

**Using plant functional traits to assess ecosystem processes and community dynamics in lowland fens: understanding the efficacy and applicability of a trait-based approach to plant ecology**

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## Abstract

The research presented here focuses on the functional aspect of biodiversity of plant communities, with emphasis placed on the functions of species within biological communities and ecosystems, rather than their identity. The prominence of plant functional traits as major contributors to ecosystem functioning is based on underlying mechanisms whereby individual species interact with each other and with their abiotic environment to influence ecological processes on different spatial scales. In this study, particular attention is given to the modulating effects of functional diversity and composition on community dynamics and ecosystem processes (e.g., soil processes relevant to the cycles of carbon and nitrogen), as well as its response to disturbance. A number of green leaf functional traits considered to be pertinent to soil processes and the biogeochemical cycles of carbon and nitrogen were measured from vascular plant species growing in lowland fens in East Anglia, UK. Such habitats are widely recognised as areas of high conservation value for providing numerous benefits to society, including nutrient cycling and soil carbon storage. The set of analyses presented here reveals the implications of different degrees of management intervention for the functional composition of lowland fen plant communities. Overall, the functional diversity of such communities were found to respond strongly to changing disturbance intensity, to significantly interact with abiotic factors to contribute to the provision of ecosystem processes and to exert major effects on species coexistence within plant assemblages. These results confirm the wide applicability of the trait approach when investigating the effects of biodiversity on the stability of biological communities and ecosystems, and is potentially informative to conservation-focused projects that aim to simultaneously enhance biodiversity and the provision of vital ecosystem services. In fact, management intervention was largely found to favour species with a set of traits conducive to enhancing soil carbon storage, lending support to current long term conservation projects that aim to positively influence soil carbon balance.

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# Chapter 1

## Introduction

### 1.1 Biological diversity, community dynamics and ecosystem functioning

The biological components of the Earth's ecosystems, particularly the autotrophic organisms that produce complex organic compounds from sunlight energy, are considered to be largely responsible for influencing community dynamics and environmental conditions from local to global scales, affecting the biogeochemical cycles of the most important nutrients and providing resources for pollinators, food, genetic resources, cultural values and many other benefits to human societies (Grime, 1998; Hooper *et al.*, 2005; Naeem *et al.*, 2012). The idea that biodiversity should positively influence the stability of communities and ecosystems gained traction as early as the 1950s, when ecologists such as Odum (1953), MacArthur (1955) and Elton (1958) emphasised the importance of biotic interactions on community dynamics and ecosystem function based on observational studies of agricultural and natural systems. Nevertheless, research during the latter part of the 20<sup>th</sup> century revealed that human alteration of the Earth's terrestrial and aquatic ecosystems had resulted in dramatic worldwide losses of biological diversity at taxonomic and functional levels (Vitousek *et al.*, 1997). A critical gap in developing strategies for biodiversity conservation remained though, particularly in the context of mitigating any potential impacts on the biogeochemical and dynamic properties of ecosystems resulting from such biotic impoverishment. This critical gap in knowledge rested mostly in the incomplete understanding of the mechanisms linking biodiversity and ecosystem processes (Grime, 2001). As a result, major international research initiatives, partly motivated by the 1992 Earth Summit in Rio de Janeiro, formed in order to understand questions related to the role of biodiversity in the functioning of ecosystems (Schulze and Mooney, 1993). Several studies in the 1990s, for instance, suggested that processes like biomass production and nutrient cycling responded strongly to changes in species diversity (Naeem *et al.*, 1994; Tilman and Downing, 1994; Tilman *et al.*, 1996; Tilman *et al.*, 1997; Hector *et al.*, 1999). Notably, long-term experimental studies began to identify causes and consequences of species diversity on ecosystems (Tilman *et al.*, 1996), confirming that positive relationships between them were mostly due to complementarity effects (i.e.,

enhanced resource use due to niche partitioning). Such studies largely focused on the effects of taxonomic diversity on ecosystems, since manipulation of species richness seemed to be the main method used.

Developing in parallel to that, however, was the increasing recognition that focusing on alternative aspects of biodiversity (other than taxonomy) was a better approach to tackle the impact of biotic loss on the integrity of ecosystem functioning (Walker, 1992). The argument was that, in order to assess the effects of taxonomic loss on communities and ecosystems, a detailed knowledge of the autecology of all species would be theoretically necessary, but unfeasible (Duckworth *et al.*, 2000). Therefore, rather than considering species solely on a taxonomic basis, one solution that later became widely adopted (Díaz *et al.*, 2007; Duffy *et al.*, 2007) was to consider species on a functional basis (Mooney *et al.*, 1997), i.e. focusing on what species '*do*' rather than on what they '*are*' (function here follows the definition given by Garnier *et al.*, 2016, as "*an activity carried out by part of a whole or by the whole itself*"). The idea of using organisms' functional attributes was actually explored in the early half of the 20<sup>th</sup> century, when authors such as Grinnell (1924), Elton (1927) and Raunkiær (1934) used species' attributes to differentiate their trophic position in ecosystems and to define arenas of actual or potential interactions according to their niche. Odum (1953) later popularised this notion in his analogy of the niche of a species as its '*profession*' in an ecosystem, while the habitat was its '*address*'. The niche concept was further developed in the 1950s by Hutchinson (1957), who identified an *n*-dimensional hypervolume to define the requirements of a species to persist, given its physiological tolerances. Although the formalisation of niche theory allowed for the development of models to describe community dynamics and to show that random food webs with high biodiversity were more stable than ones with low diversity (MacArthur, 1957; MacArthur and MacArthur, 1961; Levins, 1963), the overemphasis on the notion of interspecific competition for resources as the primary underlying mechanism driving ecological processes led to some criticism of little attention being given to the effects of organisms on their environment (Chase and Leibold, 2003). Therefore, while the links between species' performance and their niche placement had been thoroughly discussed, the question of what properties of species were responsible for driving processes at the community and ecosystem levels remained unanswered.

Numerous classification systems based on various morphological and/or functional characteristics of organisms were proposed during the 20<sup>th</sup> century in an attempt to fill that gap, including that of Mooney and Dunn (1970) and Hallé *et al.* (1978). The concept of

classifying species into plant functional types (PFTs), though introduced earlier (Raunkiaer, 1934; Grime, 1974, 1977; Noble and Slatyer, 1980; Smith and Huston, 1989; and see Duckworth *et al.*, 2000 for a historical overview), gained new currency in the 1990s as one possible framework for predicting ecosystem response to human-induced changes (Chapin III *et al.*, 1996; Woodward and Cramer, 1996; Diaz and Cabido, 1997; Lavorel *et al.*, 1997; McIntyre *et al.*, 1999). The identification of PFTs was considered an essential step in environmental change research since plants with similar responses to environmental conditions (reflecting similar attributes and strategies) could be grouped and summarised into a relatively small number of general recurrent patterns (Grime *et al.*, 1996). Notably, the development of an adaptive strategies model by Grime (1974, 1977) based on morphological, phenological and reproductive characteristics of plants also recognised the potential effects of species on ecosystems (see the definitions of response and effect traits below) and attempted to describe the ecological consequences (e.g., effects on biomass production, water level and mineral nutrients in soil) of the responses of competitive (C), stress-tolerant (S) and ruderal (R) plant species to desiccation, shading and nutrient stress. Although remarkably influential in plant ecology, Grime's C-S-R triangle remained somewhat controversial for not adequately addressing the importance of non-heterogeneous supplies of nutrients and for his rigid classification of species along nutrient and disturbance gradients, including the ways in which complex factors like light, disturbance and competition interact to influence community and ecosystem dynamics (Tilman, 1987b; Craine, 2005).

Although the functional classification approach went a step closer to answering pertinent questions related to community and ecosystem dynamics, the inadequacy of simple classification models in determining the underlying mechanisms whereby individual species interact with each other and with their abiotic environment to influence ecological processes was a considerable limitation (Tilman, 1987a). In addition, PFTs have their particular deficiencies since, in many instances, no clear breaks between different functional types can be determined, making their classification potentially subjective and arbitrary (Duckworth *et al.*, 2000), while remaining difficult to identify which property of the functional group is responsible for differences in performance in different environments.

In spite of that, functional approaches to the study of biodiversity remained useful in understanding the interactions between the different components of the ecosystem for its long-term viability, and in providing a basis for predicting changes when components

are modified or lost (Naeem *et al.*, 2012). Accordingly, there has been substantial evidence of the links between the mean functional composition of plant communities and ecosystem processes (Díaz and Cabido, 2001; Grime, 2001; Chapin III, 2003; Garnier *et al.*, 2004; Fornara and Tilman, 2008; Garnier *et al.*, 2016). One common approach taken by these more recent studies was to model the individual characteristics used to describe organisms, referred to as 'traits', to determine species' and communities' response to (and impact on) ecosystems. Functional traits can therefore be regarded as response traits, whose values respond to variations in environmental conditions (biotic or abiotic), and effect traits, which have the potential to influence the properties of an ecosystem. Arguably, a conceptual framework of response and effect traits applied to the functional approach should allow for the response of plant species to environmental factors to be linked to the potential effects of this response on ecosystem properties (Garnier *et al.*, 2016). Environmental filters select the value, range and relative abundance of response traits found in a community which, in turn, impact on ecosystem properties through the intermediary influence of effect traits. Functional traits thus became widely recognised to not only modulate organisms' fitness, but to allow for the quantification of the relationship between the different levels of organisation of ecological systems (Lavorel and Garnier, 2002; Garnier *et al.*, 2016). Therefore, the use of functional traits developed to become the key link to connect the properties of individuals/species to their performance at the community and ecosystem scales. For instance, if the key traits of an organism are known, it may be possible to quantify and predict the impacts of species invasions and/or losses on important ecosystem processes such as nutrient cycling (McGill *et al.*, 2010). In addition, plant traits have been found not only to exert major effects on ecosystem functioning (Leps *et al.*, 2006; Garnier *et al.*, 2007), but to influence the provision of multiple ecosystem services (Lavorel *et al.*, 2011; Lavorel and Grigulis, 2012).

The notion that natural habitats provide essential goods and services to society became firmly cemented in the 1990s (Costanza *et al.*, 1997; Daily, 1997; Vitousek *et al.*, 1997). It has been long recognised that the conditions and processes needed for the intermediate delivery of ecosystem processes that are vital for the production of final ecosystem services depend on the complex interactions between the biological, chemical and physical components of ecological systems (Mooney and Ehrlich, 1997). More recently though, the different possible mechanisms by which the functional diversity of biological communities affect ecosystem properties that are directly relevant for ecosystem services became the central focus of research (Díaz *et al.*, 2007; Mace *et al.*, 2012; Grigulis *et al.*,

2013), including the development of strategies to preserve and promote soil carbon sequestration through the use of regulatory plant traits (de Deyn *et al.*, 2008). Soil carbon storage is a key component of the global carbon cycle and has profound implications for the global climate (Davidson and Janssens, 2006). Some types of ecosystems, in particular wetlands, have been identified as key conservation units in the process of mitigating the effects of carbon loss from soils due to human-induced changes (Millennium Ecosystem Assessment, 2005). For instance, peatlands are well known for their ability to store carbon (Rydin and Jeglum, 2013). Although fluxes and stores of carbon in peatlands have been reliably measured (Billett *et al.*, 2004; Janssens *et al.*, 2005; Worrall *et al.*, 2009), the extent to which shifts in functional traits found in lowland fen communities affect carbon storage is still poorly understood. Most studies to date have focused on abiotic factors (Bellisario *et al.*, 1998; Updegraff *et al.*, 2001; Goll *et al.*, 2012), but Ward *et al.* (2007) and Beilman *et al.* (2009) suggested that changing vegetation composition can alter carbon dynamics and exchange rates in peatlands. However, to the author's knowledge no study to date has quantified the role of individual plant traits in driving carbon dynamics in lowland fen communities.

The present study adopts a functional approach to quantify and understand the effects of biodiversity on plant community dynamics and ecosystem processes. It is proposed that the methods adopted here (described in **Chapter 2** and in each subsequent data chapter) have great potential to answer questions related to the distribution and diversity of plant traits along disturbance gradients (Southwood, 1988; Foley *et al.*, 2005; Nelson, 2005; Garnier *et al.*, 2007; Pakeman *et al.*, 2011; **Chapter 3**), the interactions between plant functions and environmental variables that translate into ecosystem processes and services (Chapin III, 2003; Diaz *et al.*, 2004; Lavorel and Grigulis, 2012; **Chapter 4**), the rules governing community assembly processes (McGill *et al.*, 2006; Suding *et al.*, 2008; Shipley, 2010; Pakeman, 2011; Götzenberger *et al.*, 2012; **Chapter 5**) and the temporal changes in mean trait composition of plant communities through the use of palaeoecological records, with potential implications for reconstructing past ecosystem processes (Lacourse, 2009; **Chapter 6**). This study aims to highlight how taking account of the interspecific variability in plant traits helps to address these important topics, which are at the core of current ecological research (Garnier *et al.*, 2016) and form some of the most pertinent questions in contemporary ecology (Sutherland *et al.*, 2013).

Lowland fen plant communities, comprising both herbaceous and wooded sites, were selected for the current set of analyses for they reveal high levels of biodiversity

(Wheeler, 1980a), comprise about 42% of the peatland habitat in England, covering some 2880 km<sup>2</sup> (Natural England, 2010), and have been subject to little research if compared to blanket and raised bogs. However, a significant proportion of the fen habitat in Britain has been subject to profound alterations (Natural England, 2010; Mainstone *et al.*, 2016). Therefore, the type of research presented here may be particularly important for long-term restoration projects that seek to recreate peatland habitats in Britain, notably the Great Fen Project in East Anglia (Gauci, 2008), since the challenge of predicting the response of ecosystem processes to environmental change poses a significant threat to sustainable ecosystem management (Mace *et al.*, 2012). For instance, results may support maximising trait diversity and redundancy rather than taxonomic diversity. In addition, it is envisaged the present study will contribute towards:

- i. A legacy of a detailed plant functional trait database of key fen species that will be made available to the scientific community;
- ii. Quantification of soil carbon storage in lowland fens in eastern England; and
- iii. Quantification of the interactions between environmental variables, functional traits and ecosystem processes in lowland fens.

Brief descriptions of the peatland environment and of fen communities are presented next, followed by the methodological approach (Chapter 2, with a description of the study sites in East Anglia, Upton and Woodwalton). The subsequent data chapters (3 to 6) lay out their aims and objectives and the thesis concludes (Chapter 7) with an overview of the findings and some recommendations for possible future work.

## **1.2 The peatland environment**

Wetlands are generally distinguished by the persistent presence of excess water, either at the surface or within the root zone, resulting in unique soil conditions that support vegetation well adapted to wet environments (*hydrophytes*), where flooding-intolerant biota are largely absent (Mitsch and Gosselink, 2015). They are one of the most productive habitats in the world and well known to support rich biodiversity (Keddy, 2010). Wetlands are unique environments in that they form at the interface between terrestrial and aquatic ecosystems, arising when constant inundation by water produces poorly aerated substrate dominated by anaerobic processes (Mitsch and Gosselink, 2015). The resident flora of such

habitats must therefore possess unique characteristics, in that they need to cope with the direct effects of flooding and the secondary effects of anaerobic conditions (Keddy, 2010).

Under the right set of conditions, anaerobic processes can give rise to peat, which can be defined as the partially decomposed remains of plant and animal material accumulated under water-saturated conditions (Rydin and Jeglum, 2013). Peat is thus mostly organic matter that has formed in place, i.e. as sedentary material, where the content of inorganic ash by peat dry mass is normally around 25% (Moore, 1987). Different plant materials, such as woody tissue, leaves, rhizomes, roots and bryophytes (notably *Sphagnum* peat mosses), may be involved in the process of peat formation, originating above ground as photosynthetic organic matter and deposited as litter on the surface to be buried by new layers of litter on top (Rydin and Jeglum, 2013). Peat formation is thus the result of an imbalance between total energy fixation by photosynthesis and ecosystem respiration due to relatively stable standing water creating anoxic (depleted of dissolved oxygen) conditions (Moore, 1987), resulting in undecayed matter building up over the underlying mineral substratum. Therefore, peat is an important deposit of stored organic carbon due to slow mineralisation rates (Bridgham *et al.*, 1998), while its status as a greenhouse gas sink means it acts as an important buffer to rising atmospheric carbon dioxide (CO<sub>2</sub>) levels (Roulet, 2000).

The circumstances under which peat accumulates and the nature of the deposits vary widely (Waller, 1994), but the overriding physical condition controlling such processes is the height of the water table (Moore, 1987), though the acidity and nutrient status of the water appear to be other key factors (Bridgham *et al.*, 1996; Wheeler and Proctor, 2000). Peat generally forms under continuous inundation and low to moderate depths of flooding, resulting in intermittently or permanently waterlogged environments (Keddy, 2010). A positive water balance, caused by complex interactions between climate, hydrology and topography, is thus crucial for the accumulation of peat, generally occurring when poor drainage prevents water loss, such as in lowland basins, or when evapotranspiration is only about 50 to 70 percent of precipitation (Mitsch and Gosselink, 2015). Given the conditions of water surplus and organic matter build up, peat accumulation occurs either through *terrestrialisation* (the infilling of shallow lakes) or *paludification*, when terrestrial ecosystems are blanketed by overgrowth of peat vegetation (Mitsch and Gosselink, 2015).

The peat bed can be broadly divided into two layers. The upper layer, the acrotelm, is where waterlogging tends to be intermittent, resulting in rather aerobic conditions that



allow fungi and bacteria to break down recently dead organic material, though decomposition seldom proceeds to completion (Yu *et al.*, 2001; Gunnarsson *et al.*, 2008). The balance between litter production and decay processes in the acrotelm determines the peat addition rate to the thicker layer underneath it, the catotelm, where long-term peat accumulation occurs under permanently waterlogged and thus anaerobic conditions (Yu *et al.*, 2001).

Peatland is the main term used to define peat-covered land. Peatlands are now estimated to cover about 500 million hectares of the Earth's surface, or nearly 4% of the ice-free land area (Keddy, 2010). They are the most widespread type of wetlands in the world, representing 50 to 70 percent of global wetlands (Chapman *et al.*, 2003). The minimum depth of peat required to classify a site as peatland may vary, but 30 cm has been commonly used (Joosten and Clarke, 2002). Peat accumulation can often be several metres thick though, reaching depths of more than ten metres locally if undisturbed (Rydin and Jeglum, 2013).

Peatlands have been classified into several different types over the years, which have generated a great deal of terminology (Wheeler and Proctor, 2000), but the most general hydrology-based classification seems to emphasise the source of water (Keddy, 2010; Rydin and Jeglum, 2013; Mitsch and Gosselink, 2015), which will consequently affect the chemistry of the surface water such as pH, conductivity and nutrient status. Peatland sites where the water in the peat surface is connected with, or has passed over or through, mineral parent materials are commonly termed *minerotrophic*, since they are nourished by mineral soil groundwater encompassing a broad range of nutrient and pH variation (Rydin and Jeglum, 2013). Contrarily, *ombrotrophic* peatlands, occurring where the peat surface is isolated from groundwater percolating through mineral soil, are solely, or at least in most part, nourished by precipitation water and dust fallout. Although many more specialised terms have been proposed (Bridgham *et al.*, 1996), this simple but fundamental classification has been used by many peatland ecologists to generally distinguish *fen* and *bog*, where the term *fen* has been commonly used for *minerotrophic* sites and *bog* for *ombrotrophic* ones (Wheeler, 1980a; Keddy, 2010; Rydin and Jeglum, 2013). Under conducive climatic conditions, the transition from *fen* to *bog* occurs as peat accumulates and the influence of the groundwater chemistry declines, usually as a result of the development of layers of insulating peat or a lowering of the water table (Hughes and Barber, 2003), while *blanket bogs* can develop in topographic locations which shed rather than receive groundwater (Moore, 1987). This process means that peatland ecosystems

are constantly modifying their own hydrology, with fen peats superseded by bog peats, which become increasingly dominated by *Sphagnum* as the peat mass is raised above the influence of groundwater and enters its ombrotrophic stage of development (Kuhry *et al.*, 1993). Therefore, peat accumulation can change groundwater-controlled fens to rainwater-controlled bogs, resulting in progressively more acidic and generally nutrient-poor conditions, as the influence of the cations derived from mineral soil decreases with time (Rydin and Jeglum, 2013). This process of bog formation tends to become self-sustaining with increasing thickening of the peat layer, in which the peatland creates its own groundwater table, higher up than that of the surroundings, due to the capillary water transport and storage abilities of *Sphagnum*, furthering anoxic conditions and reducing decomposition rates (Kuhry *et al.*, 1993; Rydin and Jeglum, 2013). Peatlands can be further classified according to their nutrient status (i.e. chemistry-based classification related to soil fertility, mainly referring to N and P availability), ranging from *eutrophic* peatlands to include nutrient-rich sites to *oligotrophic* peatlands, displaying nutrient-poor conditions (Bridgham *et al.*, 1996), though no clear relationship between hydrology- and chemistry-based classifications seem to exist (Bridgham *et al.*, 1998).

Peatlands are known to provide numerous services to society, namely improved water quality, oxygen production, flooding regulation, nutrient cycling, biodiversity conservation and recreational and cultural services (EFTEC *et al.*, 2006; Keddy, 2010; Mainstone *et al.*, 2016). As discussed further in Chapter 6, they have also been extensively used to provide records of past plant associations and vegetation history (Waller, 1993, 1994; Waller and Marlow, 1994; Waller and Hamilton, 2000), including records of structural and functional alterations due to anthropogenic disturbances (Ireland and Booth, 2012) and ecological changes (Waller, 2013). However, it is their ability to store carbon that has been the focus of recent conservation efforts (Dunn and Freeman, 2011; Regina *et al.*, 2016), including in the UK (Gauci, 2008). Peat typically holds the vast majority of carbon found in peatland ecosystems, accounting for approximately 98.5% of the total carbon in the system, as opposed to 1.5% locked in the vegetation (Gorham, 1991). Peat deposits in the world's wetlands are substantial storages of carbon, comprising about 20 to 30 percent of the 1400 to 2500 Pg-C ( $\text{Pg} = 10^{15} \text{ g}$ ) in the Earth's soils (Roulet, 2000; Hadi *et al.*, 2005; Lal, 2008). In fact, within the terrestrial biosphere, northern peatlands are the most important terrestrial carbon store (Worrall *et al.*, 2009). Gorham (1991) estimated a figure of approximately 455 Pg of C stored in northern peatlands during the postglacial period, which represents twice the amount found in the world's forest biomass. Typical

accumulation rates have been estimated to vary between 10 and 50 g-C m<sup>-2</sup> yr<sup>-1</sup> (Mitsch and Gosselink, 2015). Peat is the single most important soil type for carbon storage in the UK (Ostle *et al.*, 2009), covering approximately 15% of the total land area and storing about 2302 Mt-C (Billett *et al.*, 2010), which accounts for more than half of the UK total soil carbon (Natural England, 2010). Notably, British peatlands have been estimated to represent a net sink of 13.9 ± 14.6 g-C m<sup>-2</sup> yr<sup>-1</sup> (Worrall *et al.*, 2003), with English peatlands alone storing some 584 Mt-C (Natural England, 2010).

Impaired decomposition due to waterlogging is the primary factor maintaining the net gain of carbon fixed in peatlands and controlling the two main gases emitted from peatlands, CO<sub>2</sub> and methane, or CH<sub>4</sub> (Updegraff *et al.*, 2001). Therefore, while decomposition is determined by complex interactions between the quality of the litter, soil pH, temperature and nutrient availability (Rydin and Jeglum, 2013), the position of the water table is key in regulating the abundance of the soil fauna and the predominant type of microbial respiration (aerobic versus anaerobic), significantly affecting gas exchange with the atmosphere. For instance, when the peat surface rises above the water table, the emission of CO<sub>2</sub> increases and that of CH<sub>4</sub> decreases (Laine *et al.*, 1995). The thicker aerated zone leads to increased aerobic respiration and higher rate of oxidation of CH<sub>4</sub> to CO<sub>2</sub>. The opposite happens when the peat surface drops in relation to the water level.

Although peatlands are particularly important in removing carbon dioxide from the atmosphere, the rate of carbon storage has been severely disrupted by human activities, including drainage for agricultural expansion, peat extraction for fuel and urban development (Natural England, 2010; Alonso *et al.*, 2012), which can increase rates of decomposition and release long-term deposits of organic carbon stored in deep layers within the peat bed in the form of CO<sub>2</sub> and CH<sub>4</sub> emissions (Waddington and Price, 2000; Updegraff *et al.*, 2001; Holden *et al.*, 2004). Pristine peatlands are still sequestering carbon at an average rate of 0.07-0.096 Pg-C yr<sup>-1</sup> (Gorham, 1991; Clymo *et al.*, 1998), but drained peatland soils are subject to decomposition and subsidence at a rate of approximately 1 to 2 cm yr<sup>-1</sup>, primarily due to oxidation (Lal, 2008). In the Fenlands of East Anglia, UK peat wastage due to subsidence of the ground surface has been estimated between 0.6 and 2.5 cm yr<sup>-1</sup>, generating annual carbon emissions of around 0.4 Tg-C yr<sup>-1</sup>, or about 0.3% of the UK's annual industrial emissions of CO<sub>2</sub> (Holman, 2009). Regular burning and grazing can also reduce carbon storage in the peatland surface, with recent carbon loss estimates of approximately 25.5 g-C m<sup>-2</sup> yr<sup>-1</sup> (due to burning alone) representing about 60% of peat surface carbon (Ward *et al.*, 2007). Despite that, large peat areas in Europe are still being

drained for pasture, cropland and forestry purposes (Janssens *et al.*, 2005). Indeed, 70% of peatlands in the UK show signs of degradation (Natural England, 2010). In some peatland areas, carbon sequestration has not only declined but been reversed, i.e. they have become sources rather than sinks of CO<sub>2</sub> (Billett *et al.*, 2004), as is now generally the case in the Fenlands in East Anglia, UK (Alonso *et al.*, 2012). While damaged peatlands can be restored and carbon sequestration increased, which are in fact stated objectives of some restoration projects in the UK like the Great Fen Project (Gauci, 2008), as yet it does not seem to compensate for the net carbon accumulation in the original system before disturbance (Waddington and Price, 2000), meaning long-term peatland protection is preferable to restoration in terms of maintaining its carbon storage capacity (Ostle *et al.*, 2009; Alonso *et al.*, 2012).

### **1.3 Fen communities**

Fens are biologically diverse minerotrophic peatlands, where peat depth is usually greater than 30 cm (Rydin and Jeglum, 2013). The total extent of different types of fen in Britain does not seem to be known, but the calcareous rich fen sites of the Broadland region in East Anglia have been estimated to cover an area of approximately 3,000 ha (EFTEC *et al.*, 2006). They have a large number of plant species organised into a variety of plant communities (Wheeler, 1980a, b, c), mostly resulting from variations in environmental conditions, natural processes of development and human interference (Wheeler and Shaw, 1995). Past floristic data have categorised some 46 plant community types supported by fens in aggregate, containing some 653 plant species, of which 294 were regarded as being particularly characteristic of fens (Wheeler, 1993). These sites are normally of high conservation value due to the entomological and ornithological diversity associated with such varied botanical richness (Ratcliffe, 1977a). Moreover, lowland fens in which deep peat deposits have been maintained are estimated to store about 144 Mt-C (Alonso *et al.*, 2012), though studies have found that fens are more susceptible to losing carbon through changing environmental conditions than bogs (Updegraff *et al.*, 2001).

The water table in fen sites is usually slightly below, at, or just above the surface (Wheeler, 1980a). Even minor variations in the level of the water may have important effects upon the composition of fen vegetation (Wheeler and Shaw, 1995). Other main physical factors controlling fens include nutrient regime, pH-base richness and soil moisture-aeration (Rydin and Jeglum, 2013). Wheeler and Proctor (2000) used the term

fen to broadly describe base-rich peatlands where water pH values are typically, but not always, greater than 5.5-6.0, are high in calcium ions and bicarbonates and have vegetation rich in dicotyledonous herbs. Fens can develop in *topogenous* environments, where impeded drainage maintains a high water table, or in *soligenous* situations, where wetness is maintained by laterally mobile water. As discussed above, fens in north-west Europe can be limited to a transitional phase in hydrosere succession, in which the accumulation of organic material in semi-terrestrial herbaceous and wooded fen can bring the soil surface above the groundwater level and lead to the formation of raised bogs. Therefore, the maintenance of fen vegetation seems to require sediment accumulation to be matched by rising groundwater levels.

The acidity and nutrient status of the soil water appear to be key factors in controlling the composition of fen vegetation (Wheeler, 1980a; Wheeler and Shaw, 1995; Wheeler and Proctor, 2000). For floristic purposes, fens have been commonly divided into rich fens and poor fens, with the former largely containing vegetation rich in calcicoles (intolerant of acidic conditions) and the latter having few, if any, calcicoles (Wheeler, 1980a). Rich fens are thus associated with calcareous soils, higher pH (occurring within the range 5-8) and base richness, while poor fen vegetation typically occur in soils with pH in the range 4-5.5 (Rydin and Jeglum, 2013). Wheeler and Proctor (2000) labelled the most nutrient-limited fen communities as small sedge fens, due to the prominence of an open field layer of small calcicole Cyperaceae (notably *Carex*) and forbs, with a rather conspicuous ground layer of brown mosses. Accordingly, tall sedge or tall herb fens were placed at the more nutrient-rich end of the continuum, where field layer growth is more vigorous and the bryophyte ground layer is largely excluded. The most eutrophic sites were classified as reed fens and other tall herb fens, where *Urtica dioica*, *Solanum dulcamara* and other ruderal species are often prominent. Reed fens, also known as reed swamps, are often species poor communities dominated by vigorous, tall monocotyledons that occur at transitions to open water, where the peat surface is seasonally or permanently submerged (Rodwell, 1995). The transition from fen to swamp is often characterised by a change in floristic composition, with a marked decrease in abundance of forbs and bryophytes (Wheeler, 1980a). Reed swamps, which have been estimated to cover about 6,500 ha in Britain (EFTEC *et al.*, 2006), tend to be dominated by reed grass (*Phragmites*), a dense-growing but non-woody plant. *Phragmites australis* is the main species often associated with reed swamps in north west Europe, though other grasses with similar growth forms can also dominate (e.g. *Phalaris arundinacea*, *Glyceria maxima*).

Fens can support both herbaceous and wooded communities, with the latter normally referred to as *fen carr*. Their occurrence seems to be largely determined by management intervention, since many herbaceous fens would be replaced by fen carrs under natural conditions (Wheeler and Shaw, 1995). In herbaceous fens, sedges often dominate, including tussock forming species (*Carex paniculata*) and those with stout shoots forming dense clumps (*Cladium mariscus*). However, other monocotyledons like rushes (e.g. *Juncus subnodulosus*) and grasses (e.g. *Calamagrostis canescens*) can be frequently abundant, while species like *Urtica dioica* and *Epilobium hirsutum* tend to be suggestive of nutrient-enrichment (Wheeler, 1980c), particularly nitrogen.

