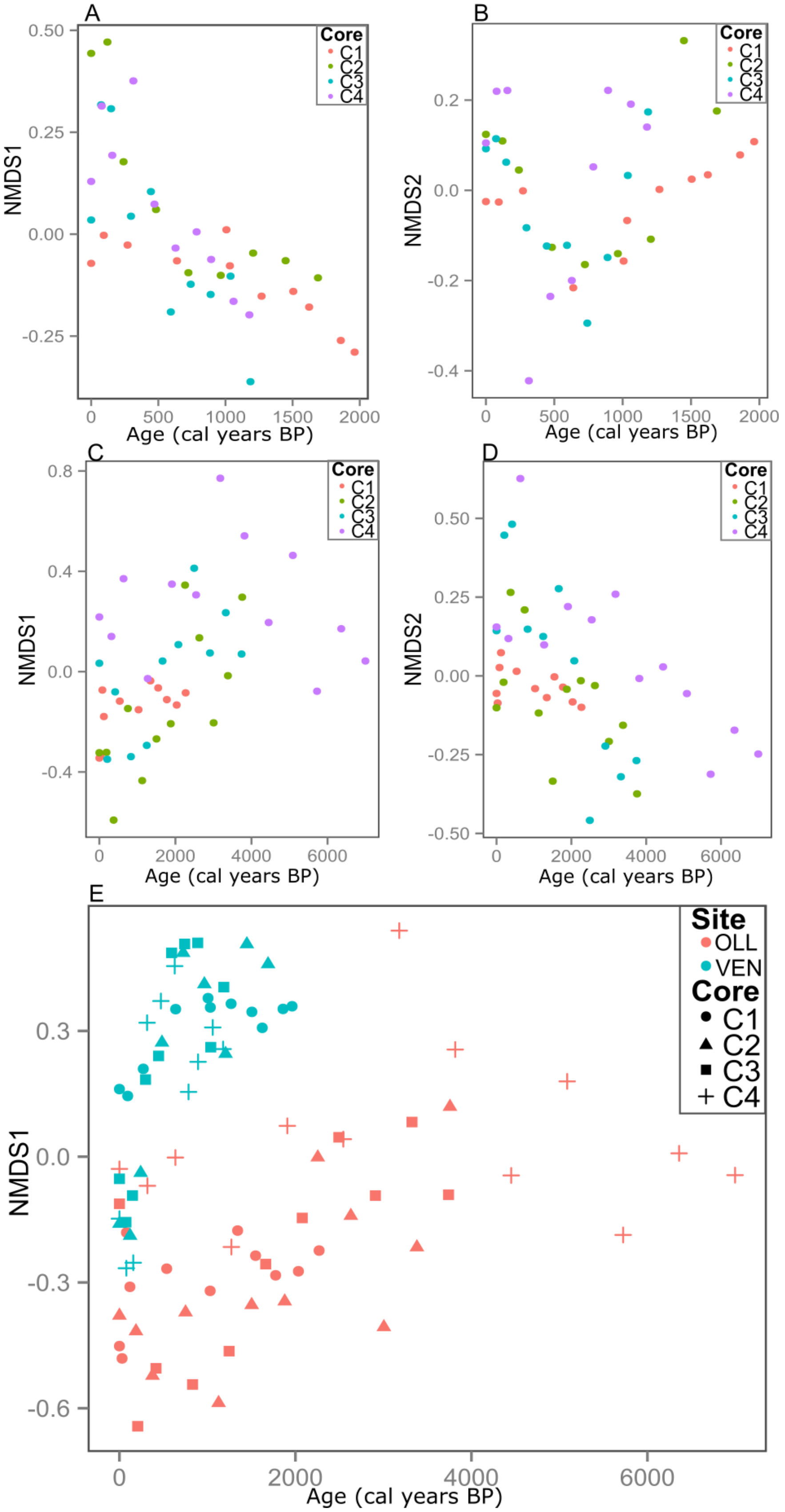

Figure 4.10 Pollen composition as represented by NMDS axis one and two scores plotted against age for the two sites individually and together. Panels A and B show scores from the four Veinte de Enero cores, panels C and D the four Ollanta cores and panel E all eight cores together.

Results from the multiple GLM framework show that across both sites sample depth, sample age, and core were all highly significant variables in explaining differences in pollen composition (Table 4.5). Additionally, there were significant interactions between depth and core at both sites, although these interactions were more marginally significant (Table 4.5). In the case of Veinte de Enero, the significant interaction effect can be attributed to the high concentration of aquatic *Pistia* pollen in the middle part of core VEN 4. Together, these results indicate that although pollen composition is well predicted by both sample depth and age, there is substantial variation between cores from within a site. Furthermore, the moderately significant interaction between depth and cores suggests that the patterns seen between composition and time are variable among cores within a site. Finally, the highly significant interaction between sample depth and site confirms the previous findings that the changes in pollen composition seen at the two sites are different from one another.

Table 4.5 P -values showing the significance of the contribution of four explanatory variables (sample depth, sample age, core and site) in determining differences in composition.

Variable	Both sites	Veinte de Enero	Ollanta
Sample depth	0.001	0.001	0.002
Sample age	0.006	0.001	0.001
Core		0.001	0.001
Site	0.001		
Core*depth interaction		0.45	0.032
Site*depth interaction	0.001		

4.5.7 Pollen sample size

The rarefaction analysis shows that for many samples in the most diverse sample, counting 300 grains is sufficient to encounter the majority of pollen types in these relatively species-poor ecosystems (Figure 4.11). However, counting 100 grains provides ~70% of the pollen types that we could expect to encounter if 500 grains were counted (Figure 4.10). This 70% of taxa will incorporate all of the most abundant taxa, but will likely miss a number of rare pollen types, which may or may not be ecologically important.

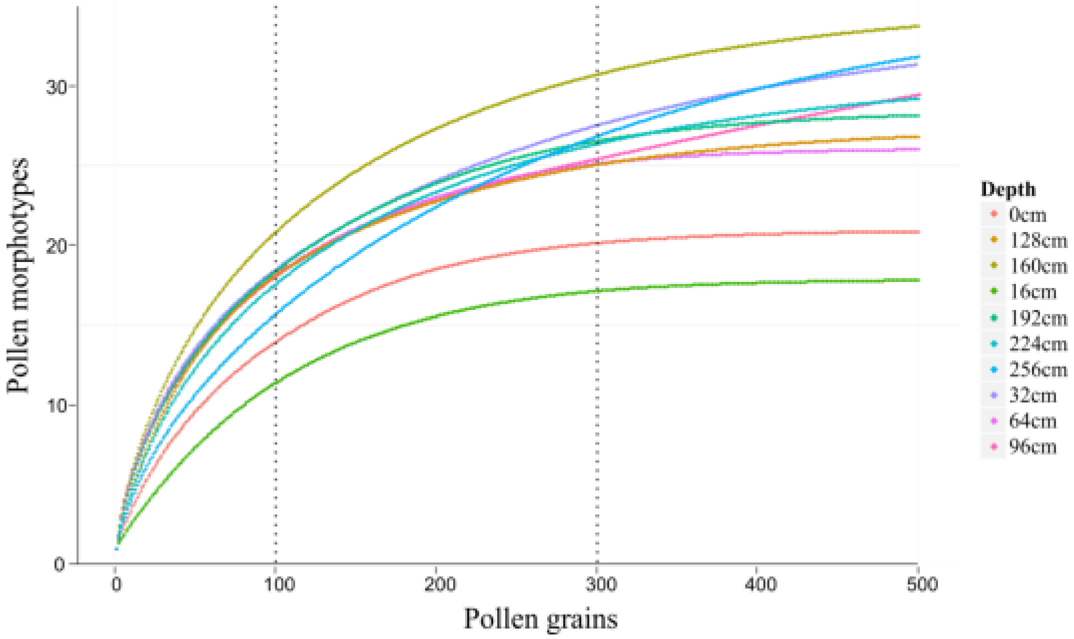

Figure 4.11 Extrapolated rarefaction curves for the most diverse core OLL 1. The rarefaction curves were generated using the estimate S programme. Dashed lines show the two count sizes employed in this study.

4.6 Discussion

4.6.1 Autogenic and allogenic determinants of peatland vegetation development

The pollen diagrams and NMDS multivariate analyses presented here suggest that at Veinte de Enero there is a consistent pattern of pollen composition change with both depth and age, across all cores. In broad outline this pattern shows that peat began to accumulate between 1000 – 2000 cal. years BP, in an open environment, perhaps a small lake, indicated by high concentrations of C*ecropia* and a lack of locally-produced pollen. This was followed by a flooded forest community, indicated by the flooded forest specialist *Symmeria paniculata* (Gentry 1994). Flooded forest was subsequently replaced by a herbaceous grass/sedge community, which may represent a floating mat or alternatively a fen community. Finally the palm swamp community which dominates much of the site at present is a relatively recent feature across the site, occurring approximately 150 cal. years BP (Figure 4.6 and Table 4.3).