Woodland and shrub communities often occur where the sediment surface is close to the average water level, and are therefore regarded as representing a relatively drier environment than herbaceous fens (Waller, 1994). *Alnus glutinosa*, a tree of wet and waterlogged conditions intolerant of nutrient poor soils and thus absent from ombrotrophic peatlands, frequently dominates the canopy layer in what are often diverse communities composed of shrubs (notably *Salix* spp.), climbers (*Lonicera* and *Humulus*) and hydrophilous tall (those associated with herbaceous fens; e.g. *Phragmites*, *Filipendula*) and short herbs (e.g. *Ranunculus*, *Solanum*), with many species of sedges and Pteridophytes possible (Wheeler, 1980c; Rodwell, 1991a). The nitrogen-fixing ability of *Alnus* has long been recognised (McVean, 1956), which is now known to occur due to a group of filamentous bacteria, known as actinomycetes, forming nodules on the roots of some trees and shrubs associated with wetlands, among them *Alnus* and *Myrica* (Keddy, 2010). *Betula* dominated communities (often with *Salix*) tend to be found in meso- and oligotrophic situations, while carr dominated by *Salix* can form distinct communities on transitional zones between herbaceous fen and *Alnus* carr (Rodwell, 1991a).

Disturbance caused by varied management practices appears to have considerable effects on the composition and diversity of plant communities in fen sites. For instance, the interchanging predominance of reed beds (*Phragmites*) and sedge beds (*Cladium*) in some areas, particularly in the Broadland region of East Anglia, UK has been attributed to certain management regimes (different mowing rotation periods) favouring one over the other (Wheeler, 1980a). Additionally, species richness in some specific vegetation types, such as rich fens and sedge beds, seems to respond strongly to mowing regimes, with managed communities presenting higher biodiversity than unmanaged sites (Shaw and Wheeler, 1991). Others, however, display a weak relationship with management, given species numbers in reed swamps and poor fens, for instance, are little changed following

disturbance (Shaw and Wheeler, 1991). The season in which mowing takes place and differences in light attenuation through the mown and unmown canopies between these different types of vegetation have been proposed as possible explanations for their distinct responses to intervention (Wheeler and Giller, 1982). Moreover, the intrinsically lower number of species associated with low-pH fen vegetation may lessen the effect of management on taxonomic diversity in these sites (Shaw and Wheeler, 1991). There is also some evidence for the interaction between vegetation management and soil fertility in relation to species richness (Wheeler and Shaw, 1995). Fertile sites can present relatively high species richness in some instances, even though the fertility of fen soils often shows a strong negative correlation with plant species diversity. That is probably due to some forms of vegetation management favouring generalist taxa (Wheeler, 1980a). Despite the effects on species diversity, the prevention of scrub invasion and subsequent development of fen woodland over low-growing herbaceous vegetation seems to be the most conspicuous consequence of management intervention in fens (Wheeler and Shaw, 1995).

## Chapter 2

### Materials and methods

#### 2.1 Study sites

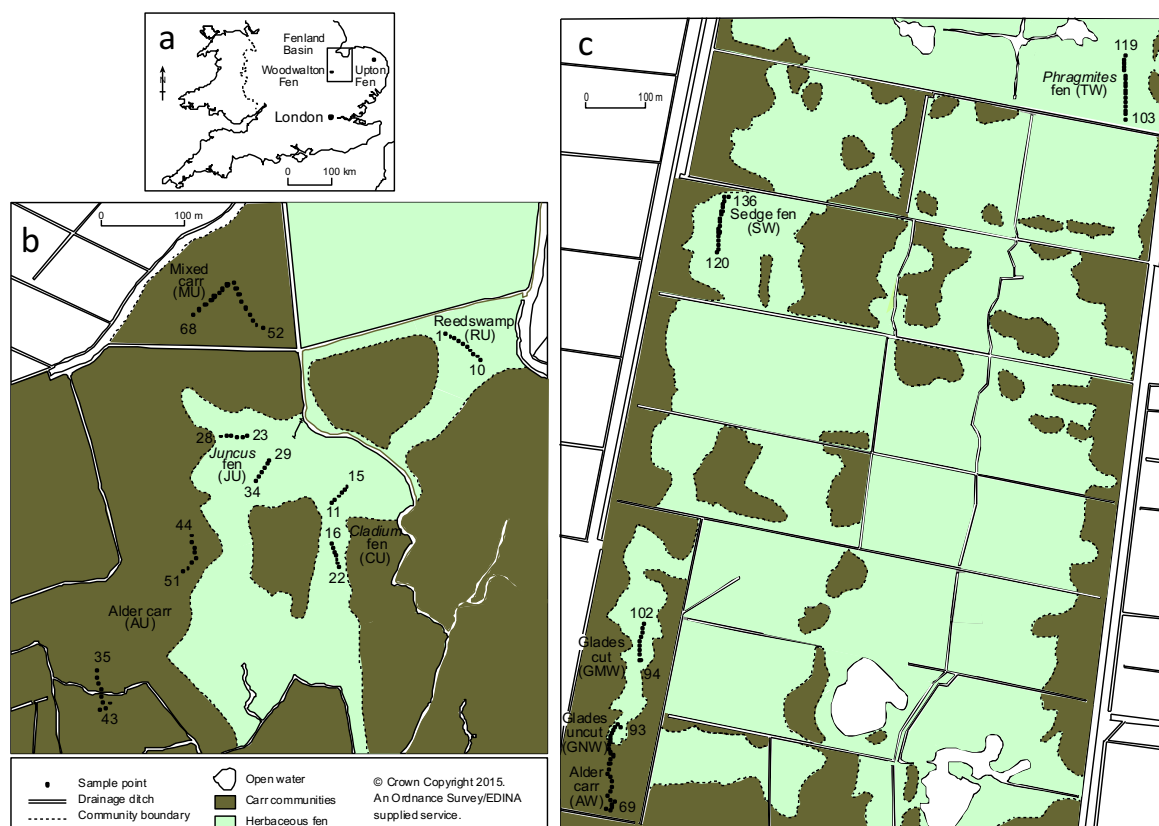
Two sites in East Anglia, eastern England (Fig. 2.1a) containing fen systems that include both herbaceous and woody vegetation (Table 2.1) were selected for investigation, namely Upton Broad, Norfolk (Fig. 2.1b) and Woodwalton Fen, Cambridgeshire (Fig. 2.1c). The lowland region of East Anglia provided the ideal setting to study fen vegetation as it is known to support more rich-fen systems than any other area of comparable size in Britain, including some of the most extensive and botanically-rich sites in the country (Wheeler, 1980a). The Broadland of Norfolk, for instance, where Upton Broad is located, contains the largest area of floodplain peatland in Britain and was the site for some of the most important investigations into the zonation of fen communities and successional pathways in fens, particularly in the Bure valley (Lambert, 1951; Lambert and Jennings, 1951). In addition, the East Anglian Fenland, the flat low-lying area surrounding the Wash where Woodwalton Fen is to be found, is the largest area of former coastal wetland in Britain (Waller, 1994).

##### 2.1.1 Upton Fen

Upton Broad (52°40'N 1°31'E) is a 105 ha Nature Reserve owned and managed by the Norfolk Wildlife Trust and surrounded by pasture and arable land. The area of open water is a designated Site of Special Scientific Interest (SSSI), partly due to the presence of a nationally rare submerged macrophyte species (*Najas marina*), and of European importance, qualified as a Special Protection Area (SPA) and as a Special Area of Conservation (SAC; Ayres *et al.*, 2008). The broad itself was classified by Ratcliffe (1977b) in the 1970s as a Grade I open water site (OW.15) of very high conservation value for representing the type of conditions that existed in many other Broadlands prior to the decline of submerged vegetation and associated fauna that happened elsewhere. The Broad lies in the Bure valley, but is landlocked and the most distant within the valley from the River Bure (Wheeler, 1980a). Its outflow dykes flow over sluices, thus preventing water inputs from



the river system (Phillips, 1977). The site is thought to receive surface water from a small local catchment dominated by drained pastureland, resulting in very low concentrations of phosphorus and organic nitrogen in comparison to other Broads in the area (Bennion *et al.*, 2001). The tall-herbaceous fen and fen carr communities sitting on peat, themselves comprising a unit of grade I conservation interest (P.108; Ratcliffe, 1977b), surround the open water and are the area of interest in this study (from here on referred to as Upton Fen).



**Fig. 2.1:** Location map of Upton and Woodwalton fens in East Anglia, UK (panel a), with position of sampling plots along transect lines in Upton Fen (panel b) and Woodwalton Fen (panel c).

The largest extent of herbaceous fen is dominated by tall monocotyledons growing on regularly mown sites (cut on a 7- to 8-year rotation; Table 2.1) upon solid peat, comprising areas of reedswamp (plots 1 to 10; Fig. 2.1b) with *Phragmites australis* and *Carex riparia* and tall-herbaceous fens (plots 11 to 34; Fig. 2.1b), where *Calamagrostis canescens* is abundant alongside *Cladium mariscus* and *Juncus subnodulosus*. Bryophytes are abundant throughout but excluded from the reed-dominated swamp, while

Pteridophytes are constant and locally abundant, most notably *Thelypteris palustris* and, to some extent, *Equisetum palustre*. Climbers are only sparsely represented, though *Calystegia sepium* is frequent and somewhat abundant in the reedswamp, while *Lonicera periclymenum* attains some prominence in the tall-herbaceous fens, particularly where *C. mariscus* dominates. *Urtica dioica* is the only herb of importance in the species-poor reedswamp, though herbaceous dicotyledons like *Solanum dulcamara*, *Galium aparine* and *Eupatorium cannabinum* are also present. *P. australis* is frequent and abundant in the more floristically variable *Cladium* fen (plots 11 to 22; Fig. 2.1b) and *J. subnodulosus* fen (plots 23 to 34; Fig. 2.1b) communities, despite growing less vigorously than in the reedswamp. That may be due to mowing practices favouring competition from other monocot species like *C. canescens*, *C. mariscus* and *J. subnodulosus* (Wheeler, 1980a). It has also been suggested that the predominance of *Cladium* over *Phragmites* in some areas may happen under conditions of reduced water flow and nutrient input from the river basin, as it seems to be the case in Upton, resulting in relatively unproductive and drier conditions reducing the vigour of *Phragmites* stands (Lambert, 1951). Some notable low-growing dicot species here include *Lysimachia vulgaris*, *Eupatorium cannabinum*, *Mentha aquatica*, *Lythrum salicaria*, *Rubus fruticosus* and *Lotus pedunculatus*. Shrubs do not feature prominently in the herbaceous sites, probably due to exclusion by regular mowing, but *Salix repens* is fairly constant in the *Cladium* fen, while *Myrica gale* and *Viburnum opulus* are somewhat frequently present. *Frangula alnus*, however, is largely absent throughout and only found on occasion.

The fen carr and mixed woodland are old and well developed. Ratcliffe (1977b) noted the presence of many old oaks that add entomological and ornithological interest to the site. *Alnus glutinosa* and *Fraxinus excelsior* are the main canopy-forming species in the alder carr (plots 35 to 51; Fig. 2.1b), while *Betula pubescens* and *Quercus robur* form the tall canopy layer in the mixed woodland (plots 52 to 68; Fig. 2.1b). The alder carr is a characteristic community of sites with fairly base-rich and eutrophic waters (W5; Rodwell, 1991a), where fen peat tends to accumulate in topogenous conditions. The mixed woodland is typical of terrestrialising conditions where the diminished influence of the groundwater, though still strong, is not sufficient to maintain swamp vegetation (W2; Rodwell, 1991a). *Salix cinerea* and *Prunus padus* are the main shrubs in the mixed woodland and alder carr, respectively, but *Crataegus monogyna* is also present. *Thelypteris palustris* is largely replaced by *Dryopteris dilatata* as the main Pteridophyte in the wooded sites, whilst *Carex acutiformis* becomes the most prominent sedge. *Poa trivialis* is rather

frequent and abundant in the alder carr, but *C. canescens* and *P. australis* are the commonest grasses in the mixed woodland. *U. dioica* is virtually absent from the alder-dominated site, but attains prominence in the field layer of the mixed woodland. Other notable dicot herbs found throughout the woody communities are *Rubus fruticosus*, *Geranium robertianum* and *Galium aparine*.

**Table 2.1:** The vegetation communities sampled in Upton Fen and Woodwalton Fen. The NVC (National Vegetation Classification) units (classified by means of identification keys) follow Rodwell (1991a, 1991b and 1995). Management categories refer to the regularity of mowing (see section 2.4.1 below). Management dates for the Upton Fen herbaceous sites refer to the last time of cutting before sampling took place.

Fen site	Community type	Main species	NVC	Management type	Management category	Plot numbers
Upton Fen	Reedswamp	<i>Phragmites australis</i> , <i>Carex riparia</i> , <i>Calystegia sepium</i>	S26/S6	Mown on a 7- to 8-year rotation; last cut 2006/07	3 (moderate)	1 to 10
	Cladium fen	<i>Cladium mariscus</i> , <i>Calamagrostis canescens</i> , <i>Juncus subnodulosus</i> , <i>Salix repens</i> , <i>Myrica gale</i>	S24	Mown on a 7- to 8-year rotation; last cut 2006/07	3 (moderate)	11 to 22
	<i>Juncus subnodulosus</i> fen	<i>J. subnodulosus</i> , <i>C. canescens</i> , <i>Thelypteris palustris</i> , <i>Eupatorium cannabinum</i>	S24	Mown on a 7- to 8-year rotation; last cut 2011	3 (moderate)	23 to 34
	Alder carr	<i>Alnus glutinosa</i> , <i>Fraxinus excelsior</i> , <i>Carex acutiformis</i>	W5	None	0 (unmanaged woods)	35 to 51
	Mixed woodland	<i>Betula pubescens</i> , <i>Quercus robur</i> , <i>Salix cinerea</i> , <i>Dryopteris dilatata</i> , <i>Urtica dioica</i>	W2	None	0 (unmanaged woods)	52 to 68
Woodwalton Fen	Alder carr	<i>A. glutinosa</i> , <i>B. pubescens</i> , <i>Crataegus monogyna</i> , <i>Poa trivialis</i> , <i>U. dioica</i> , <i>Glechoma hederacea</i>	W6	None	0 (unmanaged woods)	69 to 85
	Glade (unmanaged)	<i>C. canescens</i> , <i>P. australis</i> , <i>Symphytum officinale</i>	S24	None	1 (unmanaged herbaceous)	86 to 93
	Glade (managed)	<i>C. canescens</i> , <i>P. australis</i> , <i>C. acutiformis</i> , <i>C. sepium</i>	S24	Mown annually in summer	4 (high)	94 to 102
	<i>Phragmites</i> fen	<i>P. australis</i> , <i>C. acutiformis</i> , <i>C. canescens</i> , <i>C. sepium</i> , <i>Lysimachia vulgaris</i>	S24	Uncut for c. 20 years	2 (low)	103 to 119
	Sedge fen	<i>Carex viridula</i> , <i>Carex panicea</i> , <i>Molinia caerulea</i> , <i>Hydrocotyle vulgaris</i>	M22	Mown annually in summer	4 (high)	120 to 136

### 2.1.2 Woodwalton Fen

Woodwalton Fen (52°26'N 0°11'W) has a long and complex history of human intervention (Duffey, 1971). The site is currently under a more intricate system of management practices than Upton Fen, ranging from annually mown herbaceous fens to

regularly grazed rush pastures and unmanaged glades and woodlands (though the grazed sites were not considered in the present study; Table 2.1). Lying on the south-western edge of the Fenland basin, Woodwalton Fen is a rectangular block of relict peatland covering some 205 ha, surrounded by arable farmland but isolated from the rest of the catchment area by raised flood banks. The fen is divided into several compartments by dykes that connect to the catchment area via control sluices present at all inflows around the site. The main source of water is from the Great Raveley Drain that runs along its eastern border, which is fed by agricultural run-off and treated sewage effluent, and thus likely to be highly eutrophic. The site was listed as a grade I priority for conservation purposes in the 1970s (P.12; Ratcliffe, 1977b), having been a nature reserve since its donation by Charles Rothschild to the Society for the Promotion of Nature Reserves in 1919 (now known as The Royal Society of Wildlife Trusts). Woodwalton is indeed one of the few remaining fragments of ancient fen to survive in this region, generating a considerable degree of interest from researchers and forming a core part of the long-term Great Fen Project that aims to recreate fen communities at a landscape scale in East Anglia, linking land surrounding existing nature reserves totalling approximately 3700 ha (Gauci, 2008). Apart from rewetting the area to restore its fen character, the project seeks to positively influence soil carbon balance.

A range of wetland plant communities are present, including carr and both fen and acidophilous herbaceous sites. Poore (1956) recognised two main seral communities, including a *Molinia*-dominated acidophilic vegetation (notably containing *Calluna vulgaris*, *Erica tetralix* and *Myrica gale*) covering most of the southern end of the reserve (not surveyed for the present study). He proposed these communities were associated with areas where peat cutting had not completely removed fragments of acidic peat (Poore, 1956), suggesting a continuity of the ombrotrophic conditions recorded in this region of the Fenland basin in palaeoecological studies (Godwin and Clifford, 1938). In fact, evidence indicates that bog persisted in the Woodwalton area until extensive drainage in the mid 19<sup>th</sup> century took place (Waller, 1994). While the *Molinia*-dominated vegetation developed mostly on oligotrophic fen peat, the *Calamagrostis* herb-dominated communities, largely characteristic of the northern half of the reserve (where survey for the present study took place), grew on fen peat of various types, including *Phragmites*, *Glyceria* and wood peat (Poore, 1956). Wheeler (1980a) attributed the presence of such communities here to management practices and nutrient status.

The areas surveyed comprised woodland dominated by *A. glutinosa* and *B. pubescens*, glades (herbaceous fen surrounded by woodland), sedge fen and *Phragmites* fen. The alder carr (plots 69 to 85; Fig. 2.1c) presents a diverse field layer with nutrient-demanding herbs like *U. dioica* and *Galium aparine*. *Glechoma hederacea*, *Circaea lutetiana*, *Geranium robertianum* and *Solanum dulcamara* are also notable. *Poa trivialis* and *Holcus lanatus* are the main monocot species, while *C. monogyna* is the most prominent shrub. This community seems to closely resemble (classified by means of identification keys) the W6 vegetation unit of Rodwell (1991a), which can develop in fen peat systems that experienced some degree of enrichment through drainage and disturbance or by eutrophication of the waters. The adjoining glades, including both unmanaged (plots 86 to 93; Fig. 2.1c) and annually mown sites kept clear of carr encroachment (plots 94 to 102; Fig. 2.1c) are dominated by *C. canescens*, with *P. australis* and *C. acutiformis* also prevalent. Climbers feature prominently, particularly in the unmanaged portion, through the presence of *C. sepium* and *Vicia cracca*.

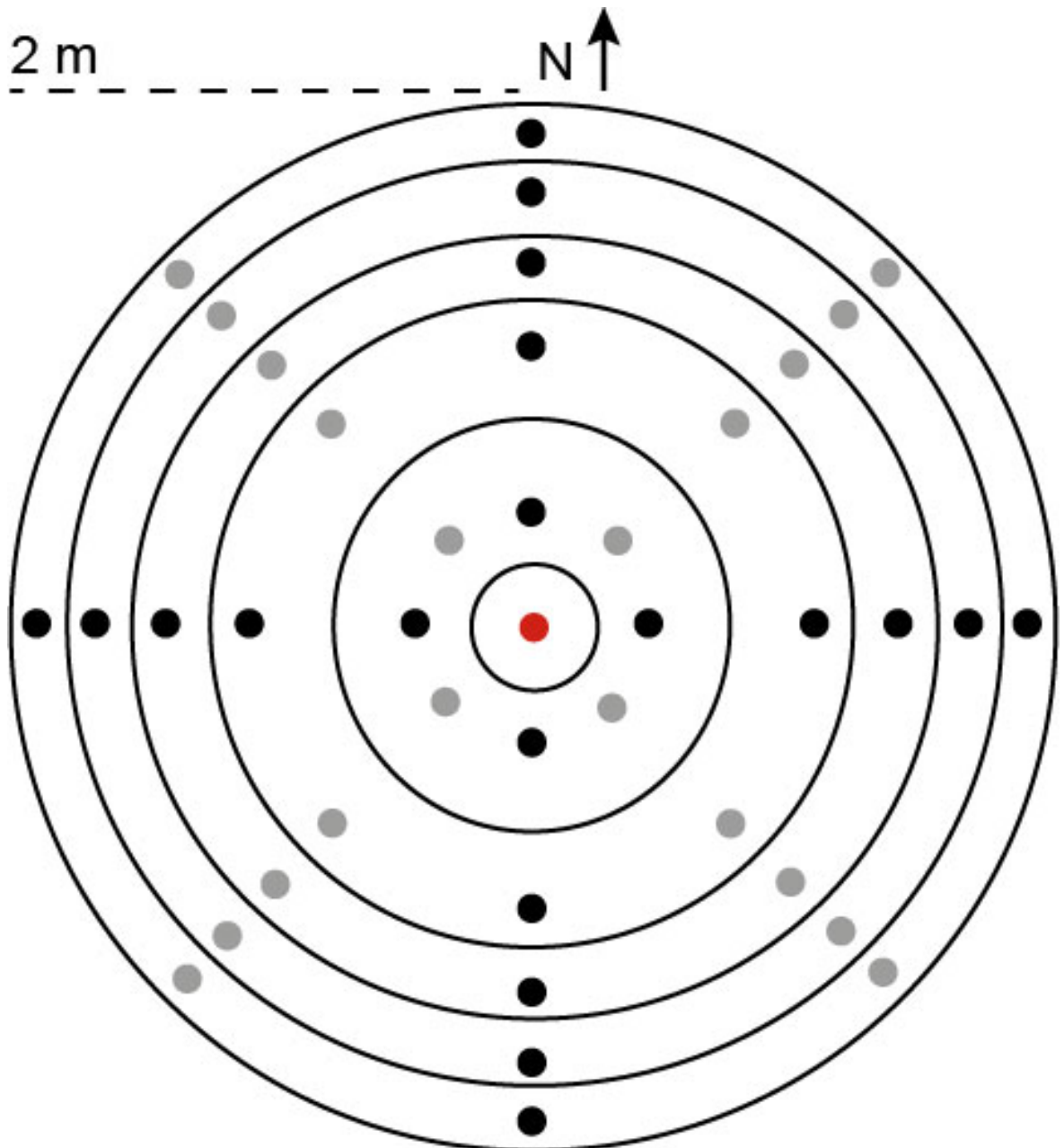
The *Phragmites* fen (plots 103 to 119; Fig. 2.1c) is classified as a reedswamp community (S26; Rodwell, 1995) in the site's management plan, and listed as being subject to a four-year cutting rotation regime. However, it has apparently remained uncut for c. 20 years (Alan Bowley, personal communication), resulting in the area now more closely resembling S24 tall-herb fen than S26 reed-dominated swamp (Rodwell, 1995), probably due to lack of recent management. Several monocots are conspicuous here, including *C. acutiformis*, *C. canescens*, *P. australis*, *Juncus effusus*, *J. subnodulosus* and *Calamagrostis epigejos*. Once again, *C. sepium* and *V. cracca* are frequent and abundant, whilst *L. vulgaris*, *Symphytum officinale*, *E. cannabinum* and *L. salicaria* are notable dicot herbs. The annually mown sedge fen (plots 120 to 136; Fig. 2.1c) is floristically rich and regarded by Poore (1956) as an intermediate community between the acidic and fen peats, though *Myrica* and the more acidophilous species are absent. The presence of this community here is probably due to incomplete removal of acid peat during peat cutting, having been subsequently liable to flooding by basic water (Poore, 1956). The dominant sedges are *Carex viridula* and *Carex panicea*, though several other monocotyledons like *Molinia caerulea*, *J. subnodulosus*, *P. australis*, *C. canescens*, *Carex elata*, *Juncus articulatus* and *C. acutiformis* are somewhat frequent and abundant. *Hydrocotyle vulgaris* is the most notable herb, but *L. vulgaris*, *L. salicaria* and *Ranunculus flammula* are also constantly present. The absence of shrubs and climbers is probably due to intensive disturbance through management.

## 2.2 Field methods

Field data collection took place between November 2012 and December 2014 in Upton and Woodwalton. Sixty-eight circular sampling plots of 2 m radius (area = 12.57 m<sup>2</sup>) were established in the Autumns of 2012 and 2013 in Upton and Woodwalton, respectively (Fig. 2.1). Plots were placed six metres apart along transect lines (Fig. 2.1). Their spatial coordinates were recorded using a hand-held GPS, while their relative elevation (m) to a temporary benchmark (TBM) was determined with a standard level mounted on a tripod and a staff rod. A stratified design (stratified by plant communities) was used to ensure a broad spatial representation of both fen carr and herbaceous fen communities. The transect lines were located in a manner to ease relocation and mostly followed a south-north direction (Fig. 2.1). Of the 136 plots between the two fens, 51 comprised woodland communities (the alder carr communities of Upton and Woodwalton and the mixed woodland in Upton) and 85 were herb-dominated plots comprising the reedswamp, *Cladium* and *J. subnodulosus* fens in Upton and the glades (managed and unmanaged), *Phragmites* fen and sedge fen in Woodwalton (Table 2.1).

### 2.2.1 Vegetation survey

Vegetation surveys were conducted over two field seasons in 2013 and 2014 in Upton and Woodwalton, respectively. In order to record the spring ephemerals and perennials present, surveys were conducted in late May in the woodlands and between July and September in the open herbaceous communities. Vascular plant species in each plot were recorded with the point quadrat method, which consisted of dropping a plumb-bob into the centre of five rings of equal area at distances of 0.45, 1.08, 1.41, 1.67 and 1.89 m from the centre of the plot (Fig. 2.2). These distances ensured equal weight to any point within the survey plot. The rings were surveyed at each of the eight cardinal and inter-cardinal directions, giving a total of eight samples per ring and 41 samples per plot (including the centre of the plot). Species 'hit' by the plumb-bob (from here on referred to as 'species encountered') were counted using proportional cover (one 'hit' per species per sample). A mirror was used to record any tree canopy above each sample point. This method allowed for species' frequency and abundance (expressed as a percentage of the total number of 'hits' with vascular plant species; i.e. as percentage cover when looking at



**Fig. 2.2:** Vegetation survey plot design using the point quadrat method. The plumb-bob was dropped at the centre of each of five rings of equal area (red, black and grey dots). Sampling took place from the centre of the plot (red dot) and followed the cardinal (black dots) and inter-cardinal directions (grey dots).

the community from above) to be more accurately estimated than by simple visual surveys. Species not encountered during the field surveys, but present within the 2-m circle area, were also recorded (from here on referred to as 'species present'). A total of 130 vascular plant species were present across the two fens. Of these, 103 species were encountered during the surveys, allowing for abundance cover calculations (species counts were transformed into relative abundances by scaling them to the total count of a sampling plot,

i.e. proportional cover). Only species with abundance cover were considered for analyses involving the computation of functional diversity metrics and community weighted means (CWMs) of plant traits (see below). Nomenclature of vascular plants follows Stace (2010). Appendix 1 presents a complete list of all species recorded at Upton and Woodwalton.

### 2.2.2 Vegetation sampling

Functional trait data used in the present work were collected *in situ* to increase the level of confidence when determining trait variability according to local conditions, since external sources of trait data (e.g., TRY plant trait database; Kattge *et al.*, 2011) do not always describe the methodologies nor the origin of the data. Vegetation sampling for the measurement of plant functional traits focused on the most abundant species across the two fen sites, based on the premises of the biomass ratio hypothesis (Grime, 1998, 2001). The hypothesis stipulates that the most abundant plant species present in a community (i.e., higher biomass) are likely to have greater modulating effects on ecosystem processes and community dynamics than rarer species, and to exert controlling influence on the fitness of their neighbours. Leaf samples from vascular plants (varying from 1 to 7 per individual) were collected from sun-exposed healthy-looking adult individuals at Upton Fen (early September 2013) and Woodwalton Fen (early September 2014). The number of specimens collected per species varied between 1 and 19. A minimum of five specimens were collected for species with abundance category of 4 or higher in the Domin scale (following Rodwell, 1991a) at the community level (see Appendix 1), except for *Carex riparia* in the reedswamp in Upton (four specimens measured; Appendix 1). A total of 69 species and just over 1300 individuals were sampled. Three of the species (*Ceratocarpus claviculata*, *Galium uliginosum* and *Rhamnus cathartica*) did not have sufficient plant material for elemental and isotopic measurements (see below), and were therefore not included in any trait analysis. Complete trait data were thus available for 66 species, of which *Frangula alnus* and *Sium latifolium*, though with fully measured traits, were not encountered during the surveys (i.e., no abundance cover calculation was possible). Therefore, a total of 64 measured species with abundance cover estimation were used in all analyses involving trait data, representing 62.1% of the total number of species encountered across Upton and Woodwalton (103 species). This represented approximately 98% of the total species cover across the sampled sites (estimated by scaling the number of 'hits' with trait measurements by the total number of 'hits' overall). Upton had 97.4% of



total species cover with trait measurements and Woodwalton 98.7%. The mean coverage per plot was 98%, and the minimum was 70.9% (one plot in the alder carr in Upton with relatively high abundance of *Prunus padus*, a species with no trait measurements; Table 2.2). Seventy five plots (55.1% of 136 plots) presented 100% trait coverage (i.e., all species encountered were sampled for trait measurements; Table 2.2). Pakeman and Quested (2007) suggested that an adequate weighted estimate of community-level quantitative single traits can be achieved by sampling the species comprising over 80% of the biomass, though sampling more species could be worthwhile in terms of accuracy. Only one plot had species with trait measurements representing less than 80% of total cover, while six plots (4.4% of 136 plots) had species with trait measurements representing less than 90% of total cover (Table 2.2). Five of these were in the alder carr in Upton, where *Prunus padus*, *Holcus mollis* and *Sorbus aucuparia* showed relatively high abundances and had no trait measurements (Appendix 1), while one plot in the sedge fen in Woodwalton revealed relatively high abundance of the grass *Anthoxanthum odoratum*, though no trait data were collected for that species. The high species cover with trait measurements presented here is most likely because all dominant tree species in the woodlands and all the main monocot species in the herbaceous sites (the most vigorous life forms in their respective communities) were sampled for trait measurements (see Appendix 1), confidently accounting for more than 80% of the biomass present in each community.

### 2.2.3 Soil sampling

Soil sampling was conducted in November 2012 and October 2013 in Upton and Woodwalton, respectively. Four peat core samples were collected from each plot using a Russian auger to a depth of 10 cm, taken at 50 cm distances marking the corners of a 0.25 m<sup>2</sup> quadrat established at 90° angles to the transect line. One core from each community was sampled to a depth of 50 cm. Core samples were wrapped in cling film and kept in cold storage at under 4°C until further analysis.

### 2.2.4 Plant litter collection

Litter traps were set up in the alder carr, unmanaged glades and *Phragmites* fen in Woodwalton in October 2013 to determine plant litter annual production rates. Two one-square-metre traps per community were placed adjacent to the transects at 50 cm above

the ground, and were roughly spaced in the middle of each half of the transects. Bamboo pegs and 100% polyethylene netting with a square mesh of 1.35 mm<sup>2</sup> were used to construct the traps. Litter collections took place regularly throughout the following year in December 2013 and March, June, September and December 2014. The managed glades and sedge fen were regarded as not producing substantial plant litter due to being cut on an annual basis (with the cuttings collected). Therefore, no litter traps were set up in these two plant communities. Litter data were not collected from Upton Fen due to logistical constraints.

**Table 2.2:** Proportion of total species cover with trait measurements for each sampled community. Proportional cover with full trait data was estimated by scaling the number of ‘hits’ on species with trait measurements by the total number of ‘hits’.

	Community	No. of plots	Plot-level % total cover with trait data		No. of plots with...		
			Mean	Minimum	< 80% trait coverage	< 90% trait coverage	100% trait coverage
Upton Fen	Reedswamp	10	100	100	0	0	10
	<i>Cladium</i> fen	12	99.7	97.9	0	0	10
	<i>Juncus subnodulosus</i> fen	12	98.1	95.2	0	0	3
	Alder carr	17	93.4	70.9	1	5	4
	Mixed woodland	17	98.3	91.2	0	0	8
Woodwalton Fen	Alder carr	17	99.3	94.8	0	0	12
	Glade (unmanaged)	8	99.3	95.1	0	0	6
	Glade (managed)	9	99.0	97.1	0	0	4
	<i>Phragmites</i> fen	17	99.2	94.9	0	0	12
	Sedge fen	17	96.6	87.3	0	1	6
Total		136			1	6	75

### 2.2.5 Aboveground biomass (AGB) harvesting

Aboveground biomass (AGB) was harvested from the herbaceous communities in Woodwalton Fen throughout summer 2014. Ten one-square-metre plots with 6 m space between them were harvested following the transect line at each of the herb-dominated communities [glades (five plots in each of the managed and unmanaged glades), *Phragmites* fen and sedge fen]. Plant material was clipped at ground level and both live and dead material were collected. The sedge fen and the glades were harvested in mid-July and mid-August prior to cutting, respectively. The *Phragmites* fen was harvested in early September, at the end of the growing season. No biomass harvesting took place in Upton Fen due to logistical constraints.

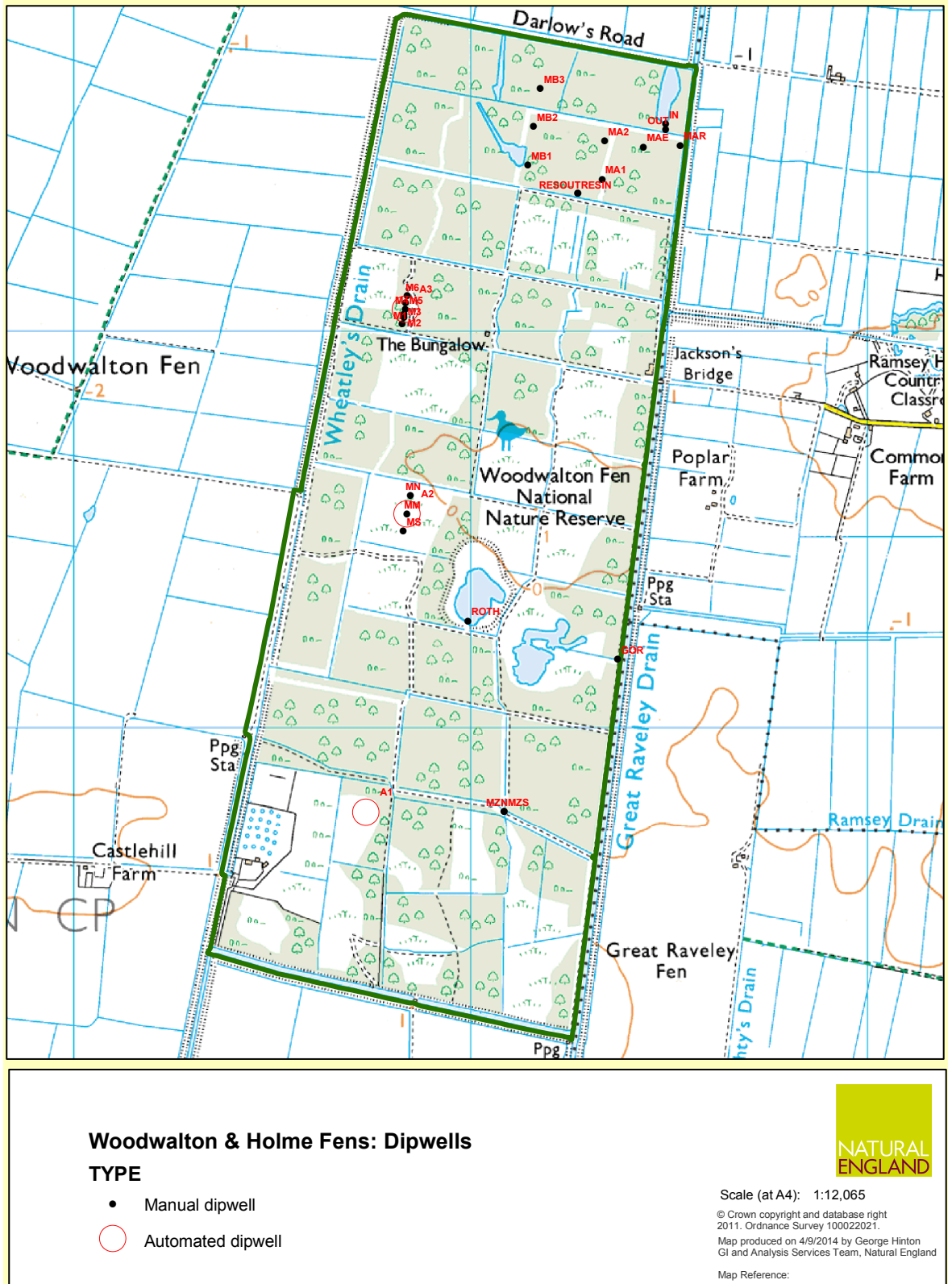
### 2.2.6 Water table height

The Environment Agency and Natural England supplied monthly dipwell data for Upton and Woodwalton, respectively. At Woodwalton Fen, plot heights and the tops of the dipwells (Fig. 2.3) were levelled relative to the vertical ordnance datum (OD) benchmark on the east side of the Rothschild Bungalow in order to compute water table height (m) in relation to each individual plot. Data from dipwell MA1 were used for the *Phragmites* fen plots, M1 to M6 supplied data to the sedge fen plots and dipwells MN, MM and MS provided data for the plots in the alder carr and the glades (Fig. 2.3). These dipwells were in close proximity to the surveyed plant communities and could be located in the field for levelling measurements. Data covering the period between 2003 and 2013 were averaged and used as the mean water table height (m) to each plot over this ten-year period. Water table data from Upton Fen were not used as it proved unfeasible to level the plot heights against OD due to logistical constraints.

## 2.3 Laboratory methods

### 2.3.1 Plant functional traits

Plant vegetative height for the species encountered was extracted from Plantatt (Hill *et al.*, 2004). Height is assumed to be the maximum stature a typical mature individual



**Fig. 2.3:** Map of Woodwalton Fen with the location of dipwells used to estimate water table height. Only data from manual dipwells were used. Kindly provided by Alan Bowley, Natural England.

of a species would attain in a given habitat. Plant leaf traits were determined following recently published standardised protocols (Perez-Harguindeguy *et al.*, 2013). Leaf samples were kept in moistened bags at under 4°C for up to 72 h prior to fresh leaf mass and leaf area measurements. Leaf lamina and petiole were used to determine fresh leaf area with a leaf area meter (LI-COR LI3000C), while leaf dry mass was computed after oven drying for 72 hours at 70°C. Oven-dried samples (leaf lamina only) were powdered by grinding and weighed to  $5 \pm 0.2$  g. These samples were then analysed for leaf C and N concentrations, and the biologically important stable isotope pairs  $^{13}\text{C}/^{12}\text{C}$  ( $\delta^{13}\text{C}$ ) and  $^{15}\text{N}/^{14}\text{N}$  ( $\delta^{15}\text{N}$ ), which can be thought of as proxy variables that reflect many physiological processes (Robinson *et al.*, 2000). Samples were analysed by GC-IRMS using a Sercon ANCA elemental analyser, coupled to a Sercon 20-20 IRMS, located at the Environmental Stable Isotope Laboratory at the University of Leicester. Measurements were carried out in triplicates of each sample, resulting in precisions of  $\leq 0.2\%$  for stable isotope and  $\leq 0.5\%$  for C and N analysis. Outlier replicates were excluded from samples with lower levels of precision when necessary and not used to compute the average values of such samples. Isotopic values are reported in the standard  $\delta$ -notation in per mil units (‰).  $\delta^{13}\text{C}$  values express the  $^{13}\text{C}$  content of a sample relative to the reference standard Vienna-Peedee belemnite (V-PDB), which has a  $^{13}\text{C}/^{12}\text{C}$  abundance ratio of  $1.1237 \times 10^{-2}$  (Staddon, 2004).  $\delta^{15}\text{N}$  values were normalised to nitrogen gas in air (AIR), which has a  $^{15}\text{N}/^{14}\text{N}$  abundance ratio of 0.0036765 (He *et al.*, 2009). They were defined as:

$$\delta^{13}\text{C} (\text{‰}) = 1000[(R_{\text{sample}}/R_{\text{V-PDB}})-1], \text{ where } R = ^{13}\text{C}/^{12}\text{C}$$

$$\delta^{15}\text{N} (\text{‰}) = 1000[(R_{\text{sample}}/R_{\text{AIR}})-1], \text{ where } R = ^{15}\text{N}/^{14}\text{N}$$

where  $R_{\text{sample}}$  and  $R_{\text{V-PDB}}$  and  $R_{\text{AIR}}$  are the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  abundance ratios of the sample and reference standards, respectively. Negative values mean that  $^{13}\text{C}$  and  $^{15}\text{N}$  are less abundant than in their respective reference standards. Table 2.3 presents a summary of all plant traits measured, as well as their ecological significance. See Appendix 3 (section 2) for mean trait values of all species sampled, as well as the mean trait values of the different life forms (section 1). Species codes, used in the bar plots in Appendix 3 (section 2), are presented in Appendix 4.

**Table 2.3:** List of plant functional traits measured for the present study. Plant height was extracted from Plantatt (Hill *et al.*, 2004). Descriptions of ecological significance were extracted from Wright *et al.* (2004), Robinson *et al.* (2000), Perez-Harguindeguy *et al.* (2013) and Jeffers *et al.* (2015).

Trait	Measurement	Unit	Ecological significance
Plant vegetative height	Shortest distance between the upper most photosynthetic tissue and the ground	cm	Associated with a species' ability to capture light and hence its competitive vigour; closely related to aboveground biomass, with implications for ecosystem processes
Specific leaf area (SLA)	One-sided area of a fresh leaf (cm <sup>2</sup> ) divided by its oven-dry mass (mg)	cm <sup>2</sup> mg <sup>-1</sup>	Frequently used in growth analysis as it potentially relates to relative growth rates; tends to scale positively with photosynthetic rate and leaf N and negatively with leaf C
Leaf mass per area (LMA)	Oven-dry mass of a leaf (mg) divided by its one-sided area (cm <sup>2</sup> ) when fresh; 1/SLA	mg cm <sup>-2</sup>	Investment in dry mass per unit of light-intercepting leaf area deployed; high LMA denotes thick leaf lamina or dense tissue, thus high C compounds and slow decomposition
Leaf dry-matter content (LDMC)	Oven-dry mass of a leaf (mg) divided by its water-saturated fresh mass (g)	mg g <sup>-1</sup>	Related to the average density of the leaf tissue; negatively related to SLA and relative growth rate, but positively related to leaf lifespan; high LDMC means slower leaf decomposition rates than low LDMC
Leaf thickness (Lth)	1/(SLA x LDMC) - approximation of whole-leaf average	cm	Related to physical strength of leaves determined by mesophyll layers; strong driver of leaf N per area, but thicker leaves often have lower %N and lower photosynthetic rate
Leaf C concentration	Total amount of C per unit of leaf dry-mass (measured via dry-combustion and IRMS analysis)	mg g <sup>-1</sup>	Investment in C compounds such as lignin and cellulose; implications for leaf decomposition rates
Leaf N concentration	Total amount of N per unit of leaf dry-mass (measured via dry-combustion and IRMS analysis)	mg g <sup>-1</sup>	Tends to correlate positively with photosynthetic rate and SLA; high leaf N associated with high nutritional quality for consumers; implications for leaf decomposition rates
Leaf C:N ratio	Total leaf C divided by total leaf N	ratio	Occasionally used as a tool to assess limitations of N availability to plants; N-fixing species tend to have lower leaf C:N ratios than other plants
Leaf δ <sup>13</sup> C	Ratio between <sup>13</sup> C and <sup>12</sup> C; expressed in relation to a reference standard; measured via IRMS	‰	Associated with the ratio of net photosynthetic rate to transpiration; used to infer the water use efficiency of a plant per unit of C assimilated; often used as a proxy for climatic conditions, water availability and irrigation practices
Leaf δ <sup>15</sup> N	Ratio between <sup>15</sup> N and <sup>14</sup> N; expressed in relation to a reference standard; measured via IRMS	‰	A measure of the fractionation of N isotopes that occurring during the assimilation, transport and loss of N; often used as a proxy for ecosystem N availability to plants

### 2.3.2 Soil analysis

Pollen analysis was performed on the soil samples to determine whether the upper 10 cm of sediment was likely to be derived from the contemporary vegetation. Palynology investigations in the 1930s dated widespread peat formation in the East Anglian Fenland to the Atlantic period between 7.5 and 5 ka BP (Godwin and Clifford, 1938). However, these same peat deposits were later subject to extensive cutting and draining (Poore, 1956; Duffey, 1971). Additional stratigraphic studies in the 1950s established the origins of the Norfolk Broads as Medieval peat cuttings between the 12<sup>th</sup> and 14<sup>th</sup> centuries (Lambert, 1960). Consequently, the removal of several metres of peat can result in sediment of antique origin occurring near the surface, and if used in this study could lead to incorrect conclusions. In fact, the close relationship between present surface conditions and past anthropogenic activities has long been recognised (Jennings and Lambert, 1951). Samples of 1 cm<sup>3</sup> were extracted at depths of 0-1, 3-4, 6-7 and 9-10 cm from the 50 cm cores from each community. Standard methods were used to extract the pollen (Moore *et al.*, 1991), and 150 pollen grains were counted per sample. The results indicated the sediment was derived from, and is therefore contemporary with, the modern vegetation (see Appendix 2 for results).

The four soil samples from each plot were split longitudinally and homogenised. The four samples from the plots with 50 cm cores were treated separately in order to inspect within plot variability. Only the top 10 cm of each core were used in all analysis. It is thought that the majority of biogeochemical processes take place in this top layer (Bennion *et al.*, 2001; Moore *et al.*, 2007), where vascular plants concentrate most of their root system (Eppinga *et al.*, 2009) and where the largest amount of carbon is stored in organic compounds (Wild, 1993). Care was taken to remove any recent plant litter from the top soil prior to analysis. Approximately one third of each homogenised sample was oven-dried at 105°C until constant mass was reached. Volume (cm<sup>3</sup>) was determined via displacement prior to drying in a 20 ml interval graduated beaker (with each ml displaced representing 1 cm<sup>3</sup> of volume), and bulk density (g cm<sup>-3</sup>) was calculated following Blake and Hartge (1986) by dividing the sample dry mass by its volume. The remaining two thirds of each sample were air-dried for 72 h for nutrient analysis to prevent carbon volatilisation at high temperatures. Samples were gently ground with a porcelain mortar and pestle and sieved in an electric shaker for 10 minutes with graded sieves of 710, 500 and 150 µm. Prepared samples were kept in cold storage at under 4°C until further analysis. Soil organic

carbon (SOC) and total soil nitrogen (total N) content (%), as well as soil  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (‰), were determined via dry combustion following similar procedures used for the leaf samples (see section 2.3.1 above). It was assumed the samples contained no inorganic carbon given the non-calcareous, neutral-acidic conditions commonly found in high-latitude peats (Chambers *et al.*, 2011), with the total carbon measured in the samples therefore assumed to represent SOC. The resulting precision was within 0.1% for total N and 1.6% for SOC, while stable isotopes data showed precisions within 0.2‰. Outlier replicates were excluded from samples with lower levels of precision when necessary and not used to compute the average values of such samples. Following Ellert *et al.* (2001) and Zubrzycki *et al.* (2013), SOC and total N were used to estimate stocks of soil C and N (i.e., the content of C and N stored in the top 10 cm of soil from the soil surface, in  $\text{g cm}^{-2}$ ):

$$\text{Soil C}_{(10\text{ cm})} = S_{bd} \cdot S_d \cdot \text{Con}_{\text{SOC}}$$

$$\text{Soil N}_{(10\text{ cm})} = S_{bd} \cdot S_d \cdot \text{Con}_{\text{totalN}}$$

where  $S_{bd}$  is soil bulk density ( $\text{g cm}^{-3}$ ),  $S_d$  is soil depth (cm) and  $\text{Con}_{\text{SOC}}$  and  $\text{Con}_{\text{totalN}}$  are SOC and total N content (%), respectively.

### 2.3.3 Annual litter production and aboveground biomass estimation

Plant material collected from the litter traps were spread out on paper tissue and air-dried for 120 h prior to weighing. Plant litter weighed in December 2013 and March, June and September 2014 were added to indicate litter annual production rate (litter produced between October 2013 and September 2014), and was converted from  $\text{g m}^{-2} \text{a}^{-1}$  to  $\text{t ha}^{-1} \text{a}^{-1}$ . See Appendix 5 for mean annual litter production rates in the alder carr, unmanaged glades and *Phragmites* fen at Woodwalton Fen. The aboveground biomass (AGB) harvested was sorted into live and dead material, oven dried at 70°C for 72 h and weighed separately. Data were converted from  $\text{g m}^{-2}$  to  $\text{t ha}^{-1}$ . See Appendix 6 for mean aboveground biomass in the herbaceous communities at Woodwalton Fen.



## 2.4 Data analysis

Data analysis methods used to answer specific questions raised by each of the subsequent data chapters (3 to 6) are presented in their respective Methods sections. However, in order to avoid repetition, the subsections below present some common methods used throughout, particularly those pertinent to the computation of multi- and single-trait diversity metrics.

### 2.4.1 Management intensity classification

Plant communities were assigned to one of five discrete management intensity categories, ranging from 0 to 4. The woodlands in Upton and Woodwalton were not under any type of management (category 0). The unmanaged glades in Woodwalton, the only herb-dominated community left undisturbed in the study sites, was given category 1. All managed herbaceous communities in both fens were under the same type of management (mowing), but were under different rotation periods. The *Phragmites* fen in Woodwalton, left uncut for c. 20 years, was given category 2 (low management intensity). The three herb-dominated communities in Upton (the reedswamp, *Cladium* and *J. subnodulosus* fens) were assigned category 3 (moderate management intensity) since they are all cut on a seven- to eight-year rotation. The managed glades and the sedge fen in Woodwalton are cut annually during summer and were assigned to category 4 (high management intensity). Table 2.1 lists the different plant communities and their management regime.

### 2.4.2 Functional trait axes

Plot-level and multi-trait functional diversity metrics used in chapters 3 and 5 were computed using three independent functional trait axes (Table 2.4) related to plant strategy: size, leaf and nutrient availability. The size axis was defined by a species' vegetative height and was associated with their ability to capture light. Height has been recognised as a key dimension of plant competitive strategy (Grime, 1977; Keddy and Shipley, 1989; Westoby *et al.*, 2002). However, a plant's capacity to achieve its upper height limit is regulated by a cost-benefit trade-off that is influenced by the density and height of competitors (Westoby *et al.*, 2002). Vegetative height thus should offer information on a species position in the competitive hierarchy within a community. The plant height variable

was  $\log_{10}$ -transformed prior to any analysis as it spanned several orders of magnitude, given the large differences in height between woody and herbaceous species.

The leaf axis was related to a plant's carbon assimilation strategy and nutrient turnover rates (Reich *et al.*, 1997; Reich *et al.*, 1999). However, most leaf traits are typically strongly correlated among species (Laughlin, 2014), with a single dimension usually accounting for the majority of the variation in leaf data (Wright *et al.*, 2004). I used principal component analysis (PCA) on three selected correlated leaf traits (SLA, leaf N and leaf  $\delta^{13}\text{C}$ ) as a means of reducing correlated dimensions within the leaf axis into a single dimension that could explain most of the variation. Other leaf traits shown in Table 2.3 (e.g. LDMC) were also strongly correlated to SLA, but the latter is thought to show stronger relationships with plant processes such as relative growth rate and leaf lifespan (Perez-Harguindeguy *et al.*, 2013), which are relevant variables to investigate biotic influences on ecosystem processes. SLA and leaf N are normally correlated with each other and with photosynthetic rate, and are hence positively related to relative growth rate as they influence carbon acquisition (Wright *et al.*, 2004). Leaf  $\delta^{13}\text{C}$  reflects the range of a plant's physiological responses to the environment, such as stomatal conductance and changes in C:N allocation to carboxylation (Seibt *et al.*, 2008). It is also closely linked to primary productivity and water use efficiency as a measure of carbon gain per unit water loss, or the ratio of net photosynthetic rate to transpiration (Cernusak *et al.*, 2009). Hence, the higher the isotopic concentration of  $\delta^{13}\text{C}$  in leaf tissue, the more water use efficient a species is considered to be. PCA was performed using the *princomp* function in R 3.1.2 (R Development Core Team, 2014). Traits were standardised to mean zero and unit standard deviation prior to PCA analysis. The scores of the first PCA axis, which was mainly correlated to leaf N, were used in all analysis since the first axis accounted for 76.0% of the total variation in the leaf axis.

The plant nutrient availability axis (referred to as the 'nutrient axis' in Chapter 5) was represented by leaf  $\delta^{15}\text{N}$ , which can be thought of as reflecting the variability of  $\delta^{15}\text{N}$  values of external N sources, as well as  $^{15}\text{N}/^{14}\text{N}$  fractionations that occur during the assimilation, transport and loss of N (Robinson *et al.*, 2000). Leaf  $\delta^{15}\text{N}$  has recently been recognised as a proxy for ecosystem N availability to plants (McLauchlan *et al.*, 2010; Jeffers *et al.*, 2015) and should reflect a species response to N availability. Mycorrhizal fungi tend to transfer less N to plants with increasing N availability, which also leads to higher N loss via soil processes such as denitrification and nitrate leaching (Hobbie *et al.*, 2005; Pardo *et al.*, 2006). Since N from mycorrhizal fungi and the N lost from soils are normally depleted

in  $^{15}\text{N}$  relative to soil organic N (Hobbie *et al.*, 2000; Pardo *et al.*, 2002; Craine *et al.*, 2009b), increasing soil N availability is generally associated with greater plant tissue  $\delta^{15}\text{N}$  (Craine *et al.*, 2009a). Leaf  $\delta^{15}\text{N}$  was hence regarded as a better proxy variable of nutrient availability to plants than any leaf mass traits (e.g. LDMC) that would simply infer nutrient content through high or low concentrations of C compounds in leaf tissue. Moreover, leaf  $\delta^{15}\text{N}$  was uncorrelated to all other leaf traits and thus provided an independent axis of trait variation (Table 2.4).

**Table 2.4:** Pearson correlation coefficients ( $r$ ) between the three trait axes.

	Size axis	Leaf axis	Nutrient axis
Size axis	1	-	-
Leaf axis	-0.25	1	-
Nutrient axis	-0.20	0.07	1

Size axis and Leaf axis:  $t = -2.04$ ,  $df = 63$ ,  $p = 0.05$

Size axis and Nutrient axis:  $t = -1.61$ ,  $df = 63$ ,  $p = 0.11$

Leaf axis and Nutrient axis:  $t = 0.52$ ,  $df = 63$ ,  $p = 0.61$

### 2.4.3 Community weighted mean (CWM) of plant traits

The community weighted mean (CWM) is a single-trait diversity measure that has been widely used in comparative studies to functionally differentiate plant communities (Garnier *et al.*, 2016). It has proved to be a robust statistic that shows little sensitivity to the method used for estimating relative abundances of species or trait values (Lavorel *et al.*, 2008). It can be seen as expressing the most probable attribute that an individual would have if drawn at random from the community (Garnier *et al.*, 2016). Because it uses relative abundances to weight mean values, CWM represents the mean trait value per unit of biomass in a community (Violle *et al.*, 2007), emphasising the traits of the most dominant species with higher performance. Moreover, relationships between traits and the abiotic environment have been found to be stronger when the abundance of species is taken into account (Garnier *et al.*, 2016), making CWM a more useful measure than the simple arithmetic mean of traits. CWMs have been used in the present study to characterise the

mean trait composition of fen plant communities individually (Chapter 6) and grouped into management intensity categories (Chapter 3) and successional stages (Chapter 5).

Species counts were transformed into relative abundances by scaling them to the total count of a given field plot. If  $p_i$  is the relative abundance of the  $i$ -th species in a given plot, and  $x_i$  its mean trait value (the average over all of its trait measures), then CWM, following Dainese *et al.* (2015), is presented as:

$$\text{CWM} = \sum_{i=1}^S p_i x_i$$

## Chapter 3

### Functional diversity and mean trait composition of lowland fens along a disturbance gradient

#### 3.1 Introduction

The diversity of species has traditionally been described by the taxonomic aspect of biological diversity. However, taking the functional components of organisms into account is essential for answering fundamental ecological questions (Mason and de Bello, 2013; Sutherland *et al.*, 2013). Function refers to the mode of action organisms employ to survive and reproduce within their environment, while ‘traits’ are the characteristics used to describe species from a functional perspective (Garnier *et al.*, 2016). Plant functional traits, be they morphological, physiological or phenological heritable individual features (Garnier *et al.*, 2016), are directly linked to species’ ability to establish, grow, compete, reproduce and migrate. Traits influence species’ fitness and performance (Pillar, 1999), affect ecosystem processes (Tilman *et al.*, 1997; Díaz and Cabido, 2001; Diaz *et al.*, 2004; de Vries *et al.*, 2012) and services (de Deyn *et al.*, 2008; de Bello *et al.*, 2010; Lavorel, 2013; Manning *et al.*, 2015), as well as community dynamics (Mouchet *et al.*, 2010; Violle *et al.*, 2011). In addition, traits have assisted in establishing links between the different levels of organisation of ecological systems (Garnier *et al.*, 2016) and in identifying axes of variation representing different plant strategies (Westoby, 1998; Westoby *et al.*, 2002; Laughlin, 2014), such as resource-use, competitive ability and sexual regeneration. The acquisition and use of resources, for instance, are highly influenced by leaf area and mass ratios (Westoby, 1998). Healthy green leaves play a central role in resource transfer between plants and the environment, for they control respiration, carbon acquisition, water transfer and other aspects of plant metabolism. In fact, leaf mass per area (LMA, the ratio of leaf dry mass to its one-sided area, the opposite of specific leaf area, or SLA) and leaf nitrogen content are involved in a leaf economics spectrum (LES) in which species with low LMA (or high SLA) and high leaf N tend to be characterised by high rates of resource acquisition and low resource conservation (the so called exploitative strategy; Lavorel and Grigulis, 2012), leading to high photosynthetic rates and consequently high relative growth rates (Wright *et al.*, 2004). They contrast with species with slow returns on investments of nutrients and

dry mass in leaves (conservative strategy), typified by high carbon investment in leaf dry mass tissue (high LMA), low nutrient concentrations and low rates of photosynthesis (Wright *et al.*, 2004). The implications for ecosystem processes, most notably the biogeochemical cycles of carbon and nitrogen, are evident as leaf construction and nutrient content will regulate the amount of recalcitrant compounds of dead litter decomposing in the soil (Cornelissen *et al.*, 1999; Cornelissen *et al.*, 2004; Cornwell *et al.*, 2008), and therefore determine microbial activity and organic matter mineralisation and accumulation rates (Wardle *et al.*, 2004; van der Heijden *et al.*, 2008). Similarly, plant stature has been proposed as one of the main functional markers of competitive ability (Westoby, 1998). Greater height confers a competitive advantage over neighbours via greater access to light, constituting a fundamental strategy of carbon acquisition (Westoby *et al.*, 2002). Moreover, plant height is related to other aspects of plant water and nutrient assimilation since high statured stems tend to correlate with deep root systems (Violle *et al.*, 2009), influencing resource depletion and nutrient cycling. Therefore, functional traits are essentially about organisms' strategies and adaptations to succeed in their own environment (see Table 2.3 in Chapter 2 for a brief description of these traits).

Given their ecological significance, plant functional traits have a long tradition in ecological studies, and have in the past been established as a means of classifying species into functional groups to better understand and identify patterns in vegetation processes (Grime, 2006). The CSR triangle of Grime (1974, 1977) and the LHS scheme of Westoby (1998) are two examples of such classifications, which are based on the assumption that species' attributes constrain their occurrence and abundance in a given environment. However, as briefly discussed in Chapter 1 (section 1.1), grouping organisms into functional groups may result in loss of information on the functional differences between individual species (Villegger *et al.*, 2008). Functional plant ecology has subsequently evolved, particularly in the last two decades (Cardinale *et al.*, 2012; Naeem *et al.*, 2012), from classifying species into broad functional groups to quantifying and isolating the role of individual traits in community and ecosystem processes and function. Consequently, the functional diversity of plant communities has emerged as an essential aspect of biodiversity (Mason and de Bello, 2013). Though the concept of functional diversity can be rather complex (Petchey and Gaston, 2006), it has been shortly described as '*those components of biodiversity that influence how an ecosystem operates or functions*' (Tilman, 2013). Functional diversity essentially refers to the variation in the degree of expression of functions and traits between species, populations and ecosystems (Garnier *et al.*, 2016). In

other words, it is concerned with understanding communities and ecosystems based on what organisms 'do', rather than what they 'are'. In the present context, 'what organisms do' means the value and range of plant functional traits that influence ecosystem processes and functioning.

A number of functional diversity measures have been proposed in recent years (Petchey and Gaston, 2002; Mason *et al.*, 2003; Mason *et al.*, 2005; Mouillot *et al.*, 2005; Cornwell *et al.*, 2006; Vileger *et al.*, 2008; Schleuter *et al.*, 2010), with the main aim of quantifying the diversity of traits within species assemblages (Mason and Mouillot, 2013). These metrics account for different aspects of functional diversity, but they mostly describe the amount of space filled by species in functional niche space and the regularity with which this space is filled. From a geometrical point of view, they describe a species' functional niche by its position in functional trait space (Rosenfeld, 2002). Their objective is thus to define a multidimensional pattern of points in trait space, with each coordinate corresponding to a measured trait and each point representing an individual species (Schleuter *et al.*, 2010).

There is evidence that biological communities with high functional diversity and redundancy are more resilient and better buffered against the vagaries of environmental change (Laliberté *et al.*, 2010; Pillar *et al.*, 2013). Such communities are in general associated with increased productivity and ecosystem functioning (Tilman *et al.*, 1997; McGill *et al.*, 2010; Cadotte *et al.*, 2011). The opposite is true for communities that exhibit low trait diversity (Brown *et al.*, 2011). Therefore, variations in the diversity of plant functions can have far-reaching consequences for the functioning of communities and ecosystems (Westoby and Wright, 2006), particularly because interspecific differences result in species and traits responding differently to changing conditions (Garnier *et al.*, 2016).