The consistency of this pattern across cores suggests that the observed pattern may be determined by autogenic succession. The GLM analysis partly supports this in that both sample depth and sample are significant determinants of pollen composition (Table 4.5). However, composition is also significantly different between cores and there is a marginally significant interaction between depth and core that is largely attributable to the *Pistia* peak in core OLL4. These results show that although there appears to be an autogenic pattern, there is also substantial variation between cores. This variation may be attributable to allogenic factors, for example, the *Pistia* peak in core VEN 4 could be due to a flooding event by sediment-rich water that only affected the site margin. Although *Pistia* has been found in palm swamps (Atrium 2014), it is normally associated with sediment-rich water (Junk & Howard-Williams 1984). Alternatively, some of this variation may be attributable to demographic stochasticity through time, as would be expected according to neutral theory (Hubbell 2001).

Overall the most parsimonious explanation for this development pattern is that this site is an abandoned river channel that has subsequently undergone terrestrialisation. This developmental pattern shares some key features with the only other published pollen record from a western Amazonian peatland (Roucoux *et al.* 2013), including high concentrations of

Cecropia and *Symmeria paniculata* at the base of the core, moving through Cyperaceae, Poaceae phases and reaching a palm swamp community towards the top of the core. The pattern described is consistent with previously proposed conceptual models of swamp development in western Amazonia, based on both inferred chronosequences and pollen records from wetland sites (Frost 1988; Kalliola *et al.* 1991a; Kalliola *et al.* 1991b; Weng *et al.* 2002). This explanation is also consistent with the geomorphological setting of this site, as this area of the PMFB contains numerous abandoned river channels, many of which appear to be in the process of infilling with peat (Rasanen *et al.* 1992).

The Ollanta cores show a different pattern of development, with few across-site consistencies. Peat developed first in what I interpret to be a small channel near the site margin, considerably earlier than the rest of the site (~ 3000 years before the next closest basal date) (Figure 4.4); peat accumulation began most recently in the centre of the site (2269 years BP). Overall, the margins of the site appear to have been dominated by phases of open herbaceous communities and flooded forests (Figure 4.7 and Table 4.4), while the centre of the site has been palm swamp for much of its history, until the relatively recent development of pole forest indicated by the appearance of *Pachira brevipes* which occurred in the past 100 cal. years BP (Figure 4.7 and Table 4.4).

This variability among cores is reflected in the multivariate statistical analyses. Firstly, the NMDS axis scores vary substantially among cores when plotted against both depth and time (Figures 4.9 and 4.10). Axis scores also vary within cores, particularly in core OLL 4, reflecting the numerous reversals between open herbaceous and flooded forest communities in this core. Results from the GLM provide further evidence that there are few consistencies in compositional change among cores (Table 4.5). The significant interaction between sample depth and core suggests that peat accumulation is resulting in different changes to pollen composition across the site. Together these results indicate that compositional changes through time at this site have not been primarily driven by autogenic succession, and instead suggest that allogenic factors have been more important determinants of vegetation development at this site.

Despite the numerous differences between cores at this site, there are some commonalties. Three out of four cores appear to be palm swamp forest at the point of peat initiation, suggesting that paludification (peat accumulation directly over a mineral substrate) may have been an important process of peat development at this site. This is further supported by the absence of flooded forest taxa at the base of all of the cores. There appears to be no published records of similar paludification patterns in tropical peatlands. However, some northern forested peatlands show similar patterns with peat developing within existing forests, directly above mineral substrates (Heinselman 1963, 1970).

Importantly, the variable flooding depth along the Ollanta transect and a published topographic survey for the other side of the peatland (Lähteenoja & Page 2011) suggest that this site is domed and that this doming may be a result of the underlying topography (Figure 4.4). This possible topographic doming is important, as it provides a potential explanation for why the margins of the site have been more influenced by inundation throughout their development, whilst the central region of the site appears to have been less influenced by flooding. Geochemical data obtained for the opposite side of this site supports this, showing that the centre of this site has become ombrotrophic and therefore isolated from fluvial disturbance, whilst more marginal parts of the site remain minerotrophic (Lähteenoja & Page 2011).

One possible explanation for the overall developmental pattern at this site is that as peat has accumulated at the edge of the site, the drainage capability of the site has been reduced, leading to a higher water table and therefore anoxia across the site. Similar patterns of upslope paludification are now well documented in Northern peatlands (Foster & Fritz 1987; Bauer *et al.* 2003). This potential mechanism may be representative of other peatlands in the Pastaza fan, which also appear to have developed on raised interfluves (Lähteenoja & Page 2011); this requires further palaeoecological testing. Furthermore, accurate topographical surveys, such as digital elevation models generated by airborne LiDAR (Vierling *et al.* 2008; Glennie *et al.* 2013), would provide valuable insight into fine scale topographic controls.

4.6.2 Linking historical processes to spatial of composition

At both sites the current vegetation communities are identifiable in the pollen surface samples, and are also found down core. However, interpreting the floristic zonation at these sites as representing chronosequences would be misleading. At Veinte de Enero there appears to be a predictable successional pattern of change in pollen composition across the four cores which is supported by the multivariate analysis. However, whilst the spatial pattern appears to reflect the successional sequence, the successional sequence does not reflect time directly. Counterintuitively, the sites which are furthest along the apparent successional sequence are those where peat initiation began most recently. Palm swamp, which consistently comes last in the succession, has been established for longest in the area which most recently began to accumulate peat. Similarly, the area where peat has been accumulating for the longest time is currently an open herbaceous community, which has been shown to be a community that precedes palm swamp in the vegetation succession at this site. Therefore, the space-for-time substitution made by inferring chronosequences is shown to be not valid.

Inferring chronosequences from floristic zonation would perhaps be even more misleading at the Ollanta site: different areas of this site have followed different developmental pathways. For example, the area of the site which has been accumulating peat the longest (OLL 4) has undergone little directional compositional change as a result of either time or peat accumulation. Instead, it appears that repeated phases of inundation and associated nutrient deposition have led to numerous reversals in the direction of change, so that flooded forest has remained the dominant vegetation community type until the present. Similar reversals resulting from repeated increases in flooding and nutrient deposition have been shown to occur in northern peatlands (Charman 1994, 1995). By contrast, the centre of the site, which began accumulating peat most recently, appears to have undergone more directional succession, resulting in the development of an apparently ombrotrophic pole forest.

Together my results show that historical processes, including succession and allogenic factors, are important in determining current patterns of peatland vegetation composition. However, I have shown that the spatial patterning in vegetation at these sites does not reflect a chronosequence. This result is consistent with other studies of succession, (e.g. (Johnson & Miyanishi 2008; Norden *et al.* 2015). In the case of Ollanta this is because allogenic influences can be more important than autogenic processes in peatland development. In the case of Veinte de Enero, although succession appears to be the most important determinant of vegetation change and the different successional communities all occur in different parts of the site, the spatial pattern still does not reflect the temporal pattern. The process of succession results not from the passing of time *per se*, but instead from the modification of the physical environment by autogenic processes (in the context of peatlands, via peat accumulation) which occurs through time but not necessarily at the same rate everywhere. This conceptual distinction appears to be one of the fundamental reasons behind the widespread rejection of chronosequences based on empirical evidence (Johnson & Miyanishi 2008; Walker *et al.* 2010a).

4.6.3 Consistencies between sites

There are few consistencies in peatland development and vegetation succession between the two sites; instead, quite different developmental patterns are seen in the data. This is supported by the GLM analysis, in particular the highly significant interaction between site and sample depth which indicates that floristic composition changes in different ways with increasing peat depth at the two sites (Table 4.5). The NMDS analysis, however, does indicate that there are some similarities in the trajectory of floristic change across the two sites (Figure 4.9 and 4.10). The consistencies in this analysis are driven by the most abundant species, and therefore probably reflect broad scale similarities including the general patterns of higher proportions of *Mauritia* pollen towards the top of the core, higher proportions of *Cecropia* and *Symmeria paniculata* towards the base, and higher proportions of Poaceae and Cyperaceae in the middle of the core. Whist these similarities mask the important details which separate the development patterns in the two sites, they also provide valuable insight into the kinds of transitions which may be common.