Plant traits have been found to respond to a number of selective biotic and abiotic pressures, including trait-shifts with climate (Wright *et al.*, 2005) and with nutrient (Grime, 2001), light (Valladares and Niinemets, 2008) and water availability (Ackerly, 2004; Ordoñez *et al.*, 2010). However, disturbance through land use change and management practices (mowing, ploughing, felling, etc.) is currently one of the most important drivers of changes in functional diversity (Pakeman, 2011) and ecosystem processes and services (Foley *et al.*, 2005; Nelson, 2005). Disturbance leads to the destruction of plant biomass by varying magnitudes, for its effects are highly dependent on the type, severity, frequency and timing of disturbance (Foley *et al.*, 2005; Garnier *et al.*, 2007), resulting in the

modification of the structure of an ecosystem or community through changes in resource availability (Grime, 2001). Correspondingly, functional diversity metrics, as well as the abundance-weighted average trait values of a community, can respond strongly to environmental changes and are therefore promising as biodiversity indicators (Vandewalle *et al.*, 2010). Disturbance has indeed been identified as one of the key factors shaping the functional characteristics of organisms (Southwood, 1988) and the functional diversity of communities (Garnier *et al.*, 2007). Interestingly though, taxonomic and functional diversity and composition of plant communities have been found to respond differently to disturbance intensity (Mayfield *et al.*, 2010; Carreño-Rocabado *et al.*, 2012).

A plant's response to disturbance is determined by its capacity to maximise either the acquisition or the conservation of resources (Grime, 2001). Therefore, according to the leaf economics spectrum (LES) continuum of fast to slow returns on resource investments, the tendency is for exploitative species with fast growth and high rates of resource acquisition (commonly associated with pioneer species colonising sites in the early stages following a disturbance event) to be gradually replaced by conservative species with slower growth rates and returns on investment (Garnier *et al.*, 2004), resulting in changes to the entire suite of traits linked to the LES (Garnier *et al.*, 2016). It has been proposed that these shifts in plant nutrient economies (from acquisitive to conservative) along management gradients (different disturbance frequencies) lead to trait trade-offs that cause feedbacks to ecosystem functioning through plant-soil interactions (de Deyn *et al.*, 2008). As pointed out previously, the quality of plant litter, determined by leaf/plant economics traits, is important to decomposability and the quality of soil organic matter, which in turn affect nutrient mineralisation and accumulation rates through changes in energy and nutrient sources for soil biota (Wardle *et al.*, 2004). Consequently, processes associated with carbon and nitrogen turnover may reflect the scaling-up from individual plant traits and the functional diversity of plant communities to key ecosystem processes (Lavorel and Grigulis, 2012).

The main aim of this chapter is to determine the impact of changing management intensity (i.e., plant communities subject to different mowing rotation regimes) on the functional ecology of lowland herbaceous and woody fen communities, and how this potentially influences ecosystem processes, particularly soil carbon and nitrogen storage. The importance of vegetation management in preventing the process of replacement of herbaceous fen by fen carr is well known (Wheeler and Shaw, 1995), but the consequences of disturbance for the functional components of fenland plant communities is poorly



understood. It is also unclear to what extent floristic changes reflect changes in community functional properties, given the large trait variation found between species within the same functional groups (e.g., pioneer vs late-stage succession species; Donovan *et al.*, 2014). I use functional traits (mostly associated with the LES, as well as plant height) and soil carbon and nitrogen data collected from two fen systems in East Anglia (described in Chapter 2) under different mowing regimes to answer three questions:

- i. How do observed taxonomic and functional diversity respond to increasing levels of management intensity?
- ii. Does the observed mean functional trait composition of plant communities in lowland fens shift with increasing management intensity?
- iii. Do ecosystem processes (soil carbon storage and soil C:N ratio) respond to disturbance following corresponding shifts (if any) in mean trait composition along a management gradient?

I hypothesise that taxonomic diversity will increase with increasing management intensity given the well-known effect of management on species diversity of rich fen communities (Wheeler and Shaw, 1995), though the effects on functional diversity are unclear and most likely dependent on the functional diversity metric used (e.g., metrics that use species presence as opposed to abundance data), as well as on the proportion of species sampled for trait measurements (Pakeman, 2014). Further, I expect a shift in mean functional composition with increasing disturbance levels, from slow growing species with conservative traits (harder and thicker leaves with low SLA and leaf N content and high LDMC and leaf C:N ratio) to species with fast growing strategies with acquisitive traits (soft leaves with high SLA and leaf N concentration and low LDMC and leaf C:N ratio). Finally, the most disturbed communities should be associated with relatively low soil C stocks compared to the least managed communities due to higher C losses resulting from faster decomposition rates of relatively low litter input, owing to the 'high' quality of plant litter deposited by pioneer exploitative species (soft, nutrient-rich leaves).

The trait data selected are thought to be important for the biogeochemical cycles of carbon and nitrogen through the processes of plant litter decomposition and primary productivity (Grigulis *et al.*, 2013). I use Petchey and Gaston's (2002) dendrogram-based measure of trait diversity (FD) and Villeger *et al.*'s (2008) functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) metrics to calculate the multi-trait functional diversity of the plant communities within the different management

category levels. Generally, these measures define functional diversity as the spread and distribution in functional trait space of the species presence and abundance in a community. They were chosen because they are independent from one another, are complementary (i.e., they measure different facets of functional diversity) and, though sensitive to changing species numbers (Villegger *et al.*, 2008; Mouchet *et al.*, 2010; Pakeman, 2014), are not trivially related to species richness (Schleuter *et al.*, 2010). In addition, despite some multi-trait functional diversity metrics (e.g. FRic, FEve and FDiv) having been shown to be sensitive to the completeness of the species' trait data coverage (Pakeman, 2014), measured species representing 90% or over of the total species abundance cover seem to provide reliable estimates of the functional diversity of a community when computed at the plot level and averaged across categories (Pakeman, 2014). As stated in Chapter 2 (section 2.2.2), only six plots (out of 136 plots) showed abundance cover of the measured species to be below 90% of the total species cover (Table 2.2).

Functional diversity can also be described in single-trait terms by community-level weighted means of trait values (CWM; see section 2.4.3 in Chapter 2), where the abundances of species are considered (Violle *et al.*, 2007). CWM has shown high sensitivity to disturbance in previous studies (Diaz and Cabido, 1997; Vandewalle *et al.*, 2010) and was used here to determine changes in mean functional composition along a disturbance gradient.

## 3.2 Methods

In order to investigate the effects of disturbance on the functional diversity and mean trait composition of lowland fens, the ten plant communities surveyed at Upton and Woodwalton (Chapter 2; section 2.1) were grouped according to their management intensity category (Chapter 2; section 2.4.1), resulting in five distinct groups (Table 3.1). Two plots in the reedswamp in Upton were excluded from these analyses due to providing fewer than four species with trait measurements, the minimum required for the computation of FRic.

Functional trait data from the 64 encountered species with full trait measurements (representing approximately 98% of the total percentage cover of all species across the sampled sites, see section 2.2.2 and Table 2.2 in Chapter 2) were used to compute community weighted means (CWMs; Chapter 2; section 2.4.3) of traits relevant to the leaf

**Table 3.1:** Plant communities arranged vertically by management intensity classification, from unmanaged to highly managed. U = Upton Fen; W = Woodwalton Fen. Field community names are as presented in Chapter 2.

Category	Management		Plant communities	Main species	No of plots
		Description			
0		Unmanaged woods	3 (Alder carr – U and W, mixed woodland – U)	<i>Alnus glutinosa</i> , <i>Fraxinus excelsior</i> , <i>Betula pubescens</i> , <i>Poa trivialis</i> , <i>Carex acutiformis</i> , <i>Urtica dioica</i> , <i>Glechoma hederacea</i> , <i>Dryopteris dilatata</i> , <i>Lonicera periclymenum</i>	51 (17 plots in each of the three woody communities)
1		Unmanaged glade	1 (Unmanaged glade – W)	<i>Phragmites australis</i> , <i>Calamagrostis canescens</i> , <i>Symphytum officinale</i> , <i>Calystegia sepium</i> , <i>C. acutiformis</i> , <i>Juncus effusus</i>	8
2		Low management, unmown for c. 20 years	1 ( <i>Phragmites</i> fen – W)	<i>C. acutiformis</i> , <i>C. canescens</i> , <i>P. australis</i> , <i>C. sepium</i> , <i>Lysimachia vulgaris</i> , <i>S. officinale</i> , <i>J. effusus</i> , <i>Eupatorium cannabinum</i> , <i>Vicia cracca</i> , <i>Lythrum salicaria</i>	17
3		Moderate management, mown on a 7- to 8-year rotation (reeds swamp and <i>Cladium</i> fen: last cut before sampling in 2006/7; <i>J. subnodulosus</i> fen: last cut before sampling in May 2011)	3 (Reeds swamp, <i>Cladium</i> and <i>J. subnodulosus</i> fens – U)	<i>P. australis</i> , <i>Carex riparia</i> , <i>Cladium mariscus</i> , <i>C. canescens</i> , <i>Juncus subnodulosus</i> , <i>Thelypteris palustris</i> , <i>C. sepium</i> , <i>E. cannabinum</i>	32 (Reeds swamp: 8; <i>Cladium</i> fen: 12; <i>J. subnodulosus</i> fen: 12)
4		High management, mown annually in summer	2 (Managed glade and sedge fen – W)	<i>P. australis</i> , <i>Carex viridula</i> , <i>Carex panicea</i> , <i>Hydrocotyle vulgaris</i> , <i>Molinia caerulea</i> , <i>Phalaris arundinacea</i> , <i>C. canescens</i> , <i>Agrostis stolonifera</i> , <i>Mentha aquatica</i>	26 (Managed glade: 9; sedge fen: 17)

economics spectrum (LES), namely specific leaf area (SLA), leaf dry-matter content (LDMC), leaf N concentration, leaf C:N ratio and leaf  $\delta^{13}\text{C}$ , to determine the dominant functional structure present in each of the management intensity categories. Plant vegetative height ( $\log_{10}$ -transformed) was also used as it is expected to be particularly responsive to disturbance. CWMs were computed in R version 3.2.4 (R Development Core Team, 2016). Multi-trait functional diversity metrics were estimated to determine the degree of trait variability across disturbance levels.

### 3.2.1 Functional diversity metrics

Plot-level, multi-trait functional diversity metrics were computed using the three independent trait axes described in Chapter 2 (the size, leaf and nutrient axes; section 2.4.2). Since such metrics account for the range of trait values and are likely to be affected by the unit of measurement (e.g. differences between stem and leaf traits), the three axes were standardised to mean zero and unit standard deviation prior to the computation of the four metrics presented here. Expected values of functional diversity under null distributions and their effect sizes are presented in Chapter 5 to determine community assembly processes along a disturbance gradient. Therefore, only observed values of functional diversity are presented in this chapter to determine the functional response of observed communities to management.

I used the dendrogram-based methods of Petchey and Gaston (2002), updated in Petchey and Gaston (2006) and discussed in Petchey and Gaston (2009), to calculate functional diversity (FD). Petchey and Gaston's FD estimates the dispersal of an assemblage of species in trait space, and automatically accounts for covariance between traits (Petchey *et al.*, 2007). Species assemblages with high trait divergence in trait space are expected to yield higher FD values than assemblages with low trait divergence. FD was calculated by converting the species by trait matrix of each plot into distance matrices, which were then hierarchically clustered to produce dendrograms describing the functional relationships between the species within each plot. FD was computed as the total branch length of the functional dendrogram. Euclidean distances and UPGMA (Unweighted Pair-Group Method using arithmetic Averages) clustering were used throughout since these produced a dendrogram with the highest cophenetic correlation (0.80) and the lowest Gower distance (933.03) when clustering the full trait by species matrix (i.e., using all 64 encountered species with complete trait data; see section 2.2.2 in Chapter 2). The advantages of using

FD are that the resulting functional diversity of a plot cannot decrease if a species is added, cannot increase if a species is removed, and remains unchanged if a species that is added or lost contains identical properties to a species that is already present (Petchey and Gaston, 2006). In addition, using the dendrogram helps to account for potential non-independence in the source of differences between species (Petchey and Gaston, 2006).

Other measures more recently proposed that account for the different facets of trait diversity and are independent of each other (and to FD) include the functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) of Villéger *et al.* (2008), who described their methods in detail and made available the R script used here to calculate the three indices. Essentially, FRic uses the convex hull volume index to measure the volume of trait space occupied by the species of a community in  $n$ -dimensional space (Cornwell *et al.*, 2006; Villéger *et al.*, 2008) and it is equivalent to a multivariate range. The convex hull volume algorithm proposed by Villéger *et al.* (2008) determines the most extreme trait values in a community (vertices), links them to build the convex hull in multidimensional trait space, and finally calculates the total volume inside it. FRic, like FD, is expected to yield higher values with increasing trait divergence in trait space, and cannot decrease with the addition of new species, since it is independent of species abundances and only considers the trait composition of a community.

Functional evenness (FEve), on the other hand, uses species relative abundances to describe the regularity (evenness) of species' abundance distribution in filled functional trait space (Mason *et al.*, 2005; Villéger *et al.*, 2008). FEve is scaled between 0 and 1 and decreases when the abundances of species are less evenly distributed or when trait distances among species are less regular. It reaches the value of 1 when species abundances are perfectly evenly distributed in trait space. The method proposed by Villéger *et al.* (2008) uses the minimum spanning tree (MST) to transform species distribution in  $n$ -dimensional functional space to a distribution on a single axis, by linking all the points contained in multidimensional space with the minimum sum of branch lengths. The index measures the regularity of branch lengths in the MST and evenness in species abundances. Because FEve considers relative abundances, unlike FD and FRic, it can decrease with the addition of species in trait space if, for instance, a new rarer species is added close to an abundant species.

Functional divergence (FDiv) refers to the distribution of abundances within the volume of multivariate functional trait space occupied by species (Villéger *et al.*, 2008). It essentially determines the degree to which the distribution of species abundances

maximises divergence in traits (Mason and de Bello, 2013). This index is a development on the single-trait approach of Mason *et al.* (2005), which measures how abundance is distributed within the range occupied by a community along a single trait axis. The FDiv of Villeger *et al.* (2008) starts by determining the coordinates of the 'centre of gravity' of the species forming the vertices of the convex hull. It then uses Euclidean distances to calculate the distances of all species to this centre of gravity, before computing a mean distance for the  $n$  species. Finally, these distances are weighted by species abundances to give abundance-weighted deviances from the centre of gravity. FDiv is also bounded between 0 and 1. The index is close to 0 when highly abundant species are very near the centre of gravity in trait space relative to rare species, and it approaches unity when the opposite happens (highly abundant species are very distant from the centre of gravity relative to rare species). Like FEve, FDiv can decrease when a species is added to the functional trait space of a community if, for example, the newly added species is highly abundant and with trait coordinates that are close to the centre of gravity of the functional trait space.

Although FD and FRic are expected to increase reasonably with the addition of species with different (or more extreme) properties than the ones already present, none of them are trivially related to species richness. On the other hand, FEve and FDiv will be independent of species richness, but highly affected by the species relative abundances in the community, which provides the benefit of weighing species' effects to reflect their relative contribution to ecosystem functioning (Grime, 1998, 2001), given the presumed greater influence some species will have on ecosystems because of their greater biomass (Díaz and Cabido, 2001). All functional diversity metrics were computed in R version 3.2.4 (R Development Core Team, 2016).

### 3.2.2 *Linear mixed effects models (LMMs)*

Linear mixed effects models (LMMs) are particularly useful when the data have a hierarchical form, such as repeated measurements and block experiments, which can have both fixed and random coefficients together with multiple error terms (Zuur *et al.*, 2007). Fixed effects can be thought of as unknown constants to be estimated from the data, while random effects govern the variance-covariance structure of the response variable (Crawley, 2015). When the explanatory variable is structured by spatial grouping (in the present case by the grouping of the neighbouring sampling plots within the different plant communities and management intensity categories), random effects that come from the

same group will be correlated and contravene independence of errors (i.e., multiple responses from the same group cannot be regarded as independent from each other, since they are likely to cause within-group correlation associated with spatial dependencies that need to be accounted for to avoid pseudoreplication). Mixed effects models account for this non-independence of errors by modelling the covariance structure (non-constant variance in the within-group errors) introduced by the grouping of the data (Crawley, 2015). Moreover, LMM assumes that the variation around the intercept (for each group) is normally distributed with a certain variance (Zuur *et al.*, 2009). A small variance means that differences per group are small, whereas a large variance means more variation.

In order to deal with idiosyncratic factors that affect the responses from the individual plots within communities and management categories, I added the random effect of sampling plots in LMMs to assume a different baseline value for the response variable of each plot. In other words, each field plot was assigned a different intercept value, with the mixed models estimating each of these intercepts, to account for spatial autocorrelation between neighbouring field plots. I used the *lme* function from the package *nlme* (Pinheiro *et al.*, 2016) in R version 3.2.4 (R Development Core Team, 2016) to fit LMMs to the data, using the functional diversity metrics, CWMs of plant traits, ecosystem processes (soil C stock and C:N ratio; see Chapter 2, section 2.3.2) and species richness as response variables, while management intensity was fitted as the explanatory variable. Sampling plots of the surveyed plant communities were used as the random effect in the models to give the following model formula:

$$\text{Response variable} \sim \text{Management intensity, random} = \sim 1 | \text{Plot} + \varepsilon$$

where the term  $\sim 1 | \text{Plot}$  assumes an intercept that is different for each plot, with the argument on the right-hand side of the  $|$  sign being a categorical variable. The formula thus anticipates that there will be multiple responses per plant community, and that these responses will depend on each plot's baseline level.

Next, I performed log likelihood ratio tests (Bolker *et al.*, 2009) to determine the significance of the effect of management intensity on each response variable via the *anova* function in R version 3.2.4 (R Development Core Team, 2016). I compared the variance structure of the full model, which included the effect of management intensity, with that of an intercept-only model (null model), where only the mean of the data was estimated:

Response variable  $\sim 1$ , random =  $\sim 1$  | Plot +  $\varepsilon$

I used the maximum likelihood method with the *lme* function (method = “ML”), since the fitted models had different fixed effects but the same random structure (Zuur *et al.*, 2009), and the  $p$  value of the log likelihood ratio statistic ( $L$ ) to determine significant effects ( $p < 0.05$ ) of disturbance intensity on the response variables. I followed the suggestion of Zuur *et al.* (2009) and corrected the  $p$  value from the *anova* output to follow the  $L$  distribution instead of the Chi-square distribution:

$$p_L = 0.5 * (1 - (L \text{ ratio}, df))$$

The associated degrees of freedom ( $df$ ) of the test statistic (and of the  $p$  value correction term) refer to the number of parameters that differ between the models (five parameters in the full model and one parameter in the null model).

### 3.2.3 Fisher’s least significant differences (LSD)

The mean species richness, functional diversity metrics, CWMs of plant traits and ecosystem processes of the different disturbance categories were compared to determine significant differences between them, given the influence of their differing management intensity. I employed multiple pairwise comparisons using Fisher’s least significant differences (LSD) on response variables that showed a significant effect of disturbance following LMM analysis (see section above). Fisher’s LSD gives the smallest difference between two means that will lead to a rejection of the null hypothesis of no difference (Sokal and Rohlf, 2012). The management categories were treated as independent entities since there were no overlapping plots between them (i.e., no plots belonging to the same plant community placed in different categories). Following Sokal and Rohlf (2012), for unequal sample sizes LSD was defined as:

$$LSD = t_{\alpha/2, df_{MSE}} \sqrt{MSE \left( \frac{1}{n_i} + \frac{1}{n_j} \right)}$$

where the square root term is the standard error of the difference, the mean square error (MSE) is the pooled error variance (weighted average of the within-treatment variances),



$n$  is the sample size of samples  $i$  and  $j$ , and the  $t$  statistic follows the  $t$  distribution with  $(n - 1)$  degrees of freedom. I used  $\alpha = 0.05$  for the  $t$  statistic. The difference between the two sample means  $\bar{Y}_i$  and  $\bar{Y}_j$  is said to be significant when  $|\bar{Y}_i - \bar{Y}_j| > \text{LSD}$ . I performed LSD analyses by using a modified version of the *LSD.test* function of the package *agricolae* (de Mendiburu, 2016) in R version 3.2.4 (R Development Core Team, 2016).

### 3.3 Results

#### 3.3.1 Species richness and functional diversity metrics

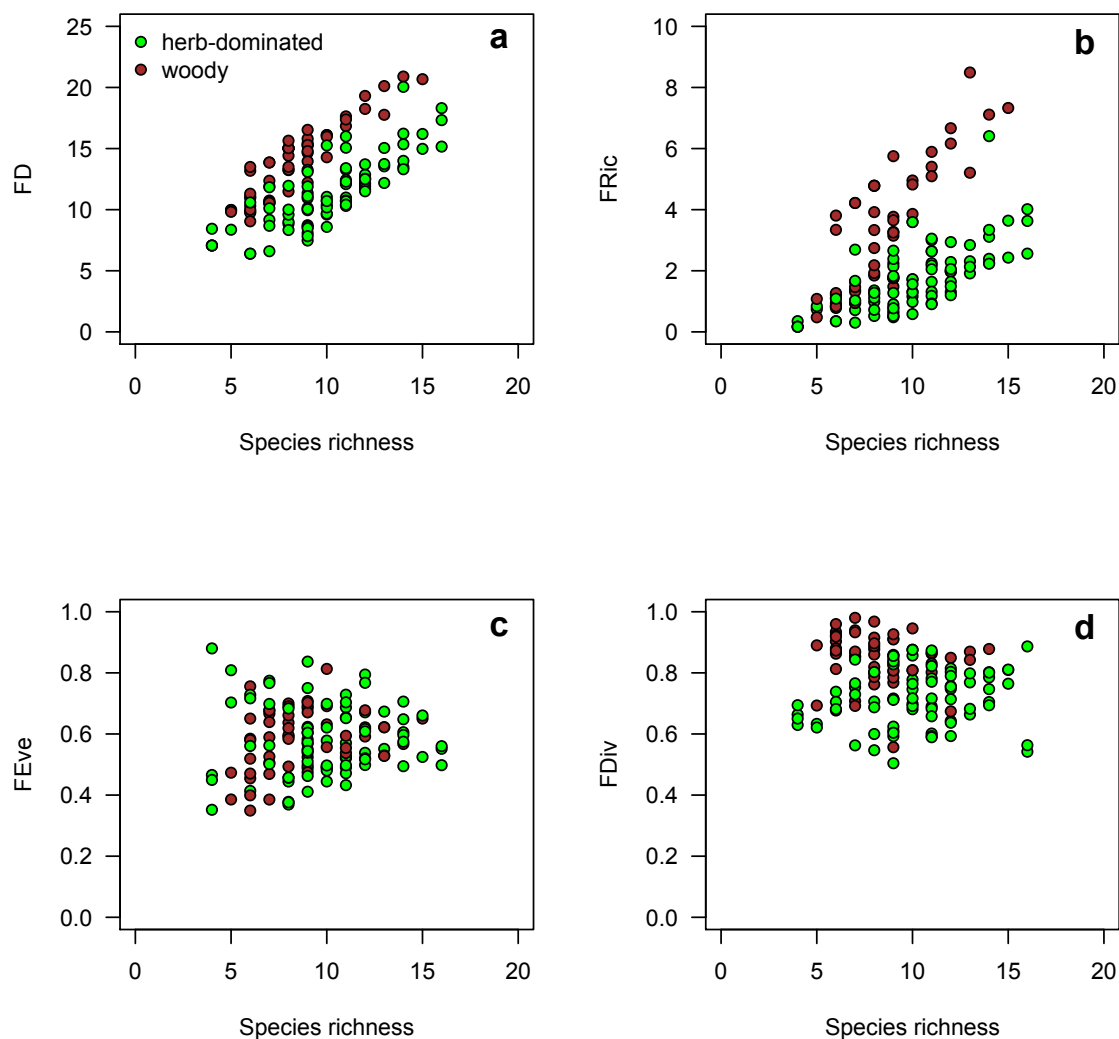
Overall, increasing plot-level species richness led to increasing functional diversity (FD) and richness (FRic; Fig. 3.1a and b). That pattern was particularly strong in the functional richness of woody communities (Fig. 3.1b). In addition, woodlands presented higher FD and FRic than herb-dominated communities (Fig. 3.1a and b). Functional evenness (FEve) and divergence (FDiv) remained constant with increasing species richness (Fig. 3.1c and d), with no discernible difference between woody and herbaceous communities. However, woodlands showed slightly higher FDiv values at the lowest levels of species richness than herb-dominated communities (Fig. 3.1d).

When accounting for the random effects of the field plots within the plant communities, the LMM results showed management intensity had a significant influence on species richness ( $L = 16.16$ ;  $df = 4$ ;  $p = 0.001$ ), FD ( $L = 43.88$ ;  $df = 4$ ;  $p < 0.0001$ ), FRic ( $L = 42.80$ ;  $df = 4$ ;  $p < 0.0001$ ) and FDiv ( $L = 65.85$ ;  $df = 4$ ;  $p < 0.0001$ ), but not on FEve ( $L = 1.24$ ;  $df = 4$ ;  $p = 0.4$ ).

The most intensively managed communities (category 4) showed significantly higher mean taxonomic diversity than the unmanaged woodlands (category 0; Fig. 3.2a;  $p < 0.0001$ , LSD analysis). However, no significant changes between the unmanaged glades (category 1) and the communities with low and moderate management (categories 2 and 3) were seen (Fig. 3.2a;  $p > 0.05$ , LSD analysis). Moreover, species diversity in management category 4 was significantly higher than in the moderately managed sites (category 3) in Upton (Fig. 3.2a;  $p = 0.02$ , LSD analysis).

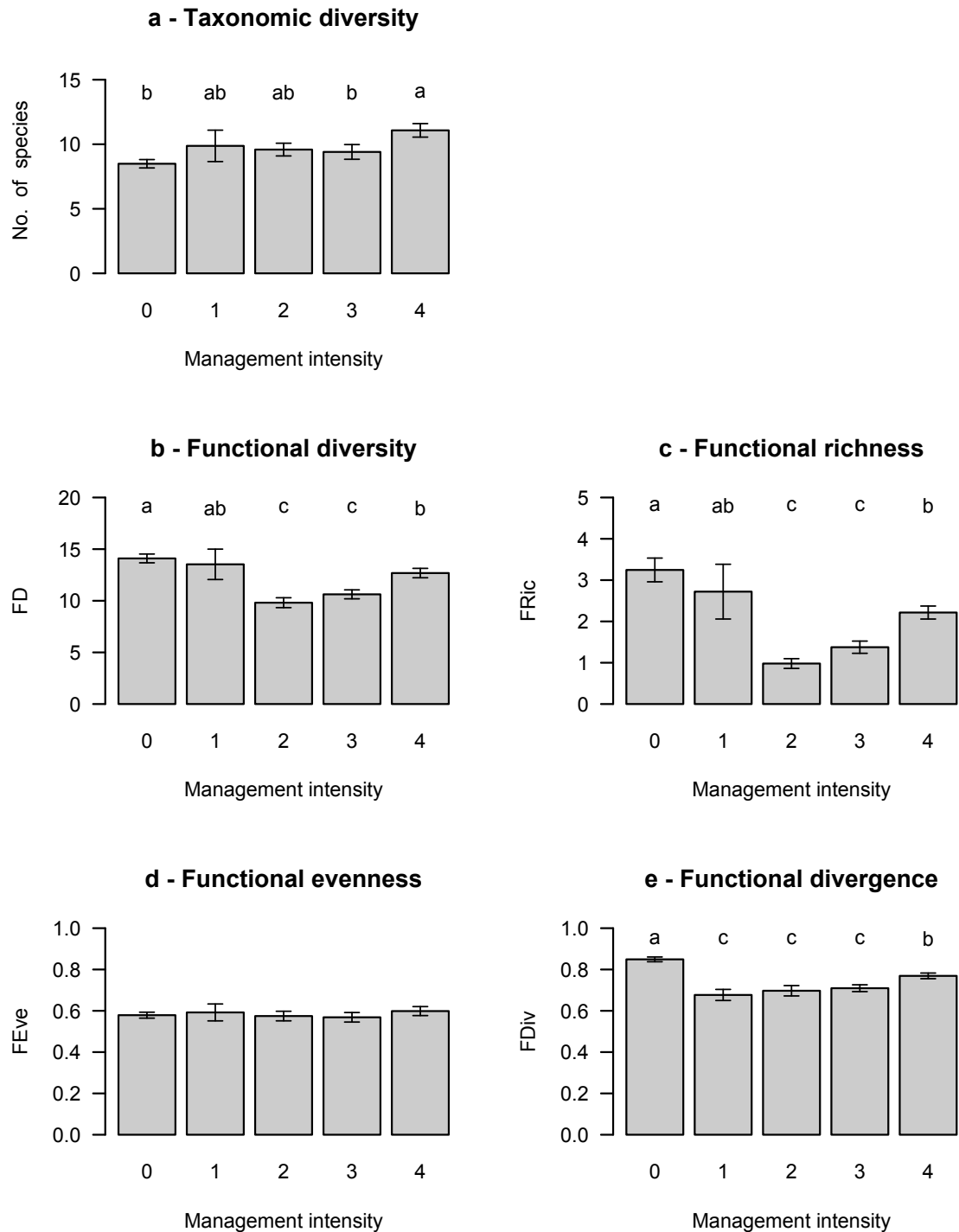
Functional diversity (FD) and richness (FRic) responded very similarly to the effects of disturbance (Fig. 3.2 b and c). Increasing the management intensity of the herbaceous sites resulted in communities with significantly higher FD and FRic (Fig. 3.2b and c, respectively;  $p < 0.05$ , LSD analysis). However, the mean FD and FRic of the unmanaged

woodlands (category 0) were significantly higher than the mean FD and FRic of the managed herb-dominated communities (categories 2 to 4; Fig. 3.2b and c;  $p < 0.05$ , LSD analysis). There were no significant differences in FD and FRic between the unmanaged woods and unmanaged glades (category 1), and between the latter and the management category 4 sites (Fig. 3.2b and c;  $p > 0.05$ , LSD analysis).



**Fig. 3.1:** Functional diversity metrics against plot-level species richness (13 levels, from 4 to 16) in Upton and Woodwalton. Green circles represent herb-dominated communities, while brown circles denote woodlands. *FD* – functional diversity; *FRic* – functional richness; *FEve* – functional evenness; *FDiv* – functional divergence.

*FEve* did not respond to changing disturbance levels following LMM analysis (Fig. 3.2d; no LSD analysis). The unmanaged woodlands and the highly managed herbaceous communities had the highest and second highest mean functional divergence (*FDiv*) respectively, and were significantly different between them and to all other herb fen sites



**Fig. 3.2:** Mean species richness (panel **a**) and functional diversity metrics (panels **b** to **d**) per management intensity category (0 – unmanaged woods; 1 – unmanaged glades; 2, 3 and 4 – low, moderate and high management intensity, respectively). Error bars show standard errors of the mean ( $\pm 1$  S.E.). Different letters above bars indicate significant differences ( $p < 0.05$ ) between means following Fisher’s least significant differences (LSD) analysis. No LSD analysis was performed for FEve (panel **d**) due to the non-significant effect of management when fitting the full model (LMM analysis,  $p > 0.05$ ). *FD* – functional diversity; *FRic* – functional richness; *FEve* – functional evenness; *FDiv* – functional divergence.

(Fig. 3.2e;  $p < 0.01$ , LSD analysis). The unmanaged glades and the low and moderate management categories (2 and 3, respectively) showed similar FDiv patterns between them (Fig. 3.2e;  $p > 0.05$ , LSD analysis).

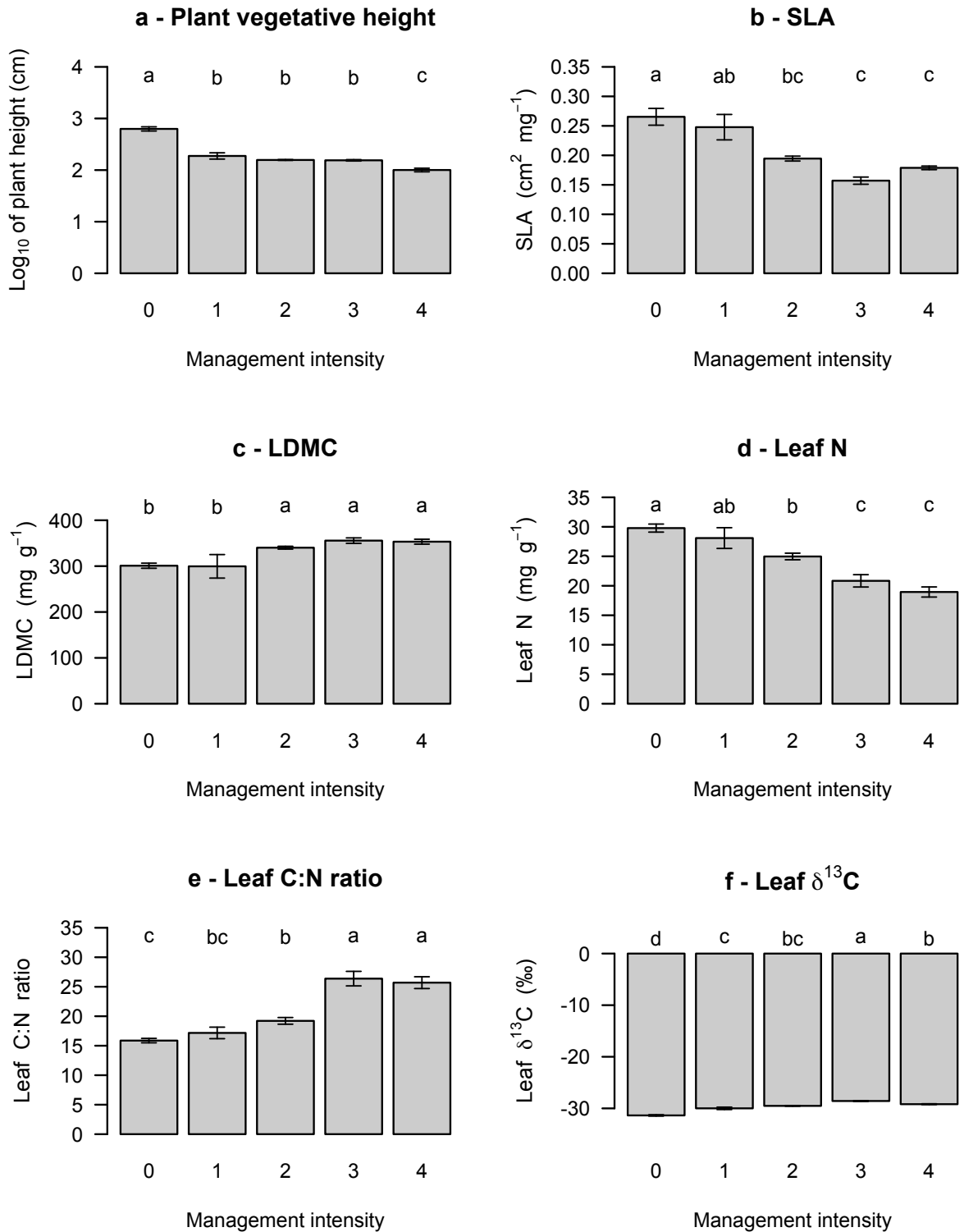
### 3.3.2 Community weighted means (CWMs) of plant traits

Surprisingly, with an increase in disturbance intensity the CWM of leaf traits changed from exploitative traits to more conservative traits associated with recalcitrant leaf litter, as shown by overall trends of decreasing SLA and leaf N and increasing LDMC and leaf C:N ratio with increasing management intensity (Fig. 3.3). As expected, disturbance led to a significant reduction in  $\log_{10}$ -transformed species' vegetative height ( $L = 175.41$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis). While the unmanaged woods (category 0) showed the highest mean plant height of all communities (Fig. 3.3a;  $p < 0.0001$ , LSD analysis), the highly managed herbaceous sites (category 4) showed the lowest (Fig. 3.3a;  $p < 0.01$ , LSD analysis). The unmanaged glades (category 1) did not differ significantly in average height from sites with low and moderate levels of disturbance (categories 2 and 3; Fig. 3.3a;  $p > 0.05$ , LSD analysis).

Management had a significant effect on SLA when accounting for the random effects of sampling plots ( $L = 52.96$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis). The mean SLA of the unmanaged woods (category 0) was significantly higher than the means of the managed herbaceous sites (categories 2 to 4; Fig. 3.3b;  $p < 0.001$ , LSD analysis). The unmanaged glades (category 1) also showed significantly higher mean SLA than the mostly managed categories (3 and 4; Fig. 3.3b;  $p < 0.05$ , LSD analysis).

LDMC presented the opposite trend of SLA, with higher disturbance levels leading to increased mean LDMC (Fig. 3.3c). Management had a significant effect on LDMC following LMM analysis ( $L = 55.07$ ;  $df = 4$ ;  $p < 0.0001$ ). With increasing disturbance intensity, the CWM of LDMC changed towards species with higher investment in leaf dry matter content, with the managed communities (categories 2 to 4) showing significantly higher means than the undisturbed sites (Fig. 3.3c;  $p < 0.05$ , LSD analysis). However, the difference between the unmanaged woods (category 0) and glades (category 1) was not statistically significant (Fig. 3.3c;  $p = 0.9$ , LSD analysis).

Leaf N content responded strongly to management ( $L = 86.94$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis) and presented decreasing mean values with increasing disturbance (Fig. 3.3d). The unmanaged woodlands (category 0) had significantly higher mean leaf N content



**Fig. 3.3:** Mean community weighted means (CWMs) of plant height (log<sub>10</sub>-transformed; panel a) and leaf traits (panels b to f) per management intensity category (0 – unmanaged woods; 1 – unmanaged glades; 2, 3 and 4 – low, moderate and high management intensity, respectively). Error bars are standard errors of the mean ( $\pm 1$  S.E.). In panel f, error bars are shown at the bottom. Different letters above bars indicate significant differences ( $p < 0.05$ ) between means following Fisher’s least significant differences (LSD) analysis.

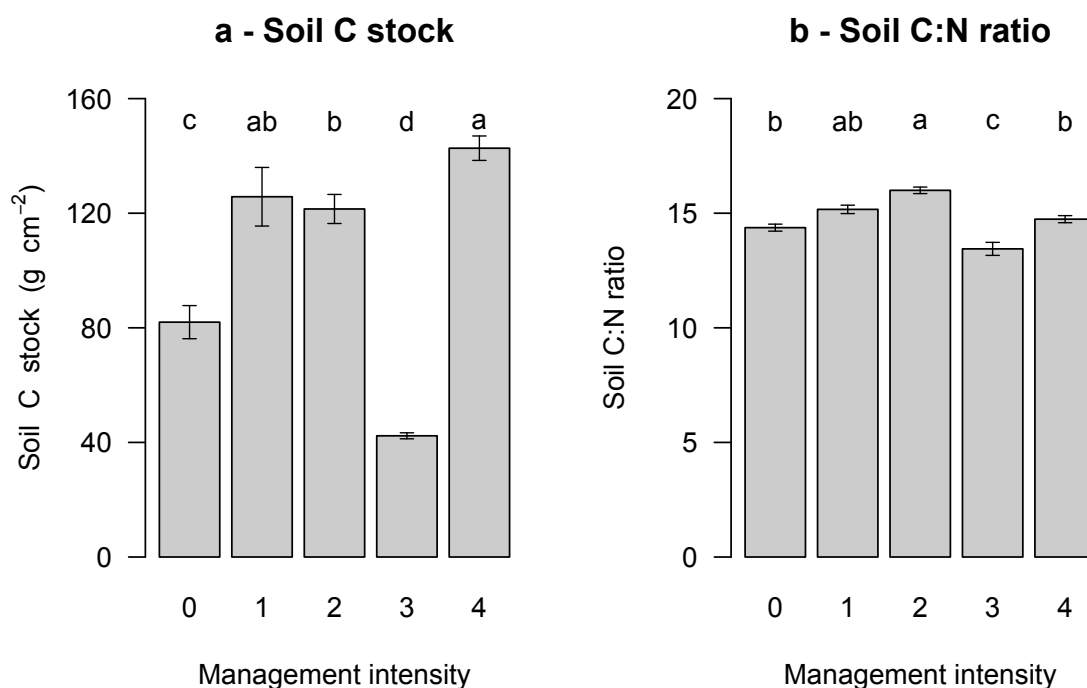
than the managed herbaceous sites (categories 2 to 4; Fig. 3.3d;  $p < 0.001$ , LSD analysis), while the most intensively managed communities (categories 3 and 4) presented the lowest means of all sites (Fig. 3.3d;  $p < 0.01$ , LSD analysis). Consequently, leaf C:N ratio revealed the same pattern of significant differences between means among management categories ( $p < 0.01$ , LSD analysis), but with an opposite tendency of increasing mean values with intensifying management (Fig. 3.3e). Once again, disturbance had a significant effect on leaf C:N ratio after accounting for the random effects of sampling plots ( $L = 101.59$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis).

Management had a significant impact on leaf  $\delta^{13}\text{C}$  ( $L = 189.22$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis). Intensifying the level of disturbance promoted communities with significantly higher water use efficiency (Fig. 3.3f;  $p < 0.005$ , LSD analysis). The only non-significant differences between mean values of leaf  $\delta^{13}\text{C}$  were those between the unmanaged glades (category 1) and the *Phragmites* fen (category 2; Fig. 3.3f;  $p = 0.1$ , LSD analysis), and between the latter and the annually mown sites (category 4; Fig. 3.3f;  $p = 0.1$ , LSD analysis). The moderately managed herbaceous communities in Upton (category 3) presented the highest mean leaf  $\delta^{13}\text{C}$  (Fig. 3.3f;  $p < 0.001$ , LSD analysis), while the unmanaged woods (category 0) showed the lowest (Fig. 3.3f;  $p < 0.0001$ , LSD analysis).

### 3.3.3 Ecosystem processes

Disturbance had significant effects on soil C storage ( $L = 126.76$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis) and soil C:N ratio ( $L = 53.39$ ;  $df = 4$ ;  $p < 0.0001$ ; LMM analysis). The highly disturbed communities (category 4) presented higher mean soil C than the unmanaged woodlands (category 0; Fig. 3.4a;  $p < 0.0001$ , LSD analysis), potentially because of intense management favouring conservative traits normally associated with reduced decomposition rates, leading to soil C build up under relatively low mineralisation rates. In fact, the annually mown sites (category 4) had the highest mean soil C stock of all communities (Fig. 3.4a;  $p < 0.05$ , LSD analysis), while the moderately managed herbaceous sites in Upton (category 3) revealed the lowest mean (Fig. 3.4a;  $p < 0.0001$ , LSD analysis). The unmanaged woods (category 0) presented the second lowest mean soil C and were significantly different to all herb-dominated communities (Fig. 3.4a;  $p < 0.001$ , LSD analysis). There were no significant differences between the unmanaged glades and management categories 2 (low management) and 4 (high management; Fig. 3.4a;  $p > 0.05$ , LSD analysis). Among the herbaceous sites, Woodwalton (categories 1, 2 and 4)

communities showed on average approximately three times higher soil C stocks than Upton sites (category 3; Fig. 3.4a; Table 3.2).

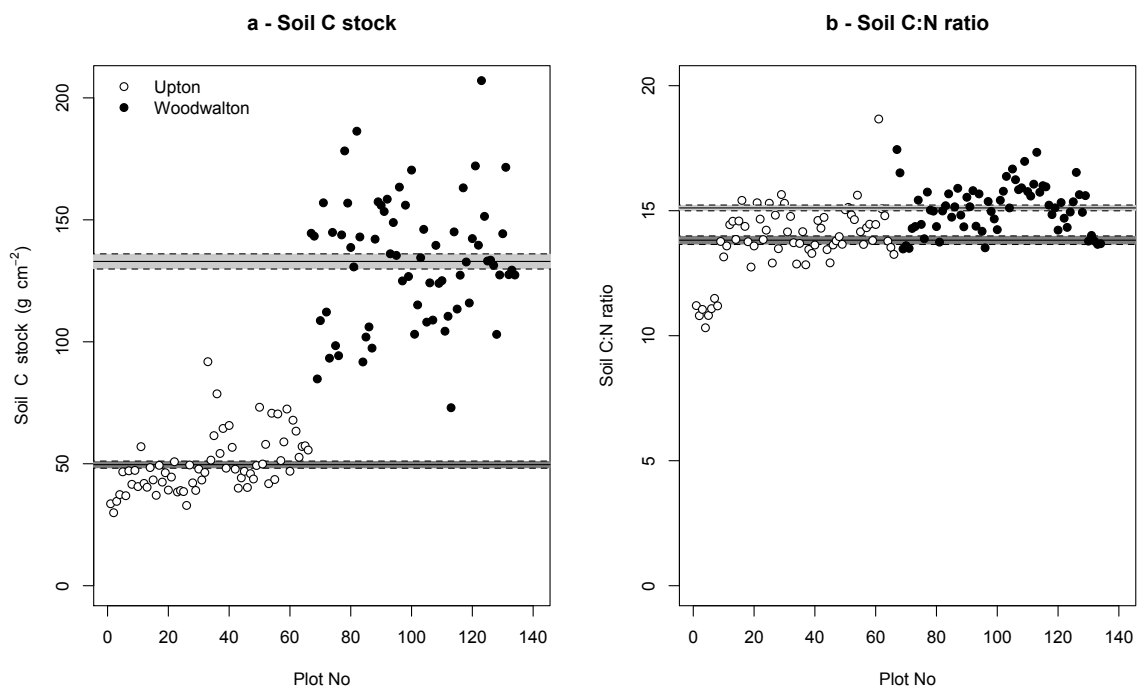


**Fig. 3.4:** Mean soil C stock (panel **a**) and C:N ratio (panel **b**) per management intensity category (0 – unmanaged woods; 1 – unmanaged glades; 2, 3 and 4 – low, moderate and high management intensity, respectively). Error bars are standard errors of the mean ( $\pm 1$  S.E.). Different letters above bars indicate significant differences ( $p < 0.05$ ) between means following Fisher’s least significant differences (LSD) analysis.

Despite the herbaceous communities in Upton (category 3) displaying the lowest mean soil C, they also revealed the lowest mean soil C:N ratio among the studied sites (Fig. 3.4b;  $p < 0.001$ , LSD analysis), suggesting relatively low soil N content in these sites. The unmanaged glades (category 1) and the *Phragmites* fen in Woodwalton (category 2) showed the highest mean soil C:N ratio (Fig. 3.4b;  $p < 0.001$ , LSD analysis), probably reflecting their relatively high mean soil C stocks (Fig. 3.4a). The unmanaged woods (category 0) and the annually mown sites (category 4) did not differ in mean soil C:N ratio (Fig. 3.4b;  $p = 0.2$ , LSD analysis), though the latter revealed significantly higher mean soil C than the former (Fig. 3.4a;  $p < 0.0001$ , LSD analysis), indicating high levels of soil N stock in the highly managed communities.

The variability in soil C stock was higher in Woodwalton, with four management intensity categories (0, 1, 2 and 4), than in Upton, with only two categories (0 and 3; Fig.

3.5a). The overall mean soil C stock in Upton was  $49.63 \pm 1.47 \text{ g cm}^{-2}$  (1 S.E. of the mean), considerably lower than in Woodwalton ( $132.94 \pm 3.11 \text{ g cm}^{-2}$ ; 1 S.E. of the mean; Fig. 3.5a). The difference in mean soil C:N ratio between the two fens was lower, with Woodwalton presenting a slightly higher overall mean ( $15.11 \pm 0.12$ ; 1 S.E. of the mean) than Upton ( $13.82 \pm 0.17$ ; 1 S.E. of the mean; Fig. 3.5b), suggesting relatively low mean N concentration in Upton soils compared to Woodwalton. Table 3.2 presents the means and standard errors of the functional diversity metrics, CWMs and ecosystem processes of the different management categories.



**Fig. 3.5:** Soil C stock (panel a) and C:N ratio (panel b) per plot. White circles are Upton plots (1 to 66) and black circles are Woodwalton plots (67 to 134). Horizontal solid lines are the means of the respective sites, and greyed areas within the dashed lines show one standard error around the mean (dark grey for Upton and light grey for Woodwalton).

### 3.4 Discussion

Determining the functional diversity of vegetation is important in unravelling the relationship between environmental change and ecosystem processes (Lavorel *et al.*, 2008). The present study elucidates the effects of disturbance on the taxonomic and functional composition of lowland fen communities and its concomitant effect on ecosystem processes. The current analyses provide some key evidence that taxonomic and functional diversity respond similarly to disturbance pressure among managed herbaceous



**Table 3.2:** Mean of functional diversity metrics, species richness, community weighted mean (CWM) of plant traits and soil variables ( $\pm$  one standard error of the mean) per management category. *n* denotes the number of sampling plots in each management category. *FD* – functional diversity; *FRic* – functional richness; *FEve* – functional evenness; *FDiv* – functional divergence; *Sp* – species richness.

	Management intensity categories				
	0	1	2	3	4
<i>n</i>	51	8	17	32	26
<b>FD</b>	14.10 $\pm$ 0.43	13.53 $\pm$ 1.47	9.81 $\pm$ 0.48	10.62 $\pm$ 0.43	12.68 $\pm$ 0.45
<b>FRic</b>	3.25 $\pm$ 0.29	2.72 $\pm$ 0.66	0.98 $\pm$ 0.12	1.38 $\pm$ 0.15	2.22 $\pm$ 0.16
<b>FEve</b>	0.58 $\pm$ 0.01	0.59 $\pm$ 0.04	0.57 $\pm$ 0.02	0.57 $\pm$ 0.02	0.60 $\pm$ 0.02
<b>FDiv</b>	0.85 $\pm$ 0.01	0.68 $\pm$ 0.03	0.70 $\pm$ 0.03	0.71 $\pm$ 0.02	0.77 $\pm$ 0.01
<b>Sp</b>	8.49 $\pm$ 0.32	9.88 $\pm$ 1.22	9.59 $\pm$ 0.49	9.41 $\pm$ 0.57	11.08 $\pm$ 0.52
<b>CWMs</b>					
<b>Log<sub>10</sub> of plant height (cm)</b>	2.80 $\pm$ 0.04	2.27 $\pm$ 0.06	2.20 $\pm$ 0.01	2.19 $\pm$ 0.01	2.00 $\pm$ 0.03
<b>SLA (cm<sup>2</sup> mg<sup>-1</sup>)</b>	0.27 $\pm$ 0.01	0.25 $\pm$ 0.02	0.19 $\pm$ 0.004	0.16 $\pm$ 0.01	0.18 $\pm$ 0.003
<b>LDMC (mg g<sup>-1</sup>)</b>	300.91 $\pm$ 5.56	299.56 $\pm$ 25.64	340.20 $\pm$ 3.07	355.63 $\pm$ 5.93	353.29 $\pm$ 5.36
<b>Leaf N (mg g<sup>-1</sup>)</b>	29.78 $\pm$ 0.68	28.09 $\pm$ 1.76	24.97 $\pm$ 0.56	20.84 $\pm$ 1.05	18.95 $\pm$ 0.86
<b>Leaf C:N ratio</b>	15.87 $\pm$ 0.37	17.17 $\pm$ 0.98	19.21 $\pm$ 0.57	26.38 $\pm$ 1.23	25.69 $\pm$ 1.00
<b>Leaf <math>\delta^{13}\text{C}</math> (‰)</b>	-31.36 $\pm$ 0.13	-29.99 $\pm$ 0.23	-29.52 $\pm$ 0.06	-28.57 $\pm$ 0.07	-29.19 $\pm$ 0.08
<b>Ecosystem processes</b>					
<b>Soil C stock (g cm<sup>-2</sup>)</b>	81.98 $\pm$ 5.78	125.75 $\pm$ 10.23	121.48 $\pm$ 5.07	42.31 $\pm$ 1.05	142.70 $\pm$ 4.27
<b>Soil C:N ratio</b>	14.37 $\pm$ 0.15	15.17 $\pm$ 0.18	16.00 $\pm$ 0.14	13.44 $\pm$ 0.28	14.74 $\pm$ 0.15

communities. However, woody and herb-dominated sites showed opposite results (lower taxonomic diversity but generally higher functional diversity in woodlands compared to herbaceous communities), confirming previous findings (de Bello *et al.*, 2006; Mayfield *et al.*, 2010; Carmona *et al.*, 2012) that these metrics measure different facets of biodiversity. Equally important, leaf traits involved in the leaf economics spectrum (LES) shifted between two competing ecological strategies with increasing disturbance frequency. The response of ecosystem processes to management intensity seemed to show a tentative link between mean soil C and shifts in aboveground plant functional traits that are pertinent to leaf litter decomposition rates and hence nutrient cycling. However, more explicit tests are required to account for the direct and indirect effects of environmental variables and plant functional traits acting simultaneously on ecosystem processes. Weighting the concurrent

effects of abiotic factors may be important to disentangle the contribution of these two components to changes in soil C and N, as determined in Chapter 4 using structural equation modelling (SEM).

The response of functional diversity was highly dependent on the metric used and the type of community sampled (woody vs herbaceous), with indices that use species presence responding differently to those that account for species relative abundances. The metrics used here were therefore shown to be independent of one another (i.e., they measure different aspects of functional diversity and are not redundant), in line with previous results (Villegger *et al.*, 2008; Schleuter *et al.*, 2010). Overall, increasing disturbance intensity led to higher taxonomic diversity and, though functional diversity (FD), richness (FRic) and divergence (FDiv) decreased from unmanaged woodlands to managed herb-dominated communities, they increased with increasing disturbance intensity among the managed herbaceous sites. Therefore, there was an overall loss of functional trait diversity from woody to herbaceous communities, but an increase in the diversity of traits and ecological strategies among herb-dominated communities with increasing disturbance. Functional evenness (FEve) was generally unaffected by disturbance effects.

Changes in taxonomic diversity and multivariate functional diversity indices were paralleled by changes in univariate community weighted means (CWMs) of plant traits. The unexpected results of increasing management leading to species at the conservative end of the LES continuum were contrary to my predictions, as well as to previous studies (Garnier *et al.*, 2007; Golodets *et al.*, 2009; Dainese *et al.*, 2015). Soil C storage behaved generally as expected, given the results of the leaf functional traits, but the differences seen between the Upton and Woodwalton herbaceous sites remain puzzling and are probably explained by changes in environmental variables not considered here, but explored in detail in Chapter 4 using SEM to quantify the direct and indirect effects of biotic and abiotic factors on ecosystem processes.

#### *3.4.1 Effects of species richness on functional diversity metrics*

As expected by the sampling effect, FD and FRic showed an overall increasing tendency with increasing species richness in both the woodlands and herbaceous sites (Fig. 3.1a and b), in accordance with the monotonicity criterion (the subset of a community is less functionally diverse than the complete community) of Mason *et al.* (2003) and Ricotta (2005), and in line with results reported elsewhere (Villegger *et al.*, 2008; Mouchet *et al.*,

2010; Schleuter *et al.*, 2010). The results confirmed the assumption that it is more likely to obtain greater trait distances between species and a larger hull volume when more species are sampled (Villegger *et al.*, 2008). However, herb-dominated sites generally displayed higher species richness than the unmanaged woods, especially at high disturbance levels (Fig. 3.2a), but lower FD and FRic (Fig. 3.2 b and c), probably because of the large differences between woody and herbaceous species in plant height (Fig. 3.3a). Nevertheless, increasing species diversity generally resulted in higher trait dispersion and a fuller occupation of the potential niche space (Fig. 3.1 a and b), resulting in increasing variability in ecological strategies to cope with increasing plot-level species density. This might indicate stronger biotic and competitive interactions at higher levels of species density, for example higher limiting similarity effects (discussed further in Chapter 5 on community assembly processes).

The striking difference between woodlands and herb-dominated sites in the FRic pattern against species numbers is most likely reflecting a larger variety of strategies in woody communities to adapt to a more heterogeneous set of conditions (e.g., open canopy vs shaded understorey). Accordingly, woody sites mostly presented higher FD and FRic values than herb-dominated communities, probably as a result of higher trait dispersion (meaning greater distances between species in the FD dendrogram) and greater differences between vertices (the most extreme trait values of the convex hull) in plant vegetative height and leaf traits (Fig. 3.3), reflecting the differences between dominant canopy species, such as *Alnus glutinosa*, *Betula pubescens* and *Fraxinus excelsior*, and the understorey and field layers comprised of shrubs, monocots and forbs (Appendix 1). That discrepancy is more accentuated in FRic than FD, probably because FRic ignores any potential functional variation within the convex hull (Mouchet *et al.*, 2010).

Contrary to FD and FRic, FEve and FDiv were shown to be independent of species richness and non-monotonic, also in accordance with previous findings (Villegger *et al.*, 2008; Mouchet *et al.*, 2010; Schleuter *et al.*, 2010). FEve is maximised by an even distribution of both species and abundances in functional space, with an increase in FEve values denoting a fuller utilisation of resources (Carreño-Rocabado *et al.*, 2012). Woodlands and herbaceous communities showed high and low values of FEve, with no clear distinction between them (Fig. 3.1c), meaning species abundances were both regularly and irregularly distributed in functional space throughout the two fen sites. However, most of the values were above 0.5, indicating a predominance of relatively high regularity in species distribution in multidimensional trait space in the majority of the

sampling plots. Moreover, woodlands showed higher variability in FEve values at relatively low levels of taxonomic diversity (between five to eight species per plot; Fig. 3.1c) than herbaceous sites. This possibly indicates differences between the bare-ground plots, where only abundant canopy species dominate and utilise resources, and plots with a rich field layer, where canopy and ground flora compete for resources and increased abundances, fully utilising light and nutrients. Accordingly, there was a slight tendency of converging FEve values at the highest levels of species numbers ( $> 12$ ; Fig. 3.1c), indicating increasing similarity between plots in terms of species abundance distribution with increasing species diversity. These tended to be dominated by herbaceous plots, where presumably species with similar fitness (regular distribution in trait space) attain similar abundances.

FDiv measures how abundances tend to concentrate on the outer margins of the functional space while accounting for the functional richness of the community (Villegger *et al.*, 2008). Most FDiv values were above 0.6 and close to 1 across species richness levels (Fig. 3.1d), meaning relatively high levels of functional divergence associated with a high degree of niche differentiation (highly abundant species very distant from the centre of gravity relative to rare species; Mouchet *et al.*, 2010). Once again, plant height seems to be the main driver of the differences between dominant and less abundant species, particularly in the woods, pushing the vertices of the convex hull 'outwards' and leaving the relatively low-abundant species closer to the centre of the functional space. In other words, the most abundant taxa seem to be very dissimilar in functional traits (particularly height) to the rarer species and to be weakly competing with them, which probably explains the overall slightly higher FDiv values in the woody communities if compared to the herbaceous sites. Species in the field layers are occupying a different niche to the tall canopy species to cope with potentially reduced levels of resources such as light and nutrients. That is particularly evidenced by the higher FDiv in the woodlands at low species richness levels ( $< 9$ ; Fig. 3.1d), where most lower-statured species were not competing directly with the dominant tall canopy species.

### 3.4.2 *Effects of disturbance on taxonomic and functional diversity*

Taxonomic and functional diversity responded mostly positively to increasing disturbance intensity among managed herbaceous sites (question i), though preventing woody vegetation from replacing herbaceous fens through vegetation management generally resulted in a loss of functional diversity and an increase in species richness.

Therefore, taxonomic diversity cannot be reliably used as a proxy for functional diversity in lowland fens. Both aspects of biodiversity responded differently to efforts of preventing the development of fen carr, even though managed herbaceous fens generally displayed similar responses (Fig. 3.2).

There was a significant increase in number of species from the unmanaged woods to the annually mown sites, in agreement with previously stated expectations and in line with other studies reporting increased species diversity following management intervention in fen sites (Shaw and Wheeler, 1991). Management often prevents scrub invasion and the development of fen woodland and helps to maintain the composition of low-growing herbaceous vegetation (Wheeler and Shaw, 1995). Similarly, the arrest of vegetation management in fens tends to result in progressive successional development leading to the ultimate development of species-poorer fen woodland or bog (Wheeler and Shaw, 1995). Though not significantly different to the least managed herbaceous sites, the three herb-dominated communities in Upton (management category 3) showed the lowest mean species richness per plot among the herbaceous sites (Table 3.2), mostly as a result of the species poor *Phragmites australis* – *Carex riparia* reedswamp community, where only 10 species were recorded in late summer. These less speciose habitats are probably a result of shading by the dominant plant, dense vigorous stands of reed that are mown on a seven- to eight-year rotation, together with the accumulation of litter or the occurrence of regular flooding, which are unfavourable to the establishment of tree seedlings and other species (Wheeler, 1980a). On the other hand, the relatively species-rich annually mown sites in Woodwalton have smaller summer biomass and likely present much less light attenuation through the vegetation stand than the lesser managed communities (Wheeler and Shaw, 1995).

Although mean FD and FRic decreased from woodlands to managed herbaceous communities, they showed similar patterns of significantly increasing diversity with increasing disturbance among managed sites (Fig. 3.2 b and c), as did mean FDiv (Fig. 3.2e), though to a lesser degree. The change in FD and FRic reflects variation in the trait distance and volume of communities (i.e., changes in trait diversity), whereas the change in FDiv is a result of variations in the distribution of abundant species in functional space in relation to rarer ones. They should hence be interpreted separately since the variation in the volume of trait space filled by a community has a different meaning to a shift in the distribution of abundance within that space (Villeger *et al.*, 2008). Decreasing functional volume in trait space from unmanaged woods to managed herbaceous fens may indicate

increasing pressure of environmental filters (Cornwell *et al.*, 2006), or in this case of management filters. Frequent disturbance in the managed herbaceous sites is filtering out high-statured species with different resource acquisition strategies to the low-growing vegetation (see below), reducing the differences between the vertices of the convex hull (smaller differences in plant height) and causing the filled functional volume (and the trait distances between species) to contract. Therefore, the diminishing FD and FRic from woody to managed herbaceous fens mostly reflect the effect of plant vegetative height. This reduction in functional diversity and richness in relatively disturbed sites compared to undisturbed communities was also confirmed by other studies (Pakeman, 2011; Dainese *et al.*, 2015). On the other hand, increasing trait diversity with increasing disturbance of herbaceous fens may be the result of significant strategic variation between pioneer-type species with adaptations for rapid growth between disturbances and for coping with regular management (Westoby, 1998), exemplified by the relatively large differences in trait values between abundant grasses (e.g., *Molinia caerulea*) and forbs (e.g., *Hydrocotyle vulgaris*) in the highly disturbed sedge fen community in Woodwalton (see Appendix 3 for mean trait values of different species and life forms).