This is illustrated in a conceptual model (Figure 4.12), which highlights the different development pathways found in this study, and superimposes them onto previous conceptual models of Amazonian swamp development that were based on inferred chronosequences (Kalliola *et al.* 1991a; Kalliola *et al.* 1991b). Overall there is much variation in developmental processes, and reversals are frequent. However, two transitions that are found at both sites are the transition from flooded forest to grass/sedge community, and from grass/sedge community to palm swamp. These transitions are also shared by the only other peatland pollen record in Amazonia (Roucoux *et al.* 2013), and pollen records from other Amazonian swamps (Frost 1988; Weng *et al.* 2002), suggesting perhaps they form part of a more general successional pattern.

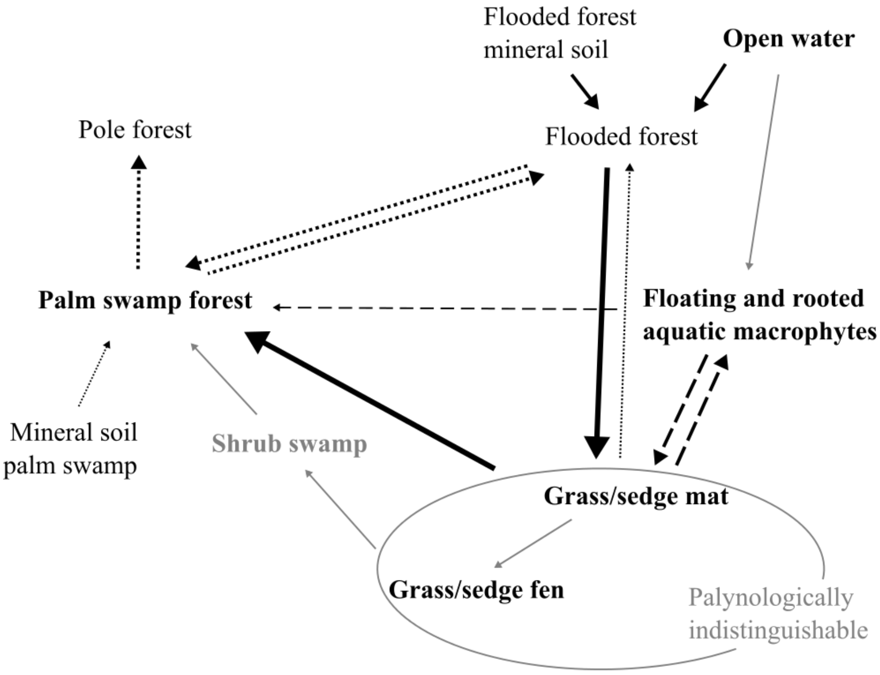

Figure 4.12 Conceptual diagram showing how the data from this study fit onto the proposed successional pathways suggested for Amazonian swamps, on the basis of vegetation surveys alone, by Kalliola *et al* (1991a; 1991b). Communities in bold represent those previously suggested, and those not in bold are communities that were observed in this study only. Arrows represent vegetation transitions, arrow thickness corresponds to how frequently transitions were observed. Solid arrows represent transitions that were found in both sites, dotted arrows are transitions only found at Ollanta and dashed arrows are transitions found only found at Veinte de Enero. Communities and arrows shaded grey are those suggested by Kalliola et al.'s model but not observed in this study.

This conceptual model also shares some functional similarities with models of hydroseral succession in temperate and boreal peatlands (Walker 1970; Klinger 1996). Like hydroseral succession, the successional trajectory is complex and highly variable between sites, cores and samples (Heinselman 1970; Charman 2002). The main similarity between the data from this study and hydroseral succession is a transition from open water, to fen/swamp, to finally ombrotrophic bog. Furthermore, some of the development patterns outlined in this study appear to share functional if not taxonomic consistencies with patterns found in tropical peatlands in South-east Asia, Central America and Amazonia (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997; Morley 2013). For example, pole forests are found in tropical peatlands in both Southeast Asia and Panama in ombrotrophic conditions and have been shown to be a late stage community in pollen records (Anderson & Muller 1975; Morley 1981; Phillips *et al.* 1997). Similarly, some inland peats in South-east Asia undergo early aquatic phases followed by open grass dominated communities, mixed swamp forests and finally stunted pole forests (Morley 1981). Whilst further investigation is certainly required to quantify these apparent consistencies, the developmental framework presented here may be applicable more widely than the PMFB or indeed Amazonia.

An important finding of this study is that the key vegetation communities that make up the developmental pathways are identifiable through both time in the pollen record, and space using satellite imagery (Lähteenoja & Page 2011; Draper *et al.* 2014). Although this study has shown there is no direct link between spatial and temporal patterns, an understanding of the more common development pathways may provide novel landscape-scale insights. For example, within the Pastaza fan, pole forests are dominant on interfluves to the east, whilst open peatlands dominate western interfluves (Draper *et al.* 2014). The conceptual model developed here would suggest that open peatlands towards the west are an earlier successional community, and therefore have either developed relatively recently or been frequently disturbed by allogenic factors. Conversely, pole forests sites to the east may be a late stage successional community. Therefore these sites have either been developing for a longer time or have been affected little by allogenic disturbances. These hypotheses are broadly consistent with the few radiocarbon dates available which suggest pole forest peatlands are older and deeper than open peatlands (Lähteenoja *et al.* 2012) Additionally, geomorphological analysis suggests that westward migration of the Pastaza over the past 8000 years has been the most important source of allogenic disturbance, which provides a mechanism for understanding why the eastern part of the Pastaza fan may be been more stable than the western part in recent millennia.

4.6.4 Historical processes and alpha diversity

A key result is that the pole forest ecosystems dominated by *Pachira brevipes* are a relatively recent feature at the Ollanta site. Pole forests dominated by *Pachira brevipes* have been shown to be perhaps the least diverse ecosystems in Amazonia in terms of α-diversity (Chapter 3). Explaining this extremely low diversity has proved difficult when historical processes are not accounted for. However, taking into account the relatively recent nature of this ecosystem type, it may be that pole forests lack diversity partly because there has been insufficient time for suitably adapted species to disperse to the site (White *et al.* 2006).

These pole forest communities seem not to be in equilibrium with their environment, and may depend more on which species are able to disperse to and survive at the site within a limited period of time, rather than which species have evolved to be the best competitor at this location. Similarly, the palm swamps at the Veinte de Enero site are low in diversity compared with other palm swamps in the region (Chapter 3). My results show that palm swamp ecosystems are also a recent feature at this site, which could provide an explanation of why they are so species poor. These historical processes are especially important in peatlands, as peatlands are particularly dynamic over short time scales. However, many other ecosystems in Amazonia are environmentally dynamic through time, such as wetland forests and forests frequently exposed to drought. Palaeoecological analysis from North-eastern Amazonia has found a comparable result, showing that current patterns of diversity are dependent on historical processes operating over the past few thousand years (Rull *et al.* 2013).

4.6.5 Novel quantitative approaches in palynology

The multivariate techniques and multicore approach used in this study enabled the investigation of ecological patterns and test relevant hypotheses, something which has been defined as a priority in palaeoecology (Rull 2010; Seddon *et al.* 2014; Jackson & Blois 2015). Tropical palynology is problematic due to the high diversity of species, and pollination strategies means interpretation of pollen records is difficult (Gosling *et al.* 2005, 2009). High pollen counts provide useful detail for understanding vegetation changes at single sites, but are resource-demanding and therefore are often limited to single sites. To develop an understanding of more generalizable patterns and processes, replication within and across sites is required. In this study, I have shown how many smaller samples can provide lots of ecologically useful information. The smaller count sizes allowed for modest replication, and analysing eight cores together using novel statistical methods allowed ecological hypotheses to be tested. There are also drawbacks of using small sample sizes, particularly when ecologically indicative taxa are rare, for example *Pachira brevipes* indicating pole forest. In these cases small sample sizes may miss these rare but ecologically meaningful taxa. One approach to get around this issue would be to develop a list of a suite of indicator taxa and then search slides for the presence of these indicator taxa only. Overall, I caution against using predetermined and arbitrary pollen counts and instead would recommend exploring data using rarefaction analysis and tailoring sample size depending on the aims of the study.

4.6.6 Conclusions

The peatland ecosystems of the PMFB exhibit substantial variation in their development, resulting from both allogenic and autogenic processes. These historical processes have played an important role in determining current patterns of composition and diversity. The importance of historical processes operating at small temporal and spatial scales is currently underappreciated in ecological studies of diversity in tropical forests, both in terms of understanding patterns in empirical data and developing theoretical models. Pollen analysis can offer ecologists unique insights into ecological processes operating over medium timescales (decadal to millennial). These timescales are a missing link between those covered by monitoring ‘long-term’ plots (decadal) and information provided by population genetics (> 10^4 years). Exploring these patterns and testing their significance was only possible using a robust statistical framework and a replicated multicore approach. Such an approach can be achieved by sacrificing pollen count sample resolutions to lower, but still informative levels. Finally, examining the relationship between ecosystem types through both space and time using multidisciplinary methods (e.g. pollen analysis and remote sensing), provides new insights into landscape development.

5. Conclusions

This final chapter concludes the thesis. First I give an overview of the most important findings from each of the three data chapters. I then go on to assess the efficacy of the interdisciplinary approach this thesis has taken. In the following section, I suggest how future research could build upon the results obtained. Finally, I discuss some of the most important implications of the results that come out of this thesis.

5.1 Overview of findings

5.1.1 The peatland carbon stock in the PMFB

Combining optical and radar satellite data with extensive field data, I have produced the first landscape scale map of peatland ecosystems in the PMFB. Combining this map with extensive ground measurements of both above-ground and below-ground carbon, I have shown the peatland ecosystems of the PMFB to be the most carbon dense ecosystems in Amazonia storing on average 892 ± 535 Mg C ha^{-1}, with approximately 90% of this carbon stored below-ground. Of the three peatland ecosystem types, pole forests are the most carbon dense storing 1392 ± 696 Mg C ha^{-1}. Compared to *terra firme* forests, pole forests store more than five times the amount of carbon per unit area. At a national level the peatland carbon stock of the PMFB is 3.14 (0.44–8.15) Pg C and although uncertain, this best estimate is equivalent to nearly 50% of the aboveground carbon stock of Peruvian forests at 6.9 Pg C (Asner *et al.* 2014a). This estimate is also substantially different and less uncertain than the previous estimate of 1.7 to 18.9 Pg C (Lähteenoja *et al.* 2012).

Using statistical resampling techniques, I produced uncertainty estimates for all aspects of the peatland carbon stock, this is arguably the most comprehensive assessment of the sources of uncertainty in a regional carbon stock assessment of tropical peatlands. This analysis demonstrated that the variables that contribute most to the large uncertainty in peatland carbon stock estimates are peat depth and bulk density. Additionally, the peatland map provided new information on the spatial distribution of different peatland types across the landscape. These findings led to the hypothesis that open peatlands may represent an early successional community and pole forests represent a late stage successional community in the development of peatland ecosystems. These hypotheses were explored later in Chapter Four using palaeoecological techniques. The findings of this study are significant, not only because they confirm the importance of the PMFB peatlands as a carbon stock, but also because the method developed here provides a novel and cost effective technique for developing large scale, spatially explicit carbon stock estimates for tropical peatlands, including a rigorous assessment of uncertainty.

5.1.2 Floristic composition and diversity in space

By establishing a network of new floristic inventories and combining this with existing plot data, I have produced the first comprehensive description of Amazonian peatland vegetation composition and diversity, providing (amongst other things) the first description of a previously undescribed ecosystem in Amazonia, peatland pole forest. I have then combined this peatland floristic dataset with an extensive network of floristic inventories from the most widespread forest types in the surrounding region (*terra firme* forests, white sand forests and seasonally flooded forests). In Chapter Three I have demonstrated that plots previously assigned to ‘palm swamp’ and ‘pole forest’ based on their structure and assumed environmental parameters, are also significantly different to each other and other ecosystem types based on their floristics.

This work revealed a number of floristic patterns that demonstrate peatland tree communities in the PMFB are distinctive in comparison to other Amazonian ecosystems. Firstly, peatland communities, in particular pole forests, are perhaps the least diverse (in terms of alpha diversity) in lowland Amazonia with as few as 15 species (dbh > 2 cm) recorded in a 0.5 ha plot. Secondly, although overall beta diversity is slightly lower in peatlands than in other ecosystem types in Amazonia, compositional similarity between pairs of plots varies much more in peatlands than in other forest types, irrespective of distance. Finally, peatlands in this dataset did not appear to contain any endemic species. Instead, pole forests contained a number of species that had previously been thought to be endemic to white sand forests, whilst palm swamps contained many species commonly found in seasonally flooded forests. This is consistent with other floristic studies undertaken in Western Amazonia, which show that, although compositional patterns do reflect environmental gradients, many species are shared between distinct and seemingly specialist communities (Phillips *et al.* 2003; Pitman *et al.* 2014). For example, in Amazonian Ecuador > 80% of tree species recorded in swamp forests were also recorded in neighbouring terra firme forests (Pitman *et al.* 2014).

In addition, I have made comparisons between the peatland communities of the PMFB and environmentally analogous ecosystems in Southeast Asia, which appear to be more species rich and harbour a specialist and endemic flora. I have shown that peatlands in the PMFB may be considered a “diversity anomaly”, in the sense that these two ecosystems have similar environmental conditions but exhibit very different patterns of diversity (Ricklefs *et al.* 2006). Placing the patterns of composition and diversity found in this study into the broader theoretical context of community assembly in tropical forests, I have investigated the relative importance of several ecological processes in determining the patterns observed. Finding that current processes such as environmental filtering and dispersal limitation, cannot fully explain these patterns, I have suggested that historical processes such as autogenic succession may have a more important role in determining local scale patterns than currently thought.

5.1.3 Floristic composition through time

Using a multiple-core palaeoecological approach, I have demonstrated that different developmental patterns and processes have been important at two different sites. At one site autogenic succession was found to be primarily accountable for changes in floristic composition through time. At the second site allogenic factors appear to have been more important for determining floristic change through time. These autogenic and allogenic historical processes were shown to have a strong influence on the spatial patterns of floristic composition seen at both sites at present. However, at both sites the patterns seen through space did not directly reflect the patterns seen through time. Therefore, assuming a space for time substitution (chronosequence) at these sites would be invalid, and caution should be taken when interpreting similar spatial patterns in the present day vegetation. This is consistent with a number of other studies that show there is often little empirical support for space-for-time substitutions in ecology (Johnson & Miyanishi 2008).

Furthermore, the pollen data, combined with radiocarbon dates, suggest that the present communities established at the sites relatively recently, and their young age probably contributes to the low alpha diversity recorded in chapter three. This highlights the importance of historical processes operating over centennial timescales in determining current patterns of composition and diversity. This finding is important because historical processes are currently poorly accounted for by ecologists interested in explaining current patterns of diversity in tropical forests.

Despite the substantial variation in floristic development patterns through time, there are also some shared features and commonalities at the two sites, such as the seemingly successional transition from a flooded forest to a herbaceous community to a palm swamp community. Some of these similarities are also shared with published pollen records from one nearby peatland (Roucoux *et al.* 2013), and from swamps more generally in Amazonia (Frost 1988; Weng *et al.* 2002). Taken together, these similarities, as well as the differences within and among sites, help to improve our understanding of Amazonian peatland development.

5.2 Discussion of approach

An overall ambition of this thesis was to use an interdisciplinary approach to address a broad range of themes concerned with improving our understanding of peatland ecosystems in the PMFB. By employing a range of techniques it has been possible to analyse a variety of data types, from a range of different perspectives. For example, remote sensing techniques were employed firstly to map the distribution of carbon at a landscape scale. From an ecological perspective this approach also provided a distribution map of a novel vegetation type, which I was then able to describe for the first time in terms of its floristic composition and diversity. Similarly, knowledge of the distribution of peatland ecosystem types gained from remote sensing led to hypotheses about ecosystem development which could subsequently be tested with palaeoecological approaches.

The integrated approach used also demonstrated the importance of the interaction between ecology and palaeoecology. Currently, ecologists rarely use pollen data to address questions related to community assembly in tropical forests, in part because pollen records are seldom available. Using a palaeoecological approach, I have been able to show how the recent nature of peatland communities may account for their exceptionally low alpha diversity. This finding challenges the current ecological thinking, which has typically overlooked the role of historical processes operating over centennial timescales in determining local patterns of composition and diversity. Additionally, ecological knowledge gained from floristic inventories across a range of sites helps to interpret the pollen record. For example by identifying key indicator taxa such as *Pachira brevipes* which is shown to be restricted to pole forests within the PMFB peatlands.

This approach has not only provided alternative perspectives for a broad range of research questions, but also by using methods across disciplines, novel method applications were possible. For example, although rarefaction analysis has been a standard technique in palaeoecology for some time (Birks & Line 1992; Odgaard 1999), more recent statistical developments in the ecological literature have provided a method for extrapolating rarefaction curves beyond the maximum observed sample (Colwell *et al.* 2012). Using this extrapolation approach I was able to estimate the importance of pollen sample count size in estimating pollen richness in a novel way. This extrapolation method provided a particularly useful way of justifying a more flexible pollen counting approach, including the use of smaller pollen sample sizes of 100 grains. There have been many studies in the palaeoecological literature to address this issue of sample count size (Birks & Birks 1980; Birks & Line 1992; Hill 1996; Odgaard 1999; Finsinger & Tinner 2005; Payne & Mitchell 2009; Van der Knaap 2009; Etienne & Jouffroy-Bapicot 2014; Keen *et al.* 2014). However, as far as I am aware, this is the first application of extrapolated rarefaction to pollen data, although it has been suggested once before (Weng *et al.* 2006).