Changes in the distribution of abundances in trait space may instead reveal shifts in the intensity of competitive interactions (Mason *et al.*, 2007; Villegger *et al.*, 2008), precipitated in this case by management effects. The unmanaged woodlands seem to be experiencing enhanced niche differentiation between the woody and the herbaceous components of the vegetation, evidenced by their higher mean FDiv than the herbaceous communities (Table 3.2). Species attaining mature heights at different depths along a vertical profile, such as commonly found in woodland environments, are operating at different light incomes, heat loads, wind speeds, humidity and with different investment costs for supporting photosynthetic tissue and lifting water and nutrients to the leaves (Westoby, 1998), leading to divergent ecological strategies to establish, grow and reproduce. In addition, species present different stem tissue properties according to the height of the photosynthetic tissue attained throughout most of their lifetime (e.g., woody vs herbaceous stem; Westoby, 1998). On the other hand, the unmanaged and lesser managed herbaceous sites are showing stronger niche overlap (lowest FDiv; Table 3.2), possibly due to more similar strategies in light and nutrient acquisition adopted by the dominant tall monocotyledons (e.g., *Phragmites australis*, *Cladium mariscus*, *Juncus subnodulosus*, *Calamagrostis canescens* and *Carex riparia*). The annually mown sites in Woodwalton presented higher mean FDiv, and thus higher niche differentiation, than the

other herb-dominated communities, likely reflecting the higher diversity of low herbs (e.g., *Hydrocotyle vulgaris*, *Ranunculus flammula* and *Galium uliginosum*) in relation to monocotyledons, with potentially different responses to light and nutrient availability (Wheeler, 1980a).

Mean FEve remained unaltered along the management gradient (Fig. 3.2d), meaning the regularity in the distribution of abundances in functional space did not respond to changing disturbance frequency. FEve has been found to be quite sensitive to niche filtering (Mouchet *et al.*, 2010), with an increase in mean FEve indicating a fuller utilisation of resources (Carreño-Rocabado *et al.*, 2012) in strongly competitive contexts where abundances are more evenly distributed (Mouchet *et al.*, 2010). Therefore, in terms of species abundance distribution in trait space, the present results are pointing to a generally similar (and moderately) competitive scenario across disturbance intensity. This is possibly because of fairly homogenous environmental conditions throughout the study sites and relatively small changes in floristic diversity across the management categories.

The findings presented here seem to be aligned with other types of habitat and management interventions, since similar results were reported for tropical forests under different logging regimes (Carreño-Rocabado *et al.*, 2012) and for mountain grasslands under the effects of grazing (Dainese *et al.*, 2015). Previous studies have also found that intensified management of ecosystems can reduce their resilience and hence increase their vulnerability to future global environmental change through simultaneous reductions in the number of species with similar effects on ecosystem functioning (functional redundancy) and the diversity of responses to disturbance (Laliberté *et al.*, 2010). Under reduced functional redundancy only minor changes in the number of species could result in significant changes in functional diversity (Flynn *et al.*, 2009) and the ability of plant communities to respond to environmental change (Elmqvist *et al.*, 2003; Folke *et al.*, 2004). However, the results presented here showed enhanced taxonomic and functional diversity of herbaceous fen communities with intensifying management, coupled with a higher number of species per functional group (grasses, sedges, rushes and forbs) in the mostly managed sites (Appendix 1), supposedly increasing their redundancy, diversity and resilience to future disturbances. The results presented here though have possibly been influenced by the type of traits chosen for this study and the aspects of plant functionality that they represent, since functional diversity metrics are likely sensitive to this choice (Lavorel *et al.*, 2008).

### 3.4.3 Effects of disturbance on the CWM of plant traits

The CWM of the plant traits considered here was an important indicator of community response to management modification, with a significant shift in mean trait composition with increasing disturbance (question ii), from species with relatively soft and easily decomposable leaves to thick-leaved species that produce recalcitrant leaf litter. This facet of community composition, which reflects the dominant type of organisms in biological communities (Vandewalle *et al.*, 2010), can be particularly useful to understand the response of ecosystems to changes in conditions following management intervention.

As would be expected, plant vegetative height showed a strong response to increasing disturbance (Fig. 3.3a), with frequent mowing regimes preventing the establishment of trees and shrubs, destroying top canopy cover, allowing for daylight to become available near the ground and excluding woody tissue from deposited plant litter (Westoby, 1998). However, contrary to the expectation previously stated, that extra amount of light penetration and nutrient availability in the absence of tall dominant species did not result in the establishment of exploitative species, but instead in the predominance of taxa at the conservative end of the range encompassed by the LES continuum. That is evidenced by significantly decreasing levels of SLA and leaf N and increasing LDMC and leaf C:N ratio with increasing disturbance (Fig. 3.3), leading to species with relatively soft, nutrient-rich leaves being replaced by those with carbon-rich, recalcitrant, nutrient-poor leaf tissue following management intervention. These findings are contrary to results reported for other types of habitat and management (Garnier *et al.*, 2007; Golodets *et al.*, 2009; Dainese *et al.*, 2015) and have implications for aboveground primary productivity (Garnier *et al.*, 2004; Lavorel *et al.*, 2011; Minden and Kleyer, 2011; Grigulis *et al.*, 2013) and litter decomposition rates (Cornwell *et al.*, 2008; Fortunel *et al.*, 2009; Grigulis *et al.*, 2013), potentially contributing to changes in soil processes and nutrient cycling as tentatively demonstrated below (section 3.4.4).

The differences in mean trait composition between managed herbaceous sites and unmanaged woods reflect marked differences in the taxa (and trait) composition of these two types of vegetation, particularly between the alder carr in Woodwalton (management category 0) and the *Cladium* and *Juncus subnodulosus* fens in Upton (category 3) and the sedge fen in Woodwalton (category 4; CWM results of individual plant communities in Upton and Woodwalton are presented in Chapter 6, but discussed here). The traits of green leaves, associated with diverse strategies for carbon gain and growth, have been shown to



vary widely within and between different phylogenetic groups and to be highly context-dependent (Cornwell *et al.*, 2008). That is evidenced here by the differences in trait composition of the diverse life forms found in the studied communities (Appendix 3). The abundant field layer in the alder carr at Woodwalton (Appendix 1) includes slender grass species, notably *Poa trivialis*, and forbs such as *Urtica dioica*, *Glechoma hederacea*, *Circaea lutetiana*, *Galium aparine* and *Geranium robertianum*. These species are mostly characterised by relatively high SLA and leaf N and low LDMC and leaf C:N ratio (Appendix 3). On the other hand, the *Cladium* and *J. subnodulosus* fens in Upton and the sedge fen in Woodwalton are rich in thick-leaved monocots like *Cladium mariscus*, *Calamagrostis canescens*, *J. subnodulosus* and *Molinia caerulea*, all species with comparatively low SLA and leaf N and high LDMC and leaf C:N ratio (Appendix 3). Therefore, taxa comprising the vegetation of these herb-dominated communities are largely typified by species with conservative economic strategies along the leaf economics spectrum, associated with conservation of resources within well-protected tissue of leaves with extended durability and relatively high dry mass-to-area ratio and low N content. Contrarily, the alder carr site in Woodwalton presents an abundance of species with opposite characteristics, typical of taxa with an exploitative strategy suitable for rapid acquisition of resources (Diaz *et al.*, 2004). Past studies of management intervention in fen systems have demonstrated that different plant groups respond differently to disturbance and hydrological conditions (Vinther and Hald, 2000; Kołos and Banaszuk, 2013), with fast-growing generalist species persisting through regular long-term mowing to produce vegetation resembling a rush community where tall monocotyledons prevail (Kołos and Banaszuk, 2013). In fact, the managed herbaceous communities in Upton and Woodwalton largely showed the prevalence of monocot graminoids over forbs, where the above-mentioned species were particularly prominent (Appendix 1). Despite graminoids (grasses and grass-like monocots) being considered fast-growing species (Bardgett *et al.*, 2008) with relatively high water use efficiency and photosynthetic rates (Fig. 3.3f and see Fig. 2.9 in Appendix 3), they have been shown to have the functional characteristics of taxa that produce slow-decomposing litter (Cornwell *et al.*, 2008), with relatively low SLA and leaf N and high LDMC, conferring high resistance to grazing and disturbance (Vinther and Hald, 2000) and resulting in the rather conservative economic strategy seen for the herb-dominated sites in general. It is also possible that yearly cutting, though regarded here as high management intensity, may still represent relatively low disturbance at an intermediate level of management if compared to, for instance, grassland vegetation subject to the impact of intensive productive

management and grazing (Pakeman *et al.*, 2009; Pakeman and Marriott, 2010; Pakeman, 2011). Evidence from such systems points to increased leaf investments in dry mass tissue (relatively high LDMC) at intermediate grazing levels under reduced land-use intensity compared to intensively managed and abandoned land (Pakeman and Marriott, 2010). Abandonment of management could thus initially favour species with acquisitive strategies to gain height following the arresting of pressure. Moreover, the time of cutting (normally at the end of the growing season in Upton and Woodwalton) may have relatively low impact on growth and hence pose reduced pressure to recruit species with exploitative strategies.

The contrasting result revealed by the unmanaged woodlands, presenting species with broadly exploitative strategies, is probably due to the coexistence of large, long-lived, tall woody plants in the alder carr communities, dominated by *Alnus glutinosa* with *Betula pubescens* and *Fraxinus excelsior* canopies (Appendix 1), with smaller, shorter-lived grasses and herbs with high investment in photosynthesis (high leaf N) and fast growth (high SLA), possibly to exploit gaps in canopy during leaf fall of the deciduous tall species. Short graminoids (*P. trivialis*) and high-canopy trees (*A. glutinosa*) have indeed been shown to have high leaf area leading to fast acquisition of resources and relatively rapid nutrient turnover rates (Diaz and Cabido, 1997). Moreover, woody deciduous species tend to produce fast-decomposing litter compared to woody evergreen species (Cornwell *et al.*, 2008), which were absent from the wooded communities. The only evergreen shrub recorded in the vegetation, *Ilex aquifolium*, was only sparsely present in the woodlands in Upton (Appendix 1). In addition, *A. glutinosa* is particularly known for being a nitrogen-fixing species with relatively high SLA, nutrient-rich and low C:N ratio leaves among woody species (Hagemann and Moroni, 2015), which were confirmed by the trait results presented here (Appendix 3, 2.2b, 2.7b and 2.8b). These results have important implications for the biogeochemical cycles of C and N, since the ease with which organic material can be decomposed is closely linked to substrate quality and the kinds and proportions of organic compounds, which are determined by the botanical make-up of the peat (Rydin and Jeglum, 2013).

#### 3.4.4 Response of ecosystem processes to disturbance and shifts in plant traits

Mean soil C largely increased with increasing disturbance intensity (Fig. 3.4a), following a corresponding shift in mean plant trait composition with intensifying

management (question iii), from relatively easily decomposable, soft, nutrient-rich leaves (exploitative strategy) to recalcitrant, nutrient-poor, high dry mass to area ratio leaves (conservative strategy). Soil C:N ratio, on the other hand, fluctuated along the management gradient and showed mostly no significant differences between unmanaged and managed sites (Fig. 3.4b). Results suggest that changes in the abundance-weighted mean functional composition of plant communities inflicted by management intervention may impact on belowground ecosystem processes. These results also lend some support to the biomass ratio hypothesis in that traits of the dominant species might help to drive ecosystem processes linked to biogeochemical cycling (Grime, 1998; Laughlin, 2011; Lavorel *et al.*, 2011; Grigulis *et al.*, 2013), rendering the variability in plant traits an important component of biodiversity that should not be separated from the environment when assessing ecosystem functioning.

Even though mean soil C responded to changes in disturbance intensity that corresponded to changes in community functional composition as expected, the surprising results of the CWM analysis showed that ecosystem processes responded in the opposite direction of the one initially expected, with the most disturbed habitats (herbaceous communities) generally presenting greater soil C than the unmanaged woodlands. This confirms previous results of the potential effects on biogeochemical cycling of LES traits that reflect the quality of plant material entering the soil (Fortunel *et al.*, 2009; Freschet *et al.*, 2010; Grigulis *et al.*, 2013). However, the moderately managed herb-dominated sites in Upton were an exception in that they showed the lowest mean soil C and N content of all communities (Fig. 3.4). In fact, there were substantial differences in soil nutrient stocks between Upton and Woodwalton, with the latter also presenting more variable soil C and N within its communities. That difference is intriguing considering that the mean CWMs of plant traits did not show consistent differences between the managed herbaceous communities in Upton and Woodwalton. Therefore, differences between the two sites in environmental variables not considered here (e.g., water table height, peat depth) might explain the discrepancy between them. Moreover, the higher variability in Woodwalton may result from a higher diversity of management practices taking place within the site, with mowing rotation periods ranging from yearly to c. 20 years, whereas all the Upton herbaceous communities are under the same cutting regime (7- to 8-year rotation).

Communities dominated by exploitative species (unmanaged woods) were generally associated with poor C and N retention, suggesting faster nutrient turnover, while dominance by conservative species (managed herbaceous sites) correlated with greater

soil C storage and N retention (higher nutrient accumulation rates). Differences in nutrient acquisition strategies among species have implications for leaf litter quality, which has been found to differ consistently across plant functional groups in peatlands (Dorrepaal *et al.*, 2005). Litter quality correlates strongly with rates of decomposition and soil heterotrophic respiration (Cornelissen *et al.*, 2007). The poor-quality leaf litter produced by the monocot plants prevalent in the herbaceous sites (Appendix 1) is possibly relatively rich in recalcitrant polymeric substances like lignin and other phenolic compounds (Cornelissen *et al.*, 2004), likely slowing decomposition due to retardation of microbial activity (Wardle *et al.*, 2004), while potentially enhancing dominance by fungi in the soil biota (Grigulis *et al.*, 2013). Moreover, the C:N ratio of sedge leaves tends to increase after senescing, as the plants withdraw N from the leaves before they wilt, resulting in relatively high C:N ratios of sedge litter (Rydin and Jeglum, 2013). The opposite happens under high-quality litter input, such as the one produced by the fast-growing grasses and forbs found in the wooded communities (Appendix 1), which is probably easily decomposed and can potentially increase rates of nitrification (Laughlin, 2011) and heterotrophic respiration (Cornelissen *et al.*, 2007), promoting nutrient uptake and loss from soil. Indeed, such conditions seem to favour soil microbial communities dominated by bacteria that perform rapid rates of mineralisation and nitrification (Skiba *et al.*, 2011). Moreover, communities dominated by tall plants and with a higher diversity of plant heights along a vertical profile, like the unmanaged woodlands in the studied sites with relatively poor nutrient retention, could promote a greater input of resources and higher diversity of micro-habitats (distinct root architectures and quality) for soil micro-organisms, enhancing microbial biomass N and leading to better nitrate uptake by plants and the soil fauna, resulting in increased N cycling (Grigulis *et al.*, 2013).

### 3.5 Conclusions

In line with previous studies (Lavorel *et al.*, 2008; Vandewalle *et al.*, 2010), the present analyses revealed that changes in univariate CWM in response to management were paralleled by changes in multivariate functional diversity indices and by changes in species diversity. Nevertheless, the impact of disturbance is context-dependent and likely influenced by other environmental variables (Garnier *et al.*, 2007), not necessarily implying a loss of trait diversity. The introduction of disturbance can lead to abiotic filtering, generating communities dominated by rather closely related species with disturbance-

adapted traits (Ding *et al.*, 2012), leading to the exclusion of not only certain species but also trait values (Dainese *et al.*, 2015), as shown here by reduced FD and FRic in disturbed sites compared to unmanaged communities. However, disturbance can also lead to niche differentiation like that seen in the undisturbed woodlands, as demonstrated by increasing FD, FRic and FDiv with increasing disturbance among the managed herbaceous sites. This suggests that abiotic filtering and strong biotic interactions (e.g., limiting similarity) can be captured simultaneously within communities and across a management gradient (see Chapter 5 on community assembly processes), confirming that results are highly dependent on the type of functional diversity metric used and most likely on the type of ecosystem being assessed. It is assumed that there are general commonalities of the effects of disturbance regime on plants (Garnier *et al.*, 2007), making these results applicable to other types of management (grazing, ploughing, etc.) and habitat.

Collectively, the results support the relevance of the leaf economics spectrum to soil processes, as expected from theoretical concepts (de Deyn *et al.*, 2008) and recent empirical results (Garnier *et al.*, 2007; Grigulis *et al.*, 2013). As shown here, communities with more exploitative plant strategies may result in greater biomass production, but potentially at the cost of poor carbon and nitrogen retention. Therefore, management practices in Woodwalton in particular seem to be promoting not only enhanced floristic diversity, which is paramount for the intrinsic character of protected fens (Wheeler, 1980a), but enhanced functional diversity and the provision of ecosystem services linked to carbon sequestration and nitrogen retention in soil, through their potential effects on plant and soil microbial community composition, satisfying some of the main goals of the Great Fen Project (Gauci, 2008). Incorporating soil microbial parameters into the type of analyses presented here may thus significantly improve our ability to explain belowground ecosystem processes, as demonstrated elsewhere (Grigulis *et al.*, 2013).

In summary, functional components can be used as indicators for biodiversity conservation in the context of land use change and complement, rather than replace, existing biodiversity monitoring, since the evaluation of the effects of management intervention on biodiversity is facilitated and is expected to positively influence conservation management practices (Vandewalle *et al.*, 2010).

## Chapter 4

# Determining the interactions between environmental variables, plant functional traits and ecosystem processes in lowland fens

### 4.1 Introduction

Determining the response of ecosystem processes and functioning to changing environmental conditions in UK peatlands, as well as modelling their interactions with other ecosystem components (e.g., plant functional traits) are becoming increasingly important, particularly for informing conservation policies for ecosystem management (Mainstone *et al.*, 2016). As discussed in Chapter 1 (section 1.2), peatlands provide numerous benefits to society, including soil carbon storage and nutrient cycling (Means *et al.*, 2016). Carbon sequestration and storage are key ecosystem services associated with peatlands, since they directly influence the global carbon cycle and consequently regulate atmospheric carbon dioxide concentrations (Gauci, 2008; Heimann and Reichstein, 2008; Billett *et al.*, 2010; Alonso *et al.*, 2012; Neubauer, 2014). Lowland fens account for between a quarter and a third of the total soil carbon stored within peatlands in the UK (see Chapter 1, section 1.2 for soil carbon statistics in Britain), mostly in deep and shallow peaty soils (Natural England, 2010). Yet, around 70% of peatlands in the UK show signs of degradation (Natural England, 2010), as they are subjected to a variety of anthropogenic pressures, such as diffuse source pollution and habitat modifications (Mainstone *et al.*, 2016).

Although fluxes and stores of carbon in peatlands and fenlands have been reliably measured (Gorham, 1991; Billett *et al.*, 2004; Janssens *et al.*, 2005; Worrall *et al.*, 2009; Billett *et al.*, 2010; Natural England, 2010), the extent to which shifts in environmental variables and plant functional traits in lowland fens affect carbon storage is still poorly understood. Abiotic factors are typically considered the primary drivers of ecosystem processes in wet environments (Keddy, 2010; Mitsch and Gosselink, 2015). Much has been attributed, for instance, to water table variation (Bellisario *et al.*, 1998; Updegraff *et al.*, 2001), which affects anaerobic conditions by regulating the thickness of the oxic zone (Morris *et al.*, 2011) and the activity of phenol oxidases (Freeman *et al.*, 2004). The latter are thought to play a central role in the breakdown of complex organic matter (Bardgett *et al.*, 2008). Soil processes such as nutrient cycling (Goll *et al.*, 2012) and the N isotopic

composition ( $\delta^{15}\text{N}$  in ‰) of soil organic matter, reflecting soil fertility and N availability to plants (He *et al.*, 2009; Jeffers *et al.*, 2015), are also crucial in controlling soil C stocks. Nitrogen deposition in soils, for example, can contribute to C uptake in N-limited ecosystems by regulating soil fertility and plant growth (Torn *et al.*, 2009). Moreover, anthropogenic influences through land use change and management practices have also been recognised as primary contributors to changes in soil carbon dynamics in various ecosystems (Vitousek *et al.*, 1997). Land management modifies community diversity and plant functional composition (Minden *et al.*, 2016) and consequently contributes to variations in stocks and fluxes of carbon and nitrogen in ecosystems (de Deyn *et al.*, 2008). For instance, removing vascular plant biomass can alter transpiration rates and advective transport of dissolved nutrients (Eppinga *et al.*, 2009), contributing to changes in stocks and fluxes of soil nutrients and water table height (Chapin III *et al.*, 2000).

Despite the evidence for the primary role of environmental variables, research over the past two decades has recognised the equally important links between plant functional traits and ecosystem processes and functioning (Cardinale *et al.*, 2012; Naeem *et al.*, 2012). The conceptual framework developed by Lavorel and Garnier (2002) emphasises the role of plant functional traits in predicting changes in ecosystem processes, highlighting the importance of both response and effect traits in ecosystem functioning. Since then, there has been growing evidence that trait diversity allows organisms and biological communities not only to respond to environmental conditions (Minden and Kleyer, 2011; Donovan *et al.*, 2014), but to regulate ecosystem processes (Chapin III *et al.*, 2000; de Bello *et al.*, 2010). Vascular plants are indeed well known for modifying the environment towards better conditions for themselves (Eppinga *et al.*, 2009), with recent research suggesting that changing vegetation and functional trait composition can alter carbon dynamics and exchange rates in peatlands (Ward *et al.*, 2007; Ward *et al.*, 2009). These studies concluded that changes in vegetation community structure has marked effects on carbon uptake and short-term  $\text{CO}_2$  fluxes, possibly due to changes in photosynthetic rates and the soil physical environment (Bardgett *et al.*, 2008). Individual functional traits have accordingly been shown to be key elements in understanding ecosystem processes and services (de Deyn *et al.*, 2008; Lavorel *et al.*, 2011), especially considering changing environmental conditions (Fortunel *et al.*, 2009). Studies accounting for the mediating effects of functional traits have thus been useful in predicting the effects of environmental change on ecosystems (Dray and Legendre, 2008; Soudzilovskaia *et al.*, 2013), as well as in quantifying the magnitude and direction of these changes on function (Suding *et al.*, 2008). Therefore, there is an

impending urgency to model the impact different ecosystem components (biotic and abiotic) have on ecosystem processes in fens (e.g., plant litter production, aboveground biomass), which will ultimately affect rates of delivery of vital ecosystem services (e.g., soil C storage).

#### 4.1.1 *Links between ecosystem processes and functioning*

The turnover of organic matter through the production and decomposition of plant litter is a major process in the biogeochemical cycles of C and other nutrients (Cornelissen *et al.*, 1999), since it determines the rate at which these nutrients are mineralised in the soil (Fortunel *et al.*, 2009). Standing litter has been hypothesised to either immobilise C and N (Lavorel and Grigulis, 2012) or to increase soil C sequestration via decomposition (de Deyn *et al.*, 2008). The outcome is dependent on the quality of litter produced, such as leaf physical toughness (Quétier *et al.*, 2007), leaf palatability (Cornelissen *et al.*, 1999) or growth-form related chemistry (Dorrepaal *et al.*, 2005; Cornelissen *et al.*, 2007). These traits can lead to either easily digestible or highly recalcitrant litter and thus affect heterotrophic respiration (Bardgett *et al.*, 2008). Litter production and decomposition rates are also responsive to abiotic factors like soil moisture and nutrient status (Aerts, 1997; Ågren *et al.*, 2001; Liski *et al.*, 2003).

While most of the carbon stored in wetlands is locked away in soils (Gorham, 1991; Bridgham *et al.*, 2006; Lawrence and Zedler, 2013), aboveground biomass (AGB) is an important temporary pool of fixed carbon (Means *et al.*, 2016) and a crucial element affecting CO<sub>2</sub> fluxes (Shaver *et al.*, 1998), making plant AGB a major component of ecosystem functioning in wet environments (Minden and Kleyer, 2011). AGB can be thus considered an ecosystem process because it is linked to the provision of a number of ecosystem services like climate regulation and soil erosion protection (Mace *et al.*, 2012). AGB responds directly to the effects of vegetation functional composition (Lou *et al.*, 2016) and to environmental variables, such as water table height (Shi *et al.*, 2015) and soil nutrient availability (Chapin III and Shaver, 1996). AGB is also influenced by the intensity of anthropogenic disturbance (Minden *et al.*, 2016), which likely has a direct effect on the partition between live and dead AGB. Moreover, AGB has been found to regulate soil organic matter accumulation and decomposition rates in wetland environments (Mueller *et al.*, 2016), therefore exerting an indirect effect on biogeochemical cycles.



Soil N has a myriad of effects in the cycles of carbon and other nutrients (Bardgett *et al.*, 2008), from regulating soil fertility and microbial activity (Hu *et al.*, 2001) to affecting plant growth and carbon transfer to soil (Diaz *et al.*, 1993), as well as causing changes in vegetation composition through indirect effects on N-fixing bacteria (van der Heijden *et al.*, 2008). More carbon will be sequestered in soils if plant productivity increases without a corresponding increase in decomposition rates (Torn *et al.*, 2009), which can be caused by the inhibition of lignin-degrading phenol oxidase (Carreiro *et al.*, 2000). However, increased soil N can also have a positive effect on decomposition by enhancing cellulase activity of microbial communities (Carreiro *et al.*, 2000), thus increasing soil respiration rates. Soil N stock has been found to respond to plant litter quality (Lavorel and Grigulis, 2012) and to water and climatic gradients in wet habitats (Eppinga *et al.*, 2010), which drive changes in mineralisation rates (Belyea and Clymo, 2001).

#### *4.1.2 Links between plant functional traits and ecosystem processes*

Once the main ecosystem processes thought to control ecosystem functioning have been determined, it is necessary to identify the key characteristics and mechanisms by which vascular plants affect these processes (de Bello *et al.*, 2010). Two independent dimensions of plant function thought to affect ecosystems have been recognised: a plant size axis and a leaf economics axis. Plant vegetative height, representing the size axis, has long been recognised as a key component of plant strategy (Grime, 1977; Westoby *et al.*, 2002; Diaz *et al.*, 2004). It is closely linked to species' light capture abilities (Westoby *et al.*, 2002) and metabolic rates (Enquist *et al.*, 1998). Plant height represents a trade-off in carbon investment between support and transport tissues and photosynthetic tissues (Westoby, 1998), thus influencing species' effect on carbon uptake and drawdown. Moreover, taller plants retain greater amounts of carbon and other nutrients and tend to produce more litter (Appendix 5), while shorter vegetation is associated with higher water conservation given low transpiration flows (Schwinning and Ehleringer, 2001). Plant height has been found to respond strongly to soil water and nutrient variables (Minden and Kleyer, 2011; Lavorel and Grigulis, 2012), and to have a positive effect on aboveground biomass and litter production (Lavorel and Grigulis, 2012). Therefore, it is reasonable to expect tall and short vegetation to have different effects on biogeochemical cycles.

As discussed in Chapter 3, the leaf economics spectrum, or LES (Wright *et al.*, 2004), represents a gradient in species' strategies, from quick to slow return on investments of

nutrients and dry mass in leaves. Species with quick returns are characterised by high leaf nutrient concentrations, high photosynthetic and respiration rates, short leaf lifetimes and low dry-mass per unit area. On the other hand, species with low leaf nutrient concentrations, low rates of photosynthesis and respiration, long leaf lifetimes and high dry-mass per unit area are at the slow end of the gradient. These contrasting strategies, referred to as exploitative and conservative by Lavorel and Grigulis (2012) respectively, of growth and resource-use have implications for nutrient and energy flows through ecosystems (Diaz *et al.*, 2004; Suding *et al.*, 2008), and have recently been linked to biogeochemical cycles in empirical studies (Lavorel and Grigulis, 2012; Donovan *et al.*, 2014). This can be attributed to their differing impacts on carbon uptake and leaf litter quality affecting the soil biota and hence decomposition rates (Wardle *et al.*, 2004). For instance, leaf chemical traits (e.g., leaf C and N concentrations) are likely related to litter nitrogen concentration or lignin:nitrogen ratio (Cornelissen *et al.*, 2004) and can be useful in understanding leaf litter quality affecting soil processes (Fortunel *et al.*, 2009). In addition, isotopic signatures of leaf tissue, such as leaf  $\delta^{13}\text{C}$  (‰), can be useful in quantifying plant-soil carbon fluxes (Staddon, 2004) and as a proxy for species-level water use efficiency and photosynthetic rate (Farquhar *et al.*, 1989; Lai *et al.*, 2004; Perez-Harguindeguy *et al.*, 2013). The water use efficiency of plants plays an important role in determining the exchange of water between terrestrial ecosystems and the atmosphere (Seibt *et al.*, 2008). According to Lavorel and Grigulis (2012), the LES should therefore scale-up to trade-offs between ecosystem properties with fast and slow turnover rates. Communities dominated by species characterised by quick return rates should have relatively high productivity, high leaf digestibility and consequently high decomposition rates and N availability and turnover. On the other end of the scale, communities with high litter accumulation due to slow decomposition and turnover rates will be dominated by species at the slow return end of the LES and tend to have high soil C accumulation (Lavorel and Grigulis, 2012).