Finally, the ability to identify proxies for vegetation communities through space (remote sensing) and time (pollen analysis), is a potentially powerful tool, especially when extensive floristic datasets are available to validate the proxies. A combined understanding of both the spatial and temporal processes that determine current patterns of diversity and composition at a landscape scale, is perhaps one way of addressing the issue of 80% of variation in local tree alpha diversity in Amazonia remains unexplained (Stropp *et al.* 2009).

5.3 Future Research directions

The work presented in this thesis has been in many ways exploratory, and therefore provides a number of possible avenues for future research. The peatland ecosystem map and associated carbon estimates that were produced in Chapter Two could be improved upon. Currently the ground reference data set used to build the map has poor coverage in the far North-western and South-western parts of the basin, due to the logistical challenges of reaching these exceptionally remote areas. Further fieldwork campaigns should target these under-represented regions. The peatland map may also be improved by the use of remote sensing products with better spectral or spatial resolution. Combined LiDAR and hyperspectral data from airborne sensors would provide this resolution and have been used extensively in this region; however, complete coverage over the entire basin may not be possible as spatial coverage is limited from airborne sensors (Asner & Martin 2009). The new Sentinel 2 sensor is the perhaps most promising prospect, as it provides superior spatial (10 m) and spectral resolution (13 multispectral bands), as well as far greater spatial (290 km swath) and temporal coverage (five day revisit time) (Drusch *et al.* 2012).

The method used in this study to produce peatland ecosystem maps and estimate carbon stocks could also be applied to other peatland regions in the tropics. Due to the unique geology of the PMFB, it is almost certainly the largest area of peatland in Amazonia. However, significant peat deposits have been confirmed elsewhere (Pitman *et al.* 2011; Householder *et al.* 2012; Lähteenoja *et al.* 2013). Future work should aim to generate below-ground carbon maps across the wider Amazon. Similar approaches are currently being employed to quantify peatland carbon stocks in the Congo basin, and initial results suggest a far larger area of peatland is found there than previously thought (G. Dargie, pers. comm.).

Perhaps the most prominent avenue for future research is to quantify not only carbon stocks but also fluxes of carbon, in order to ascertain whether the peatlands are currently operating as carbon sinks as has been suggested (Lähteenoja *et al.* 2012). It is their function as sinks or sources in addition to their role as carbon stocks, that will determine their role in the wider carbon cycle, and also their relevance to policies such as REDD+ (Murdiyarso *et al.* 2010). Peatlands can operate as hugely significant carbon sources when degraded, as has been shown in Southeast Asia (Page *et al.* 2002; Hooijer *et al.* 2010; Moore *et al.* 2013). Currently, peatlands in the PMFB are almost entirely intact and are not facing the same degradation pressures. However, threats are increasing in the region, in the form of conversion to oil palm plantation, and oil exploration for example (Finer & Orta-Martínez 2010; Finer *et al.* 2014). Another important avenue for future research will be quantifying these threats, for example, by assessing the rate of land use change and estimating the potential impact on carbon stocks.

There is much scope for greater ecological research into Amazonian peatlands. One of the most interesting results to come out of this thesis is the apparent lack of endemic species in the tree communities in peatland ecosystems. This is curious as other environmentally distinct communities, such as those found in white sand forests, have been repeatedly shown to have evolved a unique tree flora (Fine *et al.* 2005; Fine *et al.* 2010). The same is apparently true of Southeast Asian peatland forests (Posa *et al.* 2011). Therefore, the question remains: Why are there apparently no endemic trees in the peatlands of the PMFB? A first step in answering his question may be to firstly conduct more floristic inventories both in the PMFB and also perhaps in Southeast Asia to really establish that the pattern exists. To investigate these evolutionary processes further, a community phylogenetics approach will be required, in order to explore the evolutionary mechanisms that underpin this pattern. For example, it may be that lineages found in peat swamp forests are phylogenetically clustered, which would suggest that there has been some speciation in peatland forests.

Equally fascinating is the apparent discrepancy in alpha diversity between the Amazonian peatlands reported here and those of Southeast Asia (Poesie *et al.* 2010; Posa *et al.* 2011). Previous studies have been able to use similar diversity anomalies to test the importance of different aspects of community assembly theory (Ricklefs & Latham 1993; Qian & Ricklefs 2000; Ricklefs *et al.* 2006). More floristic data would be required, but this cross continent comparison in tropical peatlands could provide new insight into community assembly mechanisms. Peatlands are particularly useful in this respect because pollen preserved in the peat can provide a record of local community change through time. Furthermore, in both these regions, there are strong gradients of diversity, strong environmental gradients, and large areas of peatland that can be mapped at broad spatial scales. With additional geochemical and phylogenetic analyses, it may be possible to separate out some of the determinants of diversity in tropical ecosystems and provide answers to some of the most fundamental questions in ecology.

A further key way forward will be the development of models that can be used to predict how peatlands may function in future in response to climate change, and how any changes to peatland function may have feedback effects on the global climate. Such models require a comprehensive understanding of the key functional processes, such as litter input, decomposition rate and hydrologic conductivity (Frolking *et al.* 2010; Kurnianto *et al.* 2015). Whilst measurement of some of these processes is underway (Kelly *et al.* 2014), others remain unknown. Comprehensive field studies will be required to understand important aspects of peatland functioning in order to accurately parameterise models.

Palaeoecological records also have an important function in testing developmental models (Tuittila *et al.* 2013), and further pollen records should be obtained in order to improve our understanding of how general the patterns of peat development found in this and other studies are across the basin. Pollen records should be obtained for targeted locations, for example, in locations that are currently poorly represented, and in ecosystems that fit into current peat development hypotheses, for example the open peatlands that are widespread in the North-western part of the basin. By targeting these open peatlands it would be possible to test the current peat development conceptual model with an independent dataset. Finally, the relationship between floristics and the composition of pollen rain is currently unclear. Further work is required to find the most effective way to define the link between pollen and vegetation, as this relationship underpins our understanding of past vegetation dynamics.

5.4 Implications of this thesis

The results from this thesis have a number of important implications for international and national carbon conservation policies, biodiversity conservation planning, and for our understanding of community assembly and diversity in tropical forests.

The confirmation of the PMFB as the most carbon dense ecosystem in Amazonia, harbouring a carbon stock equivalent to nearly 50% of Peruvian AGB, has important implications in the context of carbon conservation strategies such as REDD+. REDD+ is a United Nations programme that seeks to provide a financial value for the conservation of forest carbon stocks, in order to reduce global carbon emissions (Angelsen & Brockhaus 2009). There have been recent calls for a greater focus on tropical peatlands because of their high carbon density (Murdiyarso *et al.* 2010). However, tropical peatlands are currently not well accounted for in such frameworks, predominantly because their carbon stocks and fluxes are poorly understood (Page *et al.* 2007; Murdiyarso *et al.* 2013).

REDD + has huge potential to conserve large areas of carbon rich tropical forests, but currently it has become increasingly complex and its success so far has been limited (Murdiyarso *et al.* 2012; Visseren-Hamakers *et al.* 2012; Nepstad *et al.* 2013; Matthews *et al.* 2014). One of the reasons for the lack of success is that it has proved difficult to provide the accurate, spatially explicit estimates of carbon stock that are required (Asner *et al.* 2014a). The high uncertainty in the spatial distribution of the forest carbon stock has contributed to a low market price for carbon (Asner *et al.* 2014a), which is inhibited by a lack of a binding global deal to create a large market (Nepstad *et al.* 2013). This study provides high-resolution, large-scale mapping of carbon distribution, which is one of the tools needed for the peatlands of the PMFB to be included in REDD+ schemes. Furthermore, the methodology developed here could be applied to tropical peatlands elsewhere, potentially contributing to developing a mechanism for the large scale conservation of tropical peatlands.

Peru is currently one of two tropical countries (alongside Panama) to have total coverage of high resolution AGC estimates at a national scale (Asner *et al.* 2014a). Although these AGC estimates are probably the most accurate estimates in the world to date, results from this thesis illustrate how the inclusion of only aboveground carbon is a substantial omission and can be misleading. In the existing AGC map, the PMFB is amongst the lowest scoring areas for carbon density, due to the typically small stature of the trees (Asner *et al.* 2014a). However, in this study I have shown this region to be the most carbon dense nationally, by a large margin once below-ground carbon is taken into account. Therefore, current policy decisions such as implementing REDD+ and designing protected areas to conserve carbon, must include data on below-ground carbon, such as those presented here.

Peatlands in the PMFB have been shown to have low alpha diversity, yet their high beta diversity within and among ecosystem types makes a significant contribution to regional habitat diversity. Furthermore, the floristic descriptions of pole forest peatlands made (for the first time) by this project have confirmed them to be a distinct ecosystem type that has not yet been recognised formerly. Although no endemic species were found in this analysis, only trees > 2 cm dbh were included. Currently, there is no information on the species composition of other taxonomic groups in these ecosystems, but it is quite possible that these ecosystems do hold endemic species, some of which may be new to science. Where biological inventories have been undertaken in similarly distinct ecosystems in northern Peru, many new species have been described (e.g. Pitman *et al.* 2011). Such biodiversity information can be an effective tool in establishing protected areas (Vriesendorp 2013).

The floristic similarities documented here between pole forest and white sand forests are important. Pole forests have been shown to harbour a number of species that have been described as white sand endemics. White sand forests have been a conservation priority for their high concentration of endemic bird species, several of which are critically endangered and can be found nowhere else on earth (Alonso & Whitney 2001; Whitney & Alonso 2005; Alonso *et al.* 2013). Initial research suggests that many of these endemic species are also found in the peatland forests (Lähteenoja *et al.* 2009a; S.J. Socolar, pers. comm.). This is important as the range size for these birds could be significantly increased, and meta-populations may be better connected than previously thought. Therefore, pole forest peatlands may be stabilising critically endangered bird populations.

This study also has implications for our understanding of community assembly in tropical forests. In particular, I have demonstrated the importance of historical processes such as autogenic succession and allogenic disturbance in determining current patterns of diversity and composition. At present such processes are not typically considered in studies of diversity in tropical forests at either an empirical or theoretical level (Jackson & Blois 2015).

5.5 Final summary

Peatland ecosystems in the PMFB are shown to be the most carbon dense ecosystems in Amazonia and an important carbon store at national and global scales. Peatlands are some of the most poorly understood ecosystems in Amazonia, but display remarkable floristic patterns, including exceptionally low alpha and a composition distinct from any other ecosystem type. Results from this thesis demonstrate their conservation importance, providing the kind of information policy makers require to establish protected areas. In addition, peatlands in the PMFB provide a unique system in Amazonia for testing a range of exciting questions related to community assembly. Being able to identify communities through both time and space at a landscape scale offers new insight to some of the most fundamental ecological questions in one of the most biologically complex regions on Earth.

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7 Appendices

Appendix 2.1 Site information and summaries of the key parameters used to generate carbon estimates for the 34 study sites in the Pastaza-Marañon foreland basin in north-eastern Peru. Peatland types refer to Pole Forest (PF), Palm swamps (PS) and Open Peatlands (OP).

Site	Forest plots code*	Map ref. in Fig. 1	Long. (°W)	Lat. (°S)	No. forest census plots	No. peat measurement points	AGB (Mg ha^{-1})	Mean Peat thickness (m)	Mean Dry Bulk density (g cm^{-3})	Mean C conc. (%)	Year established	Principal Investigator
Pole forest peatland												
Aucayacu	–	13	74.384	3.9354	–	8	–	4.63^{2}	0.108^{2}	49^{2}	2008	O. Lähteenoja
Miraflores	–	15	74.074	4.4149	2	8	296.31^{1}	2.1^{1,2}	0.084^{1,2}	50^{1,2}	2008 & 2012	O. Lähteenoja & F. Draper
Ollanta	–	8	74.848	4.448	4	35	94.5^{1}	3.05^{1}	0.161^{1}	54^{1}	2013	F. Draper
Nueva York	–	14	74.275	4.417	2	9	167.2^{1}	4.27^{1,2}	0.057^{1,2}	52^{1,2}	2008, 2013	O. Lähteenoja & F. Draper
Roca Fuerte	–	9	74.823	4.436	–	8	–	3.82^{2}	0.073^{2}	52^{2}	2008	O. Lähteenoja
San Jorge	–	17	73.189	4.058	1	14	208.6^{1}	2.92^{1}	0.112^{1}	44^{1}	2010	K. Roucoux

Veinte de Enero	VEN-01 to VEN-05	20	73.818	4.694	5	35	156.6[1]	1.94[1]	0.081[1]	54[1]	2009, 2012	E. Honorio and F. Draper
Palm Swamps												
Buena Vista del Maquía	–	29	74.720	6.2067	–	7	–	1.21[2]	0.088[2]	38[2]	2008	O. Lähteenoja
Charo	–	19	73.254	4.2703	–	6	–	1.26[2]	–	–	2008	O. Lähteenoja
Cuninico	–	6	75.186	4.7834	–	8	–	2.88[2]	–	–	2008	O. Lähteenoja
Fundo Junior	–	18	73.318	4.0925	–	13	–	2.68[2]	–	–	2006	O. Lähteenoja
Iricahua 1	REQ-05	21	73.820	4.8122	1	–	212.1[1]		–	–	2008	E. Honorio
Iricahua 2	JEN-14	21	73.832	4.8357	1	–	225.2[1]		–	–	2009	E. Honorio
Jenaro 1	REQ-13	26	73.646	4.8734	1	–	247.7[1]		–	–	2008	E. Honorio
Jenaro 2	JEN-15	25	73.652	4.8357	1	–	207.6[1]		–	–	2009	E. Honorio
Quistococha	QUI-01	16	73.318	3.837	1	10	214.5[3]	2.44[2]	0.095[2]	47[2]	2008, 2010	O. Lähteenoja K. Roucoux
San Roque	–	10	74.622	4.540	1	7	167.3[1]	3.53[1,2]	0.161[1,2]	42[1,2]	2008, 2013	O. Lähteenoja & F. Draper
Santa Rita	–	12	74.374	4.576	1	5	226.1[1]	0.9[1]	0.172[1]	39[1]	2013	F. Draper

Santa Rosa	–	11	74.537	4.476	–	3	–	2.1[1]	–	–	2013	F. Draper
Saramuro	–	7	74.927	4.700	1	3	100.6[1]	0.9[1]	0.214[1]	23[1]	2013	F. Draper
Tacshacocha	–	24	74.300	4.905	–	6	–	1.5[2]	0.069[2]	33[2]	2008	O. Lähteenoja
Yanashpa 1,	REQ -01	22	73.821	4.906	1	–	220.6[1]	–	–	–	2008	E. Honorio
Yanashpa 2,	REQ -04	22	73.793	4.878	1	–	193.6[1]	0	–	–	2008	E. Honorio
Open peatlands												
Maquía	–	30	74.808	6.3230	–	9	–	3.88[2]	0.074[2]	44[2]	2008	O. Lähteenoja
Nueva Alianza	–	5	75.435	4.704	–	4	–	2.6[2]	0.052[2]	46[2]	2008	O. Lähteenoja
Nuevo Encanto	–	27	74.540	5.527	–	4	–	1.96[2]	–	–	2008	O. Lähteenoja
Riñón	–	23	74.001	4.900	–	9	–	3.55[2]	0.06[2]	49[2]	2006	O. Lähteenoja
Victoria	–	28	74.624	5.670	–	7	–	1.7[2]	–	–	2008	O. Lähteenoja
Open ground reference points												
Huitoyacu 1	–	2	76.551	4.174	–	–	–	–	–	–	2006	D. Vela and R. Zaráte
Huitoyacu 2	–	1	76.557	4.162	–	–	–	–	–	–	2006	M. Flores and R. Zaráte

Palm swamp ground reference points												
Pastaza 1	–	3	76.553	4.216	–	–	–	–	–	–	2006	E. Valderrama and R. Zaráte
Pastaza 2	–	3	76.552	4.228	–	–	–	–	–	–	2006	M. Flores and R. Zaráte
Pastaza 3	–	4	76.628	4.422	–	–	–	–	–	–	2006	R. Zaráte
TOTAL	–	–	–	–	24	218	–	–	–	–	–	–

Appendix 2.2 Details of remote sensing images covering the study area in the Pastaza-Marañon foreland basin

Sensor	Path	Row	Acquisition date	Scene Code
Landsat 5 TM	06	63	22/08/2005	LT50060632005234CUB01
	06	64		LT50060642005234CUB01
	07	63	13/08/2005	LT50070632005225CUB00
	07	64		LT50070642005225CUB00
	08	63	08/09/2006	LT50080632006251CUB00
	08	64		LT50080642006251CUB00
ALOS PALSAR	02	74–78	2010	–
	03			–
	04			–
	05			–
	06			–
SRTM	21	14 and 15	02/2000	–
	22			–

Appendix 3.1 Details of all plots used in chapter 3.