The biomass ratio hypothesis postulates that the traits of individual species combine with their biomass proportion in the communities to determine the impacts of plant communities on ecosystem processes (Grime, 1998; Díaz and Cabido, 2001). Community-weighted means (CWMs; Chapter 2, section 2.4.3) of plant traits should therefore provide an ideal measure to capture such effects, since they represent the average trait value per unit of biomass within a community (Violle *et al.*, 2007). CWMs of

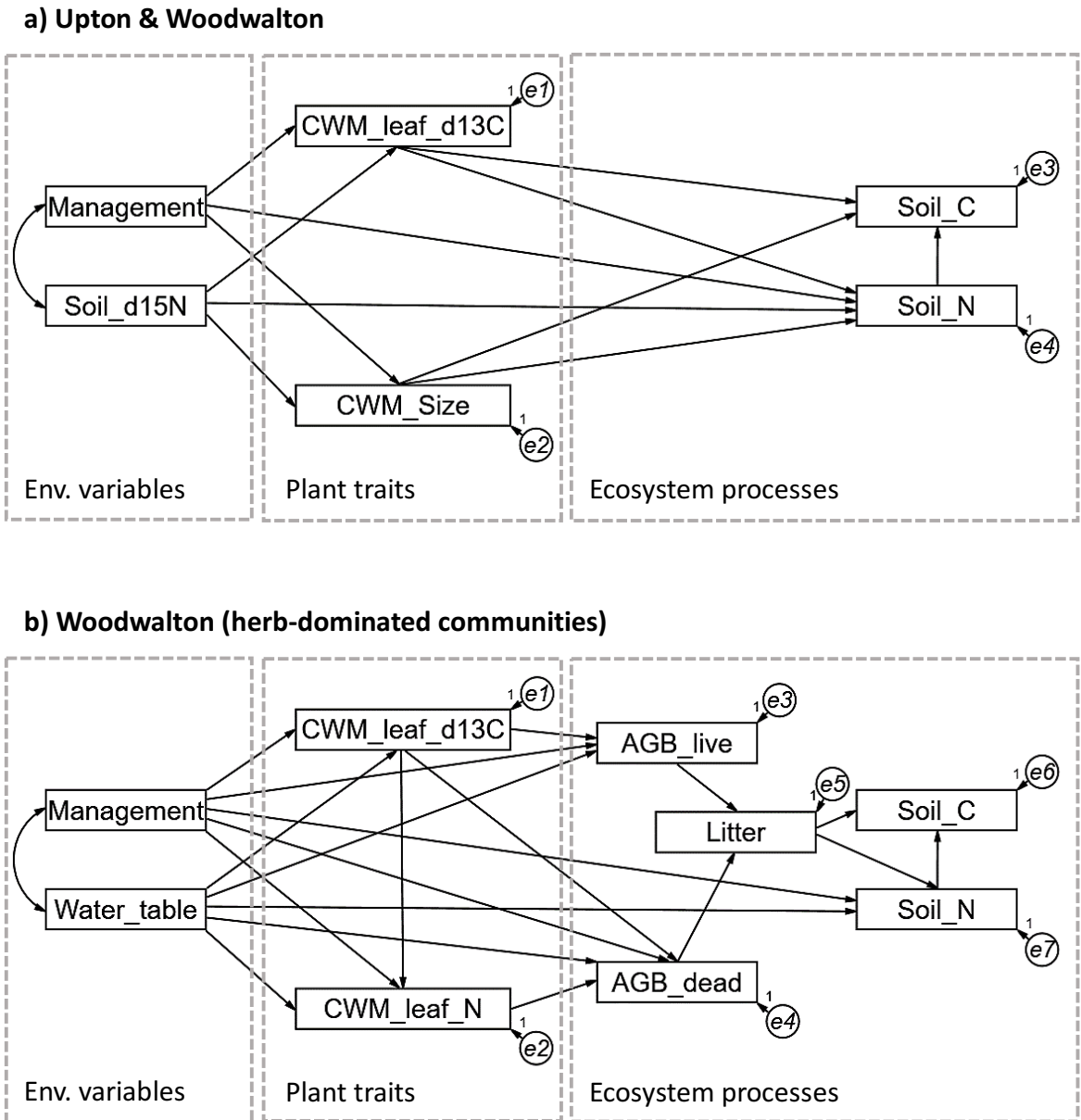
plant traits are used here to link environmental variables with ecosystem processes in hypothesised path models.

#### 4.1.3 Hypothesised models linking environmental variables, plant functional traits and ecosystem processes

Based on the evidence of the effects of environmental variables and plant functional traits on ecosystem processes and the biogeochemical cycles of C and other nutrients presented thus far, the main aim of this chapter is to quantify the size and direction of direct and indirect effects that key biotic and abiotic components have on ecosystem processes in lowland fens (Upton and Woodwalton). To that end, I constructed hypothesised models of interacting ecosystem variables (Fig. 4.1) using path analysis and structural equation modelling (SEM), which can be defined as confirmatory statistical methods allowing the *a priori* knowledge of the ecosystem to be tested against observed field data (Maruyama, 1998). Two distinct path diagrams were developed owing to different amount of data availability across replicate plots, since data on water table height, AGB and annual litter production rates were only available for Woodwalton (see Table 4.1 in Methods section below).

Three levels of ecosystem components were recognised: environmental variables, plant functional traits and ecosystem processes (Fig. 4.1). Environmental parameters were modelled as independent variables and hypothesised as having direct effects on plant traits and ecosystem processes (Fig. 4.1). Management intensity (Management) and mean water table height relative to each sampling plot (Water\_table) were used as the main environmental variables. Since water table data were not available for Upton, soil  $\delta^{15}\text{N}$  (Soil\_d15N) was used instead as a proxy variable reflecting soil fertility.

Given the tentative link between leaf traits and soil processes demonstrated in Chapter 3, functional traits were modelled as exerting direct effects on ecosystem processes (Fig. 4.1). The community weighted means of plant vegetative height (CWM\_Size) and of leaf N (CWM\_leaf\_N) and  $\delta^{13}\text{C}$  (CWM\_leaf\_d13C) were chosen as plant traits characterising the two independent dimensions of plant strategy related to the size axis and the leaf economics spectrum, respectively (Grime, 2001; Westoby *et al.*, 2002; Wright *et al.*, 2004 and see section 4.1.2 above). Only two of those trait variables were used at a time to reduce model complexity.



**Fig. 4.1:** Hypothesised path models between environmental variables, plant functional traits and ecosystem processes. Single-headed arrows denote path coefficients, double-headed arrows show correlations between independent variables. Residual error variables ( $e_x$ ) represent unexplained variance (see text). For an overview of the variables and their abbreviations see Table 4.1.

As stated previously, stocks of soil C in managed peatlands are of particular interest, given their prominence in climate change policy and mitigation strategies (Billett *et al.*, 2010; Bateman *et al.*, 2013; Means *et al.*, 2016). I expect soil C stock to respond to the environmental variables and plant traits mentioned above, as well as to other ecosystem processes like plant litter annual production rate, live and dead aboveground biomass (AGB) and soil N (Fig. 4.1). These are key ecosystem processes directly affecting the C cycle

(Torn *et al.*, 2009 and see section 4.1.1 above) and are particularly susceptible to change under human influence (Vitousek *et al.*, 1997).

In Model a (Fig. 4.1a), I used data collected from all 136 plots in Upton and Woodwalton and included management and soil fertility as environmental variables, plant height ( $\log_{10}$ -transformed) and leaf  $\delta^{13}\text{C}$  as plant traits and soil C (Soil\_C) and N (Soil\_N) stock as the ecosystem processes of interest. In Model b (Fig. 4.1b), which comprised the 51 herb-dominated plots in Woodwalton, live and dead aboveground biomass (AGB\_live and AGB\_dead) and litter annual production rate (Litter) were added as ecosystem processes. Plant size was removed from the model and replaced with leaf N content, given the low variability in plant height within herbaceous communities (Chapter 3). Water table height replaced soil fertility as one of the environmental variables.

All dependent variables are shown with an associated error term (*ex*), representing the proportion of their variance not explained by their predictor variables (see section 4.2.1 below). Here, positive effects mean an increase in the explanatory variable is accompanied by an increase in the dependent variable, whereas a negative effect indicates the dependent variable responds negatively to an increase in the explanatory variable.

#### 4.1.3-a Upton and Woodwalton (Model a)

Soil  $\delta^{15}\text{N}$  was used in *Model a* as a proxy variable reflecting N availability to plants (soil fertility). As discussed in Chapter 2 (section 2.4.2), sites that have experienced increased N availability may promote vegetation with relatively high foliar  $\delta^{15}\text{N}$  due to increased availability of  $^{15}\text{N}$ -enriched nitrogen from soil organic matter in relation to mycorrhizal fungi (Craine *et al.*, 2009a). As plant material decay into soil organic matter, the  $^{15}\text{N}$ -enrichment of plant material following high N availability is reflected in the  $^{15}\text{N}$  signature of soil (Amundson *et al.*, 2003). Additionally, the inclusion of leaf  $\delta^{13}\text{C}$  in *Model a* was meant to represent species' productivity through their water use efficiency and photosynthetic rates (see section 2.4.2 in Chapter 2).

The first links to be considered are between environmental variables and plant traits (Fig. 4.1a). Following the results presented in Chapter 3, increasing management should result in communities dominated by low-statured, fast-growing species that produce recalcitrant leaf litter (see section 3.4.3 in Chapter 3), which will consequently lead to low decomposition rates and high soil C retention. Therefore, I expected the management variable to have a negative effect on plant vegetative height and a positive

effect on leaf  $\delta^{13}\text{C}$  (expectation **I**), since higher management intensities were shown to exclude trees and shrubs and favour fast-growing graminoids with relatively high water use efficiency and photosynthetic rates (see Fig. 3.3a and f in Chapter 3). Moreover, soil  $\delta^{15}\text{N}$  should be associated with higher plant sizes and higher leaf  $\delta^{13}\text{C}$  (positive effects) due to increased N availability to plants leading to enhanced productivity and C acquisition (**II**).

I also hypothesised a direct link between the environmental variables and soil N stock, with management intensity expected to have a positive effect on soil N retention (**III**), given the recalcitrant nature of leaf litter in the highly-managed communities promoting the build-up of soil nutrients (see Chapter 3). Moreover, as stated above soil  $\delta^{15}\text{N}$  is also expected to reflect positively on the total amount of N in the soil organic matter that is available to plants (**IV**).

Considering the modulating effects of plant traits on ecosystem processes, increased plant size was hypothesised to lead to reduced soil C and N stocks (negative effects; **V**) through higher input of relatively fast-decomposing plant litter from trees and shrubs (see Chapter 3), leading to higher nutrient loss from soils. Leaf  $\delta^{13}\text{C}$  was hypothesised to be positively related to soil C and N (**VI**), due to the enhanced signal of  $\delta^{13}\text{C}$  of decomposing leaf litter of highly managed communities (Fig. 3.3f, Chapter 3) that are associated with high soil C and N retention (Chapter 3). Finally, soil N was expected to be positively related to soil C (**VII**) through stoichiometric relationships between them (Cleveland and Liptzin, 2007).

#### 4.1.3-b Woodwalton (herb-dominated communities; Model b)

Data on water table height, live and dead aboveground biomass (AGB) and litter annual production rate were available for the herb-dominated communities in Woodwalton, and were therefore added to *Model b* (Fig. 4.1b). For the purpose of path analyses, data on plant litter annual production rate originating from the two traps in each community (see section 2.2.4 in Chapter 2) were treated separately and assigned to the plots belonging to the half of the transect where the traps were placed. While water table height replaced soil  $\delta^{15}\text{N}$  as an environmental variable, leaf N replaced plant height due to the negligible variability in plant size among the herbaceous communities (see Chapter 3).

I expected management intensity to be negatively related to leaf N and positively to leaf  $\delta^{13}\text{C}$  (**VIII**), since results presented in Chapter 3 (Fig. 3.3d and f) showed that increasing management intensity in herbaceous fens tends to favour species with low leaf

nutrient content but high carbon isotopic signature. Despite the difficulty in predicting the effects that changing water regime will have on the vegetation, given the considerable variation wetland species show in their response to waterlogging (Wheeler and Shaw, 1995), I hypothesised increasing water table height to adversely affect plant productivity, given reduced levels of ecosystem respiration (Updegraff *et al.*, 2001) and a decrease in the release of soil nutrients by mineralisation (Mitsch and Gosselink, 2015). Therefore, higher water table should negatively impact on leaf N and leaf  $\delta^{13}\text{C}$  (IX) due to reduced soil fertility through reduced mineralisation rates and the tendency of decreasing  $\delta^{13}\text{C}$  values in plant tissue under wetter conditions (Robinson *et al.*, 2000).

Considering the direct effects of environmental variables on ecosystem processes, the positive effect of management on soil N stock expected in *Model a* (III) was again hypothesised. Moreover, water table height should have a negative impact on soil N (X) due to reduced microbial mineralisation of plant litter. Given the positive effect of management on plant biomass recently reported by Minden *et al.* (2016), I expected increasing management intensity to increase live AGB and, since cuttings are routinely removed after mowing, reduce dead AGB (XI). On the other hand, given the negative effect of depleted oxic zone on net ecosystem productivity (Bellisario *et al.*, 1998) and hence plant growth and vitality, water table height should negatively impact on live AGB and positively on dead AGB (XII).

Considering the effects of plant traits, I hypothesised a negative relationship between leaf  $\delta^{13}\text{C}$  and leaf N (XIII). The opposite response to disturbance of these two leaf traits (Fig. 3.3d and f, Chapter 3) suggests that graminoid species tend to produce N-impooverished but  $^{13}\text{C}$ -enriched leaves under disturbance. In addition, there should be a positive association between leaf  $\delta^{13}\text{C}$  and live AGB (XIV), based on the positive relationship between highly managed sites with relatively high proportions of live biomass (Appendix 6) and communities colonised by species showing high water use efficiency (Fig. 3.3f, Chapter 3). Consequently, leaf  $\delta^{13}\text{C}$  was expected to be negatively associated with dead AGB (XV). On the other hand, leaf N should scale positively with dead AGB (XVI), given the characteristically nitrogen-poor leaves found in the most managed communities (Fig. 3.3d, Chapter 3) with the lowest proportion of dead AGB (Appendix 6). Moreover, live and dead AGB were hypothesised to result in lower and higher litter input to the soil (XVII), while litter production rates were expected to positively affect soil C and N stocks (XVIII). The final link in the model was again the positive relationship between soil N and C stocks (VII).

## 4.2 Methods

Table 4.1 lists all the environmental variables, plant functional traits and ecosystem processes used in the hypothesised path diagrams, as well as the number of plots with data available for each variable. See Chapter 2 for data collection and sample processing methods.

### 4.2.1 Path analysis and structural equation modelling (SEM)

Structural equation modelling (SEM) has been shown to be a powerful statistical tool to analyse ecological networks with multiple variables (Grace and Pugsek, 1997; Minden and Kleyer, 2011; Lavorel and Grigulis, 2012). It is particularly useful for partitioning direct and indirect relationships between observed variables of hypothesised models through the use of path analysis (Sokal and Rohlf, 2012). Path analysis uses correlation coefficients and regression analyses to model complex relationships among multiple dependent (endogenous) and independent (exogenous) variables (Schumacker and Lomax, 2010). It therefore provides an opportunity to use observed field data to test hypotheses about causal interactions between ecosystem components like environmental variables, plant functional traits and ecosystem processes that affect ecosystem functioning (Shipley, 2000). Moreover, these complex interactions can be illustrated in path diagrams (Fig. 4.1), where cause-and-effect relationships are depicted by straight, single-headed arrows denoting path coefficients (standardised partial regression coefficients, or standardised beta weights) between cause and effect variables (Sokal and Rohlf, 2012). Path coefficients are standardised to provide a comparable metric between all variables, and indicate that for every unit increase in standard deviation of the predictor variable there is an  $x$  change (either increase or decrease depending on whether it is a positive or negative sign) in units of standard deviation of the response variable. Following Lavorel and Grigulis (2012), path coefficients  $> 0.8$  are interpreted as exerting large effects,  $\approx 0.5$  indicate moderate effects and  $< 0.2$  suggest small effects. Direct pathways between two variables are the value of path coefficients, while indirect pathways involve intermediary variables (Krzanowski and Marriott, 1995). Curved, double-headed arrows indicate unanalysed correlations between exogenous variables. The endogenous variables in path diagrams are indicated as completely determined, since all the factors contributing to their total variation are drawn



**Table 4.1:** List of variables used in the hypothesised path diagrams, showing abbreviations used in the models and the number of plots with data available.

	Name in model	Unit	No. of plots with data available	Sites where data available
<b>Environmental Variables</b>				
Management intensity	Management	Categorical (0 to 4)	136	Upton & Woodwalton
Mean water table height	Water_table	m	68	Woodwalton
Soil $\delta^{15}$ N	Soil_d15N	per mil (‰)	136	Upton & Woodwalton
<b>Plant traits (CWMs)</b>				
Plant vegetative height	CWM_Size	cm	136	Upton & Woodwalton
Leaf N content	CWM_leaf_N	per mil (‰)	136	Upton & Woodwalton
Leaf $\delta^{13}$ C	CWM_leaf_d13C	per mil (‰)	136	Upton & Woodwalton
<b>Ecosystem processes</b>				
Soil C storage	Soil_C	g cm <sup>-2</sup>	136	Upton & Woodwalton
Soil N storage	Soil_N	g cm <sup>-2</sup>	136	Upton & Woodwalton
Plant litter annual production rate	Litter	t ha <sup>-1</sup> a <sup>-1</sup>	68	Woodwalton
Aboveground biomass (live)	AGB_live	t ha <sup>-1</sup>	51	Woodwalton (herb-dominated communities)
Aboveground biomass (dead)	AGB_dead	t ha <sup>-1</sup>	51	Woodwalton (herb-dominated communities)

in, including unknown (residual) factors represented by the predictor error ( $e$ ) terms (Sokal and Rohlf, 2012). This method therefore produces path coefficients between exogenous and endogenous variables, and shows the amount of variance of each endogenous variable explained by its predictor variables ( $r^2$ ) and residuals ( $e$ ).

Path analysis, as implemented by SEM software, calculates all the paths simultaneously and produces overall goodness-of-fit measures for the model (Grace and Pugsek, 1998), allowing significance tests to be performed on both the overall structure of the model (all the relationships between variables) and on specific parameters, such as correlations and regression weights between two variables (Grace, 2006). Path analysis starts with an initial conceptual model based on *a priori* knowledge of the functioning of the system, which is then tested against the covariance matrix of the observed data (Maruyama, 1998). The model is then evaluated by a chi-square ( $\chi^2$ ) test of fit, in which a significant  $p$ -value indicates that the covariance structure of the data differs significantly from that of the hypothesised model, meaning the model does not adequately summarise the relationships in the data (Byrne, 2010). On the other hand, a non-significant  $p$ -value denotes that the model is a credible representation of the data, indicating the two covariance structures do not differ significantly. A good fit of the hypothesised model to the data will also result in a low  $\chi^2/df$  ratio, and should ideally be  $< 2$  (Byrne, 2010). The NFI (normed fit index) and CFI (comparative fit index) are other measures commonly used to evaluate model fit, and indicate the proportion of improvement of the overall fit of the model relative to the independence model (where all correlations among variables are

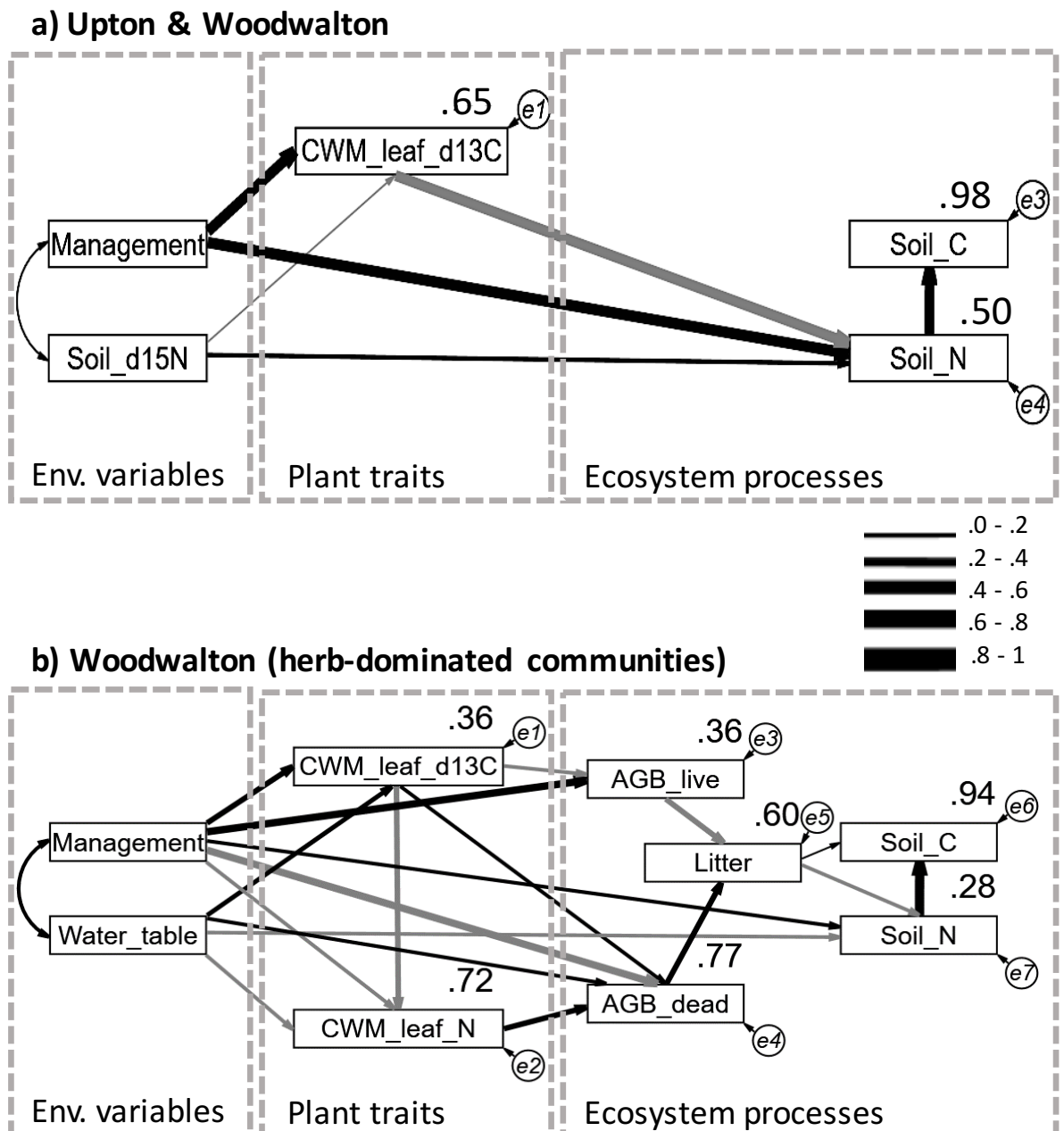
zero). Values close to 1 are generally considered to indicate a good fit, and should ideally be  $> 0.9$  (Byrne, 2010). The RMSEA (root mean square error of approximation) index evaluates the extent to which a model fails to fit the data per degree of freedom, and tends to favour more complex models (Browne and Cudeck, 1993). It is considered to indicate a poor fit if it is  $> 0.1$ , but should ideally be  $< 0.05$  (Byrne, 2010). Therefore, good fitting models have relatively low  $\chi^2$ ,  $p > 0.05$ ,  $\chi^2/df < 2$ , NFI and CFI  $> 0.9$  and RMSEA  $< 0.05$  (or at least  $< 0.1$ ).

Once ecologically meaningful models of the system in question have been identified, they can be tested against the aforementioned goodness-of-fit indices to determine their statistical feasibility. Here, I adopted a similar approach to recent studies (Minden and Kleyer, 2011; Lavorel and Grigulis, 2012) in adapting the hypothetical models to improve their overall fit, while maintaining their theoretical credibility and ecological relevance. Therefore, non-significant path coefficients ( $p > 0.05$ ) were excluded from the hypothetical (full) models, unless their inclusion contributed to explanatory power and did not significantly affect model quality. Similarly, path coefficients were added to improve model fit where needed, as long as the addition was theoretically justified. Akaike's Information Criterion (AIC) was used to compare the full and reduced models, with the model presenting the lowest AIC value considered as producing the best overall fit to the data structure. The functioning of the ecosystem can then be discussed by examining the strength and direction of the interactions between variables in the reduced models. Path analysis and SEM were implemented using IBM SPSS Amos 23.0.0 (Amos Development Corporation, Spring House, PA, US).

## 4.3 Results

### 4.3.1 Upton and Woodwalton (Model a)

The hypothesised full model was not well supported by the observed data ( $\chi^2 = 23.776$ ,  $df = 3$ ,  $p < 0.001$ ,  $\chi^2/df = 7.925$ , NFI = 0.975, CFI = 0.977, RMSEA = 0.226, AIC = 71.776). However, removing the  $\log_{10}$ -transformed plant size variable from the model and the non-significant ( $p > 0.05$ ) path coefficient between leaf  $\delta^{13}\text{C}$  and soil C (Table 4.2a) significantly improved model fit ( $\chi^2 = 4.334$ ,  $df = 3$ ,  $p = 0.228$ ,  $\chi^2/df = 1.445$ , NFI = 0.994, CFI



**Fig. 4.2:** Final models derived from hypothesised models in Fig. 4.1. Path coefficients between variables are standardised partial regression coefficients of direct effects. Arrow widths are proportional to the standardised path coefficient (see legend). Black arrows indicate positive associations, while grey ones denote negative associations. Numbers on the top right-hand-side of dependent variables show the proportion of their variances explained by the model ( $r^2$ ). See Table 4.1 for abbreviations and Table 4.2 for the values of path coefficients, with their respective  $p$  values.

= 0.998, RMSEA = 0.057, AIC = 38.334). This reduced model was adopted as the final model explaining soil C and N storage in Upton and Woodwalton (Fig. 4.2a), with all the standardised partial regression coefficients (path coefficients) retained in the model being

significant at  $p < 0.05$  (Table 4.2a). However, acceptance of the null model should be viewed with caution since other untested models may be at least as good.

Management intensity and soil  $\delta^{15}\text{N}$ , the two environmental variables, were only weakly correlated ( $r = 0.106$ ). Both environmental variables explained about two-thirds of the total variability in leaf  $\delta^{13}\text{C}$  (Fig. 4.2a). Between them, management intensity showed higher overall effects than soil nitrogen availability (soil  $\delta^{15}\text{N}$ ), suggesting it was the main explanatory independent variable in the model. Management showed a strong positive effect on leaf  $\delta^{13}\text{C}$ , confirming previous results (Chapter 3) that communities under higher disturbance were more likely to recruit species with increased water use efficiency. Soil  $\delta^{15}\text{N}$  presented a negative and weak effect on leaf  $\delta^{13}\text{C}$ , suggesting higher soil fertility was associated with species with relatively low water use efficiency.

Both environmental variables had a significant direct effect on soil N storage. Adding the direct negative effect of leaf  $\delta^{13}\text{C}$ , they explained half of the total variance in soil N (Fig. 4.2a). Management again showed the strongest (positive) effect, while soil  $\delta^{15}\text{N}$  only had a weak to moderate positive effect, indicating that sites with higher nitrogen storage are associated with higher management intensity.

The only variable to present a significant relationship with soil C storage was soil N, which explained nearly all of the total variability in soil C storage (Fig. 4.2a). Increasing soil N directly led to a significant increase in the soil C pool through the indirect effects of both environmental variables (management intensity and soil fertility) and one functional trait (leaf  $\delta^{13}\text{C}$ ).

#### 4.3.2 Woodwalton (herb-dominated communities; Model b)

*Model b* was well supported by the field data ( $\chi^2 = 23.650$ ,  $df = 16$ ,  $p = 0.097$ ,  $\chi^2/df = 1.478$ , NFI = 0.936, CFI = 0.977, RMSEA = 0.098, AIC = 99.650). Removing the non-significant path coefficient between water table height and live aboveground biomass (AGB\_live) slightly improved its fit to the data ( $\chi^2 = 23.822$ ,  $df = 17$ ,  $p = 0.124$ ,  $\chi^2/df = 1.401$ , NFI = 0.936, CFI = 0.979, RMSEA = 0.090, AIC = 97.822). Five non-significant coefficients ( $p > 0.05$ ; underlined numbers in Table 4.2b) were retained in the final model (Fig. 4.2b) as their inclusion improved model fit and helped explain a higher proportion of the total variability in the model (Fig. 4.2b). Three of them were still significant at the 0.1 level (Table 4.2b). As mentioned above though, accepting the null model does not necessarily mean it

**Table 4.2:** Standardised partial regression coefficients of direct effects and their respective  $p$  values, based on the critical ratio of each regression weight, for each of the two hypothesised models and their respective final models. Underlined coefficients are non-significant at  $p > 0.05$ , but were retained in the final model for reasons of model fit (see text). See Table 4.1 for abbreviations.

Explanatory variable	Response variable	Hypothesised model		Final model	
		Coefficient	$p$ value	Coefficient	$p$ value
<b>a) Upton &amp; Woodwalton</b>					
Management	CWM_leaf_d13C	0.807	<0.001	0.807	<0.001
Management	CWM_Size	-0.799	<0.001	-	-
Management	Soil_N	0.549	<0.001	0.849	<0.001
Soil_d15N	CWM_leaf_d13C	-0.114	0.028	-0.114	0.028
Soil_d15N	CWM_Size	-0.159	<0.001	-	-
Soil_d15N	Soil_N	0.310	<0.001	0.338	<0.001
CWM_leaf_d13C	Soil_N	-0.810	<0.001	-0.886	<0.001
CWM_leaf_d13C	Soil_C	0.004	0.828	-	-
CWM_Size	Soil_N	-0.305	0.006	-	-
CWM_Size	Soil_C	0.009	0.665	-	-
Soil_N	Soil_C	0.991	<0.001	0.988	<0.001
<b>b) Woodwalton (herb-dominated communities)</b>					
Management	CWM_leaf_d13C	0.479	<0.001	0.479	<0.001
Management	CWM_leaf_N	-0.351	<0.001	-0.351	<0.001
Management	AGB_live	0.696	<0.001	0.712	<0.001
Management	AGB_dead	-0.760	<0.001	-0.759	<0.001
Management	Soil_N	0.399	0.014	0.399	0.014
Water_table	CWM_leaf_d13C	0.223	0.068	<u>0.223</u>	0.068
Water_table	CWM_leaf_N	-0.266	0.001	-0.266	0.001
Water_table	AGB_live	0.071	0.640	-	-
Water_table	AGB_dead	0.327	0.002	0.320	0.002
Water_table	Soil_N	-0.232	0.073	<u>-0.232</u>	0.074
CWM_leaf_d13C	CWM_leaf_N	-0.440	<0.001	-0.440	<0.001
CWM_leaf_d13C	AGB_live	-0.309	0.070	<u>-0.289</u>	0.081
CWM_leaf_d13C	AGB_dead	0.292	0.022	0.295	0.021
CWM_leaf_N	AGB_dead	0.487	0.003	0.488	0.003
AGB_live	Litter	-0.469	<0.001	-0.470	<0.001
AGB_dead	Litter	0.434	<0.001	0.430	<0.001
Litter	Soil_N	-0.212	0.164	<u>-0.212</u>	0.164
Litter	Soil_C	0.058	0.122	<u>0.058</u>	0.123
Soil_N	Soil_C	0.994	<0.001	0.994	<0.001

represents the best depiction of the system, since other models not tested here may be at least as good.

Management intensity and water table height were only moderately correlated ( $r = 0.363$ ), perhaps due to the relatively homogeneous water level within the herb-dominated plots. Overall, management showed higher effect sizes on plant traits (leaf  $\delta^{13}\text{C}$  and leaf N) and ecosystem processes (live and dead AGB and soil N) than water table height. Management and water table had positive and negative effects on leaf  $\delta^{13}\text{C}$  and leaf N respectively, though the effect of water table on leaf  $\delta^{13}\text{C}$  was insignificant. In addition, leaf  $\delta^{13}\text{C}$  had a moderately negative impact on leaf N concentration. Their combined effects explained almost three-quarters of the variability in leaf N, but only slightly over a third of the variability in leaf  $\delta^{13}\text{C}$  (Fig. 4.2b). Essentially, increasing disturbance and water table height lead to species with relatively higher water use efficiency and lower leaf N content.