Plot Code	Locality	Lat.	Long.	Plot area (ha)	Min stem dbh (cm)	Ecosystem type	Reference or senior team for RAINFOR plots
OLL-01	Ollanta	-4.448	-74.848	0.5	10 (2)	PF	This study
OLL-02	Ollanta	-4.452	-74.856	0.5	10 (2)	PF	This study
OLL-03	Ollanta	-4.454	-74.861	0.5	10 (2)	PF	This study
OLL-04	Ollanta	-4.457	-74.867	0.5	10 (2)	PF	This study
MIF-01	Miraflores	-4.407	-74.063	0.5	10 (2)	PF	This study
MIF-02	Miraflores	-4.415	-74.074	0.5	10 (2)	PF	This study
MIF_03	Miraflores	-4.410	-74.060		10 (2)	PF	This study
NYO-01	Nueva York	-4.417	-74.280	0.5	10 (2)	PF	This study
NYO-02	Nueva York	-4.395	-74.265	0.5	10 (2)	PF	This study
NYO_03	Nueva York	-4.400	-74.270		10 (2)	PF	This study
SJO_P1	San Jorge	-4.062	-73.192	0.5	10 (2)	PF	Kelly *et al.* 2014
VEN-05	Veinte de Enero	-4.686	-73.819	0.5	10 (2)	PS	This study
VEN-04	Veinte de Enero	-4.679	-73.819	0.5	10 (2)	PS	This study
VEN-03	Veinte de	-4.676	-73.819	0.5	10 (2)	PS	This study

	Enero						
VEN_02	Veinte de Enero	-4.668	-73.819	0.5	10 (2)	PS	Honorio Coronado *et al.* 2015
VEN_01	Veinte de Enero	-4.672	-73.820	0.5	10 (2)	PS	Honorio Coronado *et al.* 2015
REQ-05	Requena	-4.812	-73.820	0.5	10	PS	Honorio Coronado *et al.* 2015
REQ-13	Requena	-4.836	-73.833	0.5	10	PS	Honorio Coronado *et al.* 2015
REQ-01	Requena	-4.906	-73.821	0.5	10	PS	Honorio Coronado *et al.* 2015
REQ-04	Requena	-4.879	-73.793	0.5	10	PS	Honorio Coronado *et al.* 2015
JEN_P1	Jenaro Herrera	-4.873	-73.647	0.5	10	PS	Honorio Coronado *et al.* 2015
JEN_P2	Jenaro Herrera	-4.836	-73.652	0.5	10	PS	Honorio Coronado *et al.* 2015
QUI_P1	Quistococha	-3.840	-73.319	0.5	10 (2)	PS	Roucoux *et al.* 2013
SRI-01	Santa Rita	-4.576	-74.374	0.5	10 (2)	PS	This study
SRO-01	San Roque	-4.532	-74.630	0.5	10 (2)	PS	This study
PRN_01	Parinari	-4.524	-74.469	1	10 (2)	PS	This study
NAP-01	PV7 terrace	-0.880	-75.210	1	10	TF	Pitman *et al* 2008
NAP-02	PV7 polvorín	-0.880	-75.210	1	10	TF	Pitman *et al* 2008
NAP-03	Vencedores	-1.140	-75.020	1	10	TF	Pitman *et al* 2008

NAP-04	Santa María	-1.420	-74.620	1	10	TF	Pitman *et al* 2008
NAP-05	Ingano Llacta	-1.870	-74.670	1	10	TF	Pitman *et al* 2008
NAP-06	Boca Curaray	-2.380	-74.090	1	10	TF	Pitman *et al* 2008
NAP-07	San José	-2.510	-73.660	1	10	TF	Pitman *et al* 2008
NAP-08	Santa Teresa	-2.830	-73.560	1	10	TF	Pitman *et al* 2008
YAR-01	Curacinha	-5.050	-72.730	1	10	TF	Pitman *et al* 2008
YAR-02	Buenavista	-4.830	-72.390	1	10	TF	Pitman *et al* 2008
QBC-01	Quebrada Blanco	-4.360	-73.160	1	10	TF	Pitman *et al* 2008
QBC-02	Quebrada Blanco	-4.360	-73.160	1	10	TF	Pitman *et al* 2008
YAG-01	Yaguas	-2.860	-71.420	1	10	TF	Pitman *et al* 2008
MAR-01	Maronal	-2.970	-72.130	1	10	TF	Pitman *et al* 2008
APY-01	Apayacu	-3.120	-72.710	1	10	TF	Pitman *et al* 2008
ORS-01	Río Orosa	-3.620	-72.240	1	10	TF	Pitman *et al* 2008
SAP-01	Sabalillo	-3.340	-72.310	1	10	TF	Pitman *et al* 2008
NAU-01	Nauta	-4.440	-73.610	1	10	TF	Pitman *et al* 2008
ALP-01	Allpahuayo -Mishana	-3.949	-73.435	1	10	TF	Abel Monteagudo, Tim Baker, Javier Silva Espejo, Oliver Phillips, Roel Brienen, Yadvinder Malhi; RAINFOR

ALP-02	Allpahuayo -Mishana	-3.952	-73.438	1	10	TF	Abel Monteagudo, Tim Baker, Oliver Phillips ,Roel Brienen ; RAINFOR
YAN-01	Yanamono	-3.435	-72.845	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker; RAINFOR
YAN-02	Yanamono	-3.434	-72.845	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker; RAINFOR
SUC-01	Sucusari	-3.252	-72.908	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker, Nestor Jaramillo; RAINFOR
SUC-02	Sucusari	-3.250	-72.904	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker, Nestor Jaramillo; RAINFOR
SUC-03	Sucusari	-3.250	-72.917	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker ;RAINFOR
SUC-04	Sucusari	-3.251	-72.891	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker ;RAINFOR
SUC-05	Sucusari	-3.256	-72.894	1	10	TF	Oliver Phillips, Rodolfo Vasquez, Roel Brienen, Tim Baker, Nestor Jaramillo; RAINFOR
JEN-11	Jenaro Herrera	-4.878	-73.629	1	10	TF	Euridice Honorio, Oliver Phillips, Roel Brienen, Tim Baker ; RAINFOR
JEN-13	Jenaro Herrera	-4.924	-73.538	1	10	TF	Euridice Honorio, Oliver Phillips, Roel Brienen, Tim Baker ; RAINFOR
SMU-01	Saramuro	-4.707	-74.924	0.5	10 (2)	SF	this study
BVA_P1	Buena vista	-4.240	-73.200	0.5	10 (2)	SF	Kelly *et al.* 2014
REQ-02	Requena	-4.917	-73.788	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-03	Requena	-4.885	-73.791	0.5	10	SF	Honorio Coronado *et al.* 2015

REQ-06	Requena	-4.823	-73.806	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-07	Requena	-4.811	-73.803	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-08	Requena	-4.815	-73.790	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-09	Requena	-4.819	-73.789	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-10	Requena	-4.915	-73.746	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-11	Requena	-4.955	-73.720	0.5	10	SF	Honorio Coronado *et al.* 2015
REQ-12	Requena	-4.959	-73.725	0.5	10	SF	Honorio Coronado *et al.* 2015
AMB	Allpahuayo -Mishana	-3.951	-73.400	0.1	5	WS	Fine *et al.* 2010
AMC	Allpahuayo -Mishana	-3.948	-73.412	0.1	5	WS	Fine *et al.* 2010
AMD	Allpahuayo -Mishana	-3.942	-73.439	0.1	5	WS	Fine *et al.* 2010
ANV	Upper Nanay	-3.741	-74.122	0.1	5	WS	Fine *et al.* 2010
ANC	Upper Nanay	-3.741	-74.133	0.025	2.5	WS	Fine *et al.* 2010
JEB	Jeberos	-5.300	-76.267	0.1	5	WS	Fine *et al.* 2010
JH1	Jenaro Herrera	-4.850	-73.600	0.1	5	WS	Fine *et al.* 2010
JH2	Jenaro Herrera	-4.850	-73.600	0.1	5	WS	Fine *et al.* 2010
JHC	Jenaro	-4.850	-73.600	0.025	2.5	WS	Fine *et al.* 2010

	Herrera						
MP	Morona	-4.267	-77.233	0.1	5	WS	Fine *et al.* 2010
MB	Morona	-4.267	-77.233	0.1	5	WS	Fine *et al.* 2010
TA1	Tamshiyacu	-3.983	-73.067	0.1	5	WS	Fine *et al.* 2010
TA2	Tamshiyacu	-3.983	-73.067	0.1	5	WS	Fine *et al.* 2010
TAC	Tamshiyacu	-3.983	-73.067	0.025	2.5	WS	Fine *et al.* 2010
MAT	Matses	-5.855	-73.754	0.1	5	WS	Fine *et al.* 2010
ALP-18	Allpahuayo-Mishana	-3.954	-73.429	0.1	2	WS	Oliver Phillips, Rodolfo Vasquez; RAINFOR
ALP-24	Allpahuayo-Mishana	-3.955	-73.430	0.1	2	WS	Oliver Phillips, Rodolfo Vasquez; RAINFOR
ALP-25	Allpahuayo-Mishana	-3.953	-73.437	0.1	2	WS	Oliver Phillips, Rodolfo Vasquez; RAINFOR
ALP-26	Allpahuayo-Mishana	-3.952	-73.411	0.1	2	WS	Oliver Phillips, Rodolfo Vasquez; RAINFOR
ALP-30	Allpahuayo-Mishana	-3.954	-73.427	1	10	WS	Abel Monteagudo, Tim Baker, Javier Silva Espejo, Oliver Phillips, Yadvinder Malhi ; RAINFOR
ALP-40	Allpahuayo-Mishana	-3.941	-73.440	1	10	WS	Abel Monteagudo, Freddy Ramirez, Oliver Phillips; RAINFOR
ALP-50	Allpahuayo-Mishana	-3.951	-73.410	1	10	WS	Rooselvelt Garcia, Oliver Phillips; RAINFOR

JEN-12	Jenaro Herrera	-4.899	-73.629	1	10	WS	Euridice Honorio, Oliver Phillips, Roel Brienen, Tim Baker ; RAINFOR

Appendix 3.2 List of peatland specialist taxa

Taxa	**Peatland ecosystem where specialist**
Buchenavia_amazonia	Pole forest and palm swamp
Crudia_glaberrima	Pole forest and palm swamp
Cybianthus_reticulatus_cf	Pole forest and palm swamp
Ilex_vismiifolia	Pole forest and palm swamp
Macrolobium_multijugum	Pole forest and palm swamp
Mauritia_flexuosa	Pole forest and palm swamp
Tabebuia_insignis	Pole forest and palm swamp
Macrolobium_angustifolium	Pole forest and palm swamp
Lueheopsis_hoehnei	Pole forest and palm swamp
Ficus_americana	Pole forest and palm swamp
Bocageopsis_muliflora	Pole forest
Chrysophyllum_amazonicum	Pole forest
Ecclinusa_lanceolata	Pole forest
Himatanthus_bracteatus	Pole forest
Inga_alba	Pole forest
Machaerium_macrophyllum	Pole forest
Mouriri nigra	Pole forest
Platycarpum sp1	Pole forest
Ryania_pyrifera	Pole forest
Amanoa_oblongifolia	Palm swamp
Bactris_borgniatti	Palm swamp
Bactris_concinna	Palm swamp
Diospyros_artanthifolia	Palm swamp
Elaeis_oleifera	Palm swamp
Inga_maginata	Palm swamp
Klarobelia_inundata	Palm swamp
Macrolobium_gracile	Palm swamp
Protium_glabrescens	Palm swamp
Pterocarpus_santalinoides	Palm swamp
Ruptiliocarpon_caracolito	Palm swamp
Sloanea_guianensis	Palm swamp
Terminalia_dichotoma	Palm swamp
Tococa_caudata	

Appendix 4.1 Details of pollen Taxonomy, CDM refers to (Colinvaux *et al.* 1999); WHH refers to (Weber *et al.* 1999), R & M refers to (Roubik & Moreno 1991); LPRC refers to the Leeds pollen reference collection.

Pollen Type	**Constituent taxa**	**Reference**	**Notes**
Apocynaceae *Macoubea* t.	Apocynaceae *Macoubea, Malouetia*	CDM	
Aquifoliaceae *Ilex*	Aquifoliaceae *Ilex*	CDM	
Araceae *Pistia*	Araceae *Pistia stratiotes*	WHH	
Arecaceae *Bactris t.*		R&M	
Arecaceae *Euterpe*	Arecaceae *Euterpe precatoria*	CDM	
Arecaceae *Mauritia t.*		LPRC	Monoporate grains with echinate-scabrate surface. Echinae sit in conspicuous depressions in the tectum. Pore circular to elliptic with ragged edges. Grains spheroidal to oblate-spheroidal. Includes grains belonging to both Mauritia sp. and Mauritiella sp.
Begoniaceae *Begonia*		RM	Trizonocolporate, sexine finely striate, striae longitudinally orientated, colpi thin and as long as grain. Prolate in equatorial view, lobed in polar view.
Combretaceae *sp.*	Combretaceae *Combretum decandrum*	R&M	
	Combretaceae *Combretum sp.*	R&M	
	Combretaceae *undiff.*	R&M	Grains strongly hexalobulate, polar diameter 17–41 μm, pores circular or lalongate and conspicuous.
Compositeae *undiff*		CDM/RM	tricolporate, strongly echinate, psilate, pores inconspicuous
Cyperaceae *undiff*		LPRC	Monoporate, scabrate, generally irregularly shaped grains. Often rather triangular in shape. Pore

			inconspicuous, raged. Exine has lacunae (areas where scabrae are absent).
Elaeocarpaceae *Sloanea*	Elaeocarpaceae *Sloanea zuliaensis*	R&M	
	Eleocarpaceae *Sloanea guianensis*	NPD	
Euphorbiaceae *Croton*			
Euphorbiaceae *Mabea*			
Fabaceae *Machearium*	Fabaceae *Machearium arboreum*	CDM/RM	tricolporate, slightly reticulate, subprolate, very thin colpi, very large slightly lalongate pore.
	Fabaceae *Machearium floribundum*		
Fabaceae *Macrolobium*		CDM	Tricolporate, striato-reticulate, prolate grain, pores conspicuous and circular to slightly lalongate
Malvaceae *Apieba t.*			
Malvaceae *Lueheopsis*	Malvaceae *Lueheopsis hoenhii*	LPRC/CDM	tricolporate, reticulate, prolate to subprolate, colpi 2 µm wide and length of grain, pores eliptic and large.
Malvaceae *sp.*			
Melastom/combretaceae		CDM/RM	Heterocolporate, 3 colpi alternating with 3 pseudocolpi, colpi and pseudocolpi as long as grain, typically small (< 20µm polar diamter), colpi and pseudocolpi same depth,
Melastomataceae *Miconia t.*		CDM/RM	Polar diameter < 20 µm (12–20 µm), psilate-scabrate, pseudocolpi inconspicuous, pores pores faint, equatorial constriction to copi,
Moraceae *Brosimum*		B&M	
Moraceae *Ficus*		B&M	
Moraceae *undiff*	Moraceae *Maclura*	B&M	Small (6–22 µm), psilate to scabrate, di- to tetraporate grains

	tinctoria		are assigned to this category when there is insufficient detail preserved/visible to enable them to be keyed out using B&M.
	Moraceae *Olmedia sp.*	B&M	
	Moraceae *Pourouma sp.*	B&M	
	Moraceae *Pseudolmedia sp*.	B&M	
	Moraceae *Sorocea guilleminiana*	B&M	
	Moraceae *Sorocea hirtella*	B&M	
	Moraceae *Urera sp.*	B&M	
	Moraceae *undiff.*	R&M	
Myristicaceae *Virola*		R&M	
Myrtaceae *undiff*	Myrtaceae *Calycopus warszewiczianus*	R&M	
	Myrtaceae *Eugenia principium*	R&M	
	Myrtaceae *Myrcia fosteri*	R&M	
	Myrtaceae *Psidium anglohondurensis*	R&M	
	Myrtaceae *Psidium sp*.	R&M	
	Myrtaceae *undiff.*	R&M	Often not very well preserved with detail of morphological characters difficult to see clearly. Includes trizonocolporate, syncolporate or parasyncolporate, psilate to scabrate grains.
Pachira brevipes		SS	brevi-tricolpate, heteroechinate,

		very oblate, colpi short
Poaceae *undiff*	CDM	Spherical, psilate to scabrate grains with a single annulate pore
Polygonaceae *undiff*	RM	
Rubiaceae *Psychotria*	CDM/RM	
Rubiaceae sp.		
Sapotaceae *Pouteria*	CDM	
Symmeria *paniculata*	CDM Absy (1979)	
Symphonia *globulifera*	R&M	
Tabebuia insignis	LPRC	
Tapiria *guianensis* t.	LPRC	
Urticaceae *Cecropia*	B&M	