Management had strong direct positive and negative effects on live and dead AGB respectively, indicating the effect of biomass removal through management practices, with no dead biomass left standing on highly managed sites. Water table height showed a weak to moderate positive effect on dead AGB and a non-significant effect on live AGB. Live AGB was not significantly regulated by leaf  $\delta^{13}\text{C}$ , and dead AGB was only weakly to moderately affected by leaf  $\delta^{13}\text{C}$  and leaf N. Overall, the direct and indirect effects of environmental variables and plant traits explained over a third of the variance in live AGB, and over three-quarters in dead AGB (Fig. 4.2b).

About 60% of the variability in annual litter production rate was regulated by the amount of aboveground biomass present (Fig. 4.2b), with live and dead AGB showing moderate negative and positive effects on litter production respectively (i.e., sites with higher dead AGB also produced higher amounts of litter on an annual basis). Litter production had no significant direct impact on either soil N and soil C storage. Management intensity was the only variable to have a significant effect on soil N, albeit moderate, explaining less than a third of its total variance (Fig. 4.2b). Soil N was once again the only variable to be significantly and positively related to soil C, explaining more than 90% of its total variability (Fig. 4.2b).

#### **4.4 Discussion**

Quantifying the effects of environmental variables and plant traits on ecosystem processes in lowland fens is a crucial first step in understanding ecosystem functioning, particularly to better inform conservation policies aimed at increasing biodiversity and reducing carbon loss from long-term deposits. This type of study should thus be of

particular interest to conservation projects that aim to prevent the loss of carbon from long-term soil stores, such as the Great Fen Project in the Fenland region of East Anglia, UK (Gauci, 2008).

I hypothesised that plant traits associated with the leaf economics spectrum and plant size were directly regulated by environmental parameters, while mediating the effects of these same parameters on ecosystem processes. Though results have generally met my expectations, most of the variability seen in ecosystem processes were explained by direct effects of environmental variables rather than plant traits. Management intensity accounted for the majority of the variability seen in ecosystem processes, especially aboveground biomass and soil N. These results thus suggest that plant traits, such as vegetative height and leaf nutrient composition, only play a relatively minor role in the regulation of ecosystem processes in this type of ecosystem, where human intervention seems to be the major cause of change. This confirms some previous results showing that abiotic factors can sometimes be sufficient in explaining most of the changes in ecosystem processes (Díaz *et al.*, 2007). Moreover, the mapping of some common leaf traits (e.g., SLA, LDMC, leaf N concentration) to function may be affected by low variation in leaf life span (LLS) between co-occurring species within a community, which seems to occur in many herbaceous and woody deciduous communities (Funk and Cornwell, 2013). LLS is a key component of leaf trait variability within the concept of the leaf economics spectrum (LES), since it influences variation among species in resource acquisition (e.g., fast vs. slow carbon gain). The strength of the LES relationship with ecosystem function may thus depend on the variation of LLS present (not measured here), and be weakened if the range of variation is not enough under similar habitat conditions (Funk and Cornwell, 2013).

Despite that, both models confirmed my hypotheses of plant function strongly responding to changes in environmental conditions and anthropogenic disturbance, with the intensity of management explaining the largest share of plant trait variability. Moreover, by responding to management practices, plant trait diversity has, to some extent, contributed to explaining the variability in ecosystem processes, particularly leaf nutrient and isotope traits that influenced soil N and aboveground biomass. Although model fit improved after excluding the plant trait variables from the models (*Model a*:  $\chi^2 = 1.211$ ,  $df = 2$ ,  $p = 0.546$ ,  $\chi^2/df = 0.605$ , NFI = 0.998, CFI = 1, RMSEA = 0, AIC = 25.211; *Model b*:  $\chi^2 = 16.143$ ,  $df = 10$ ,  $p = 0.096$ ,  $\chi^2/df = 1.614$ , NFI = 0.939, CFI = 0.974, RMSEA = 0.111, AIC = 66.143), the fraction of total explained variation in soil N in *Model a* ( $r^2 = 0.22$ ) and in

AGB live ( $r^2 = 0.31$ ), AGB dead ( $r^2 = 0.70$ ) and litter annual production rate ( $r^2 = 0.59$ ) in *Model b* decreased (see Fig. 4.2 for comparisons).

As expected, soil C storage was shown to be very responsive to other ecosystem components, both directly and indirectly, confirming changing environmental conditions and management practices may have a cascading effect on the ability of lowland fens to store carbon.

It can be argued that goodness-of-fit measures accepting multivariate statistical tests of complex hypothesised models do not necessarily provide strong support for a given model, especially considering that other untested models may be at least as good. As stated in section 4.3, they only show that the hypothesised models of the system cannot be rejected. However, the use of path analysis and structural equation modelling were shown to be useful multivariate tools to broadly analyse complex relationships between different ecosystem components, since they separate and quantify direct and indirect effects of ecological variables acting simultaneously on ecosystem functioning.

#### 4.4.1 Upton and Woodwalton (*Model a*)

Although some of the path coefficients between plant height and other ecosystem variables were significantly different from zero (Table 4.2), plant size did not seem to be a generally important variable in the functioning of the system in *Model a*. That result was unexpected, especially given the range of plant height variation between woody and herbaceous fens included in the model. As expected though, increasing management intensity favoured those with higher leaf  $\delta^{13}\text{C}$ , partially meeting expectation I. This finding is consistent with previous studies that show carbon fixed by low-statured species is often derived from recycled  $\text{CO}_2$  from soil respiration with a higher  $^{13}\text{C}/^{12}\text{C}$  ratio (Farquhar *et al.*, 1989), resulting in relatively high  $\delta^{13}\text{C}$  in leaf tissue. Moreover, management may be favouring species with higher water use efficiency and hence higher leaf  $\delta^{13}\text{C}$ . However, contrary to my expectation (II), soil fertility, represented by N availability to plants in the form of soil  $\delta^{15}\text{N}$ , did not significantly impact on plant vegetative height. This may be due to a greater proportion of net primary production in the woodlands being allocated to belowground organs as nitrogen availability increases (Thomas and Mead, 1992), which eventually provides a competitive advantage to tree species by enhancing their ability to access soil nutrient and water. Another explanation is that *Sphagnum* peat may sequester mineral nutrients from the acrotelm and reduce mineralisation rates (Eppinga *et al.*, 2009),



reducing the N that is available for vascular plant growth. Also contrary to my expectation, increased N availability in the soil resulted in reduced leaf  $\delta^{13}\text{C}$  (II), albeit with a small effect size (Table 4.2a), perhaps due to reduced C storage in leaves under high N levels (Farrer *et al.*, 2013). Isotopic composition of plant tissues in nutrient-poor ecosystems can reflect differences in acquisition strategies by different species (Gavazov *et al.*, 2016). The change in C storage of some wetland species susceptible to increases in soil N may be a result of reduced belowground transfer of C during the growing season (Farrer *et al.*, 2013), as well as a decrease in their ability to offset increased uptake of N with increased photosynthesis and growth (Farrer *et al.*, 2013).

The strong positive effect of management on soil N stock was in accordance with my expectation (III) of higher disturbance rates resulting in communities with recalcitrant leaf litter promoting the build-up of soil nutrients (see Chapter 3). Graminoid species growing in the mown sites are characterised by shallow roots that are well adapted for N acquisition from slow mineralisation of organic matter on the soil surface (Mládková *et al.*, 2015). This can potentially lead to increased net N mineralisation, which has been shown to be positively and strongly related to total soil N (Parfitt *et al.*, 2005). Moreover, mowing has been found to mitigate N losses through its effect on vegetation types and soil properties, by reducing soil moisture content and increasing soil temperature (Lu *et al.*, 2015).

The weak to moderate positive effect of soil fertility on soil N stock was also expected (IV) due to higher microbial activity and hence N mineralisation rates under increased fertility (Bardgett *et al.*, 2008). Contrary to my expectations (V and VI), plant height and leaf  $\delta^{13}\text{C}$  did not significantly regulate soil C stock. The only significant effect of plant traits on ecosystem processes was the strong negative effect of leaf  $\delta^{13}\text{C}$  on soil N stock, also contrary to my expectation (VI). Plant traits may affect soil nutrient properties by regulating leaf litter quality. Leaf  $\delta^{13}\text{C}$  signals may reflect altered C:N allocation to carboxylation and leaf structure (Seibt *et al.*, 2008), leading to reduced leaf N concentration under increased  $\delta^{13}\text{C}$  and thus affecting litter decomposability and N mineralisation. Finally, following my expectation (VII) soil N stock was strongly positively related to soil C stock. The biogeochemical cycles of C and N are tightly coupled. The limiting effect of nitrogen usually present in many ecosystems causes carbon uptake and storage to be strongly regulated by the nitrogen cycle (Vitousek and Howarth, 1991), leading plant communities to match any changes in the total N capital of the system to parallel changes in total carbon through fluctuations in photosynthetic rates (Asner *et al.*, 1997). In other

words, high N requirements during photosynthesis means that increases in primary production are dependent on the availability of N to fuel increased photosynthetic C acquisition. In addition, this strong relationship might probably reflect the stoichiometrically balanced nature of the soil microbial biomass C:N ratio (Cleveland and Liptzin, 2007).

#### 4.4.2 Woodwalton (herb-dominated communities; Model b)

As in *Model a* and according to my expectations, leaf  $\delta^{13}\text{C}$  responded positively to management intensity (VIII), while leaf N scaled negatively with disturbance (VIII). As discussed in Chapter 3, this is due to the predominance of sedges and rushes in the most managed herbaceous communities, with relatively low leaf N when compared to other life forms (Appendix 3, 1g). Moreover, there is evidence of the species-specific responses to disturbance in the use of C and N reserves for leaf regrowth (de Visser *et al.*, 1997). According to my expectation (IX), leaf N was negatively regulated by water table height, albeit weakly, probably indicating reduced mineralisation rates and N availability to plants under wetter conditions in the substratum. However, the insignificant effect of water table height on leaf  $\delta^{13}\text{C}$  (Table 4.2b) contradicted my expectation of a significant negative effect between the two variables (IX). As pointed out previously, management regime seems to be the main variable controlling plant traits in this ecosystem, overriding any effects of varying water table on plant function.

Management intensity showed the same positive effect, albeit weaker, on soil N stock as in *Model a* (III), whereas the negative effect of water table height on soil N, while expected (X), was not significant (Table 4.2b). The strong positive and negative effects of management on live and dead AGB respectively met my expectation (XI). The main reason for this result is the prevalence of dead over live AGB in the unmanaged glades and *Phragmites* fen communities (Appendix 6). The height of the water table did not have any significant impact on live AGB (Table 4.2b), though it was moderately and positively associated with dead AGB, partly meeting one of my expectations (XII). This may be an effect of a reduced oxic zone impacting plant growth and productivity (Bellisario *et al.*, 1998), but it is most likely due to the higher water table height measured in the *Phragmites* fen community, which is one of the lesser managed herbaceous sites and with the highest rates of dead AGB accumulation (Appendix 6).

Most of my expectations regarding the effects of plant traits on ecosystem processes were not met, possibly because of the choice of traits used in the models (see section 4.5 below) or, as discussed above, the potentially low variability in leaf life span within herbaceous and woody deciduous communities (Funk and Cornwell, 2013). However, the expected negative relationship between leaf  $\delta^{13}\text{C}$  and leaf N (**XIII**) might be reflecting an increased net influx of carbohydrates relative to growth-related influx of N in expanding cells of leaves (de Visser *et al.*, 1997), possibly due to higher C assimilation following increased photosynthetic rates under higher irradiance experienced by the herb-dominated communities (Farquhar *et al.*, 1989). The positive association between leaf  $\delta^{13}\text{C}$  and live AGB (**XIV**) was insignificant (Table 4.2b). In addition, contrary to expectation **XV** but in accordance with expectation **XVI**, leaf  $\delta^{13}\text{C}$  and leaf N were positively related to dead AGB. The unmanaged glades, where most of the aboveground biomass is dead (Appendix 6), have shown relatively strong positive signals of leaf N concentration (Fig. 3.3d, Chapter 3), probably reflecting its proximity to the alder carr where a nitrogen-fixing species (*A. glutinosa*), with high leaf N content (Appendix 3, 2.7b), prevails. Moreover, monocot species like *Calamagrostis canescens* and *Phragmites australis*, which revealed relatively high leaf  $\delta^{13}\text{C}$  values (Appendix 3, 2.9e), tended to be prominent in communities with high dead AGB, such as the *Phragmites* fen and the unmanaged glades (Appendices 1 and 6). In addition, past studies have also found a negative relationship between isotope discrimination in leaves and aboveground dry mass (Wright *et al.*, 1988), though the reasons for that still seem to be unclear.

Live and dead AGB contributed negatively and positively to litter input rates respectively, as would be expected of senescing standing biomass contributing larger amounts of litter than recently cut vegetation (**XVII**). The amount of litter input, on the other hand, did not significantly affect soil C and N stocks (Table 4.2b) as expected (**XVIII**), perhaps due to the relatively low amount of litter produced by the herbaceous communities (Appendix 5). Finally, as seen in *Model a* and for the reasons discussed above, soil N was strongly and positively related to soil C (**VII**).

## 4.5 Conclusions

The models presented here provide a plausible representation of the interactions among ecosystem components in the lowland fens studied. However, they are not intended as full descriptions of ecosystem functioning, since potentially important

feedbacks from biogeochemical cycles and the biotic component on environmental variables were not depicted. In fact, changing plant functional composition and life forms have been reported to stimulate a lowering of the water table by increasing the rate of evapotranspiration and affect the amount of precipitation that reaches the surface (Rietkerk *et al.*, 2004; Eppinga *et al.*, 2009). Therefore, the relative abundances of *Sphagnum* and vascular plant species must be crucial in the regulation of the water table depth in fens, which has been repeatedly shown to be very important for overall carbon balance in wet habitats (Funk *et al.*, 1994; Shaver *et al.*, 1998; Freeman *et al.*, 2004; Bardgett *et al.*, 2008).

Despite the tentative links between leaf traits and soil processes established in Chapter 3, the plant traits used in these analyses displayed relatively low effect sizes on ecosystem processes when considered in conjunction with environmental variables. That may be due to the fact this study only considered leaf chemical traits and aboveground organs of plant species. Given the importance of belowground organs of wetland species in adapting to waterlogged and nutrient poor conditions (Keddy, 2010), quantifying the role of belowground traits on ecosystem processes, and how they respond to changing environmental factors, would be a promising development on the current study. It is possible that this was a limitation of the analyses presented here, since aboveground and belowground linkages are now recognised to be crucial in understanding ecosystem dynamics (Bardgett and Wardle, 2010). Further studies should therefore attempt to investigate not only the role of belowground organs, but the interactions between above- and belowground traits, abiotic factors and soil microbial communities (de Vries *et al.*, 2012). Furthermore, establishing the role of belowground communities and processes is vital in understanding the effects of climate change on carbon dynamics in ecosystems (Bardgett *et al.*, 2008).

While these limitations are acknowledged, I believe they do not alter the main conclusions: ecosystem processes respond strongly to environmental variables and anthropogenic disturbance, and to a certain extent to plant functional traits. This type of study is particularly pertinent today given the growing interest in managing carbon in the context of ecosystem services as a viable climate mitigation strategy. In fact, the value of ecosystem services, such as soil carbon storage for example, has been increasingly recognised in the last two decades (Costanza *et al.*, 1997; Costanza *et al.*, 2011), making the present study a valuable tool in informing conservation policies. It is believed that peatlands in the UK continue to act as a long-term sink for carbon (Billett *et al.*, 2010), but

continuous monitoring of the potential source-sink status of peatlands is key in accompanying the analyses presented here, in order to understand the drivers of carbon loss and uptake in peatlands. In addition, peatlands are under constantly changing conditions imposed by human intervention, which makes the conclusions reached here particularly helpful in anticipating what can cause long-term deposits of carbon to continue to act as a carbon sink, or to shift to a source of carbon in the future.

## Chapter 5

### Unravelling neutral- and niche-based community assembly processes acting along a successional and management gradient in lowland fens

#### 5.1 Introduction

The proposal in the 1970s (Diamond, 1975) that processes driving species coexistence within ecological communities could be described by a set of ‘assembly rules’ has led to forty years of an ongoing and sometimes contentious debate (Connor and Simberloff, 1979; Ricklefs, 1987; Wilson, 1994; Weiher and Keddy, 1995b; Hubbell, 2001; Wilson, 2007; Ricklefs, 2008; Brooker *et al.*, 2009). Community assembly rules are said to lead to non-random co-occurrence patterns in species composition (Gotelli and McCabe, 2002), caused by ecological processes acting on the regional species pool (Keddy, 1992; Davis *et al.*, 2005) and resulting in greater than expected divergence or convergence of species functional traits. These processes, commonly referred to as niche-based processes (Weiher *et al.*, 2011), are thought to impose constraints on species coexistence (Weiher and Keddy, 1999) and can potentially be used to predict community structure (Weiher and Keddy, 1995b). However, there has been contradictory evidence for the existence of non-random community processes over the past three decades (Gotelli and McCabe, 2002; Götzenberger *et al.*, 2012), resulting in persistent questions about the ecological processes that drive community assembly. The main argument surrounding this debate can be distilled down to the question of whether niche-based (deterministic) or neutral (stochastic) processes provide better explanations for species coexistence, and therefore community assembly (Callaway, 1997; Gaston and Chown, 2005; Weiher *et al.*, 2011; Fridley, 2013).

Arguments supporting niche-based, deterministic processes assume that species presence and abundances are determined by their ecological niche breadth and adaptability of their functional traits (Clements, 1916; Hardin, 1960; MacArthur and Levins, 1967; Zobel, 1997). The hypothesis of limiting similarity asserts that species’ niche breadth can predict whether they occupy or invade empty niche space (MacArthur and Levins, 1967). Coexisting species should possess differing resource use strategies and be sufficiently functionally dissimilar to allow stable coexistence along functional niche axes.

Interspecific niche differentiation would result in a greater divergence of traits and biotic strategies than expected under a random assembly, and enable a diverse set of species to exploit the same resource pool without interfering with each other's abundances. Alternatively, the hypothesis of habitat filtering predicts a convergence of morphological traits and species strategies in functional niche space due to common traits adapted to the local physical and chemical settings (Ordoñez *et al.*, 2009), with species functions responding primarily to a set of filters imposed by environmental (Sommer *et al.*, 2014) and climatic constraints (Diaz *et al.*, 1998). Ultimately, a community is composed of species from the regional pool and possesses the optimal combination of trait values to survive through these filters (Zobel, 1997). As the environment becomes more favourable and the restrictions on species are reduced, a more variable mixture of species should be able to coexist via niche differentiation (Villegger *et al.*, 2008). Thus, niche assembly focuses on stabilising mechanisms, such as niche partitioning, and abiotic filters regulating species recruitment.

The early individualistic approach of Gleason (1926), on the other hand, argued that community patterns depended solely on species' individual migration behaviour and environmental requirements, irrespective of associational affiliations and biotic constraints. More recently, the wide-ranging neutral theory of Hubbell (2001) contended that communities are assembled via trait-neutral, stochastic factors like species' arrival sequence and their dispersal ability. Neutral assembly theory (Hubbell, 2001) suggests that equalising mechanisms, such as random dispersal, ecological drift and stochastic local extinction, lead to a per capita ecological equivalence among individuals and species, and allow for coexistence in time and space (Chesson, 2000). The diversity of an assemblage thus results from stochastic ecological and evolutionary processes acting on both local and regional scales (Gaston and Chown, 2005), with species dispersal abilities and arrival sequence taking a central role in structuring ecological communities (Robinson and Dickerson, 1987). Therefore, demographic stochastic models should enable us to predict species relative abundances under random dispersal and speciation. Neutral theory has provided an alternative view to niche-based models (Weiher *et al.*, 2011) and has broadened the field with a wide range of relevant hypotheses to community assembly (Alonso *et al.*, 2006).

Current approaches to the study of community assembly processes involve the use of species functional traits and null models to assemble communities via neutral (random) processes (Pakeman, 2011; Liu *et al.*, 2013; Sommer *et al.*, 2014; Chalmandrier *et al.*, 2017)

to disentangle the role of stochastic and deterministic processes acting on observed patterns of species functional diversity and composition. Trait-neutral processes may be inferred by organising species randomly in functional space using traits that are perceived as important, with non-random distributions revealing filtering processes that shape community functional composition in a characteristic way (Grime, 2006). The presence of stochastic influences on niche-based assembly (Weiher *et al.*, 2011) and the simultaneous interaction of opposing assembly processes (Mason *et al.*, 2011) make such studies valuable tools in defining the functional patterns of field plant communities.

Wetlands may provide an excellent model system for this type of investigation, since physical and chemical factors guide and constrain biological communities and ecological processes that occur within them (Mitsch and Gosselink, 2015). Moreover, they experience changing levels of nutrient supply and waterlogged conditions throughout the year (Wheeler, 1980a). It is believed that constantly changing conditions determine the ecological attributes of fen vegetation (Keddy, 2010), imposing controls on their composition and leading to a common set of organismal functional traits. Nonetheless, fens generally reveal high levels of biodiversity (Wheeler and Shaw, 1995) and are hence suitable habitats for community ecology studies, particularly given the multitude of environmental and anthropogenic factors that act on the range of plant communities present.

Protected fens in the UK are commonly subjected to diverse types and levels of management (Wheeler and Shaw, 1995). The effects of management on community assembly processes in wetland habitats have seldom featured in the literature (but see Weiher and Keddy, 1995a; Pakeman, 2011 and Pakeman *et al.*, 2011), despite the fact that an understanding of community processes can be useful in the management of natural and semi-natural communities (Morin, 2011). For instance, different mowing regimes have been shown to have positive and negative effects on species richness in different fen vegetation types (Wheeler and Shaw, 1995). Similarly, vegetative functional traits in grassland communities also seem to respond strongly to mowing treatments (Mason *et al.*, 2011), with trait divergence (limiting similarity) and convergence (habitat filtering) said to alternate along disturbance intensity gradients (Laliberté *et al.*, 2013). Nevertheless, questions remain as to the effects of management on species trait convergence and divergence. For instance, would increasing levels of disturbance limit aboveground competition (and thus trait divergence) and lead to stronger trait convergence among species?



The importance of vegetation management in preventing the process of replacement of herbaceous fen by fen carr is well known (Wheeler and Shaw, 1995), but the relative importance of neutral and niche processes during succession is poorly understood (Schleicher *et al.*, 2011). It is thought that species tolerance to stress and their competitive abilities will shift from early to late stages of succession (Schleicher *et al.*, 2011). For instance, environmental stress at early stages of succession may lead to a convergence of stress tolerance traits (vegetative height, leaf nutritional content) that are adapted to cope with this set of conditions (Weiher and Keddy, 1995b). Such a scenario is likely to result in strong habitat filtering patterns seen in the functional composition of pioneer plant communities. Conversely, competition among species becomes stronger as succession progresses and denser canopies develop (Weiher and Keddy, 1999). This tends to lead to limiting similarity patterns with communities showing divergent trait composition associated with growth and resource use strategy (Stubbs and Wilson, 2004), such as tall versus short canopy, large versus small leaves. Such conditions are more likely to occur at small spatial scales, like sampling plots measured at the cm scale (Holdaway and Sparrow, 2006; Weiher *et al.*, 2011).

How environmental stress, management disturbance and biological competition shape community assembly during succession are important questions. Recent research suggests that questions of interest should focus on whether stochastic and deterministic processes alternate across gradients of changing environmental conditions, or if they operate concurrently within communities and successional stages (Sutherland *et al.*, 2013). Current consensus indicates that neutral and niche processes may operate simultaneously in the assembly of plant communities (Fukami *et al.*, 2005; Leibold and McPeck, 2006; Kembel, 2009; Vergnon *et al.*, 2009). Therefore, comparing observed functional diversity patterns with random expectations should allow for the evaluation of the relative contribution of trait-driven versus trait-neutral assembly processes, and of the simultaneous interactions between them.

In order to address these questions, I use orthogonal functional trait axes of vascular plant species (see Table 2.4 in section 2.4.2 in Chapter 2) and null models to examine whether observed functional diversity patterns of managed and unmanaged herbaceous and woodland lowland fen communities significantly depart from random expectations to resemble niche-driven (limiting similarity and habitat filtering) processes. Trait convergence and divergence denote that the functional diversity of an assemblage will be respectively smaller and greater than the corresponding diversity of a random

assembly. I use Petchey and Gaston's (2002) functional diversity (FD) metric in multi and single functional trait space to determine the trait diversity and variability of both observed and simulated communities. Firstly, I consider the three independent dimensions of plant resource use strategy described in Chapter 2 (section 2.4.2), namely the size, leaf and nutrient axis of plant function. These axes are considered separately (univariate analysis) and simultaneously (multivariate analysis). Secondly, I employ species clustering methods to categorise the field sampling plots into successional stages, equivalent to a hypothetical hydroseral sequence. The six resulting successional stages are placed on a wetter-to-drier scale, varying from seasonally submerged herbaceous fen vegetation to relatively drier fen carr, dominated by woodland and shrub communities. The effects of the successional gradient on the relative importance of neutral and niche processes are determined with an index of variance (*IV*) that compares the observed and expected FDs. Thirdly, I overlay the different levels of management intensity (Chapter 2, section 2.4.1) on the derived successional stages to investigate their effects across herbaceous and woodland communities. Finally, I compute community-weighted means (CWMs; Chapter 2, section 2.4.3) of the traits and trait axes used here to determine the mean functional composition of each successional stage.

Considering that the early herbaceous stages of succession currently experience management intervention (see Table 5.1 in the Methods section below), I expect results to show the following observed functional diversity patterns: **(I)** convergence (habitat filtering) in traits related to productivity (height and leaf size and nutrient traits) during the initial stages of succession (herbaceous fens) as a direct result of management practices and the trait-convergence effect disturbance stress may induce (Weiher and Keddy, 1995b); **(II)** divergence (limiting similarity) in traits at the more advanced stages of succession as denser canopies develop (Weiher and Keddy, 1999), since species in the unmanaged woodlands should be under higher niche differentiation to compete for resources (e.g., tall versus short canopy, high SLA tree leaves versus high LDMC graminoid leaves; see Chapter 3); **(III)** convergence, divergence or randomness in the leaf and nutrient single axis results, due to the range of plant growth and resource use strategies found in both woody and herbaceous communities (Westoby *et al.*, 2002). Moreover, the CWMs of the successional stages should reveal similar patterns to the ones presented in Chapter 3 as a result of management, with herbaceous stages displaying relatively low SLA and leaf N but high leaf  $\delta^{13}\text{C}$  when compared to the wooded stages **(IV)**.

The key questions here are: 1) which type of assembly processes are most important in shaping the functional composition of herbaceous and woody fenland plant communities? and 2) how do the different community assembly processes behave over successional and management gradients?

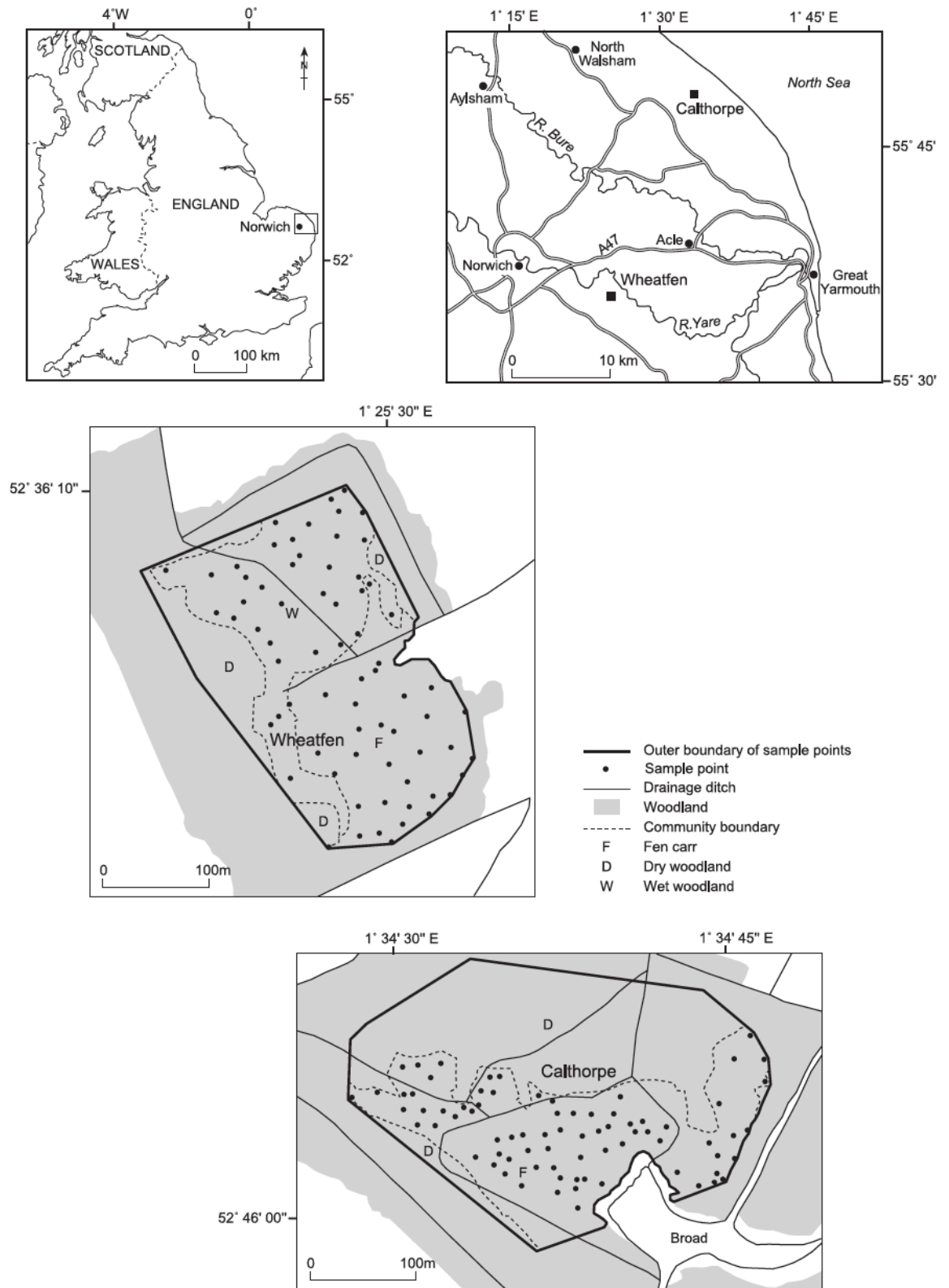
## 5.2 Methods

The 136 plots from Upton and Woodwalton were added to 76 vegetation plots from Calthorpe Broad, Norfolk and 72 from Wheatfen, Norfolk from a previous study (Fig. 5.1; for details of the sampling design at these two sites see Binney *et al.*, 2005 and Waller *et al.*, 2005). A total of 284 surveyed plots were thus considered for these analyses. Vegetation composition at Calthorpe and Wheatfen was determined in the summer of 2001 using similar methods to the ones described in Chapter 2 (section 2.2.1). A total of 178 vascular plant species were present across the four fen sites, of which 150 were encountered during the surveys. A pool of 65 species with functional trait measurements were used for data analysis, including the 64 species encountered in Upton and Woodwalton (section 2.2.2, Chapter 2) and *Frangula alnus*, a species encountered in Calthorpe but not in Upton and Woodwalton (Appendix 1).

Differences between plant species in the way they obtain and process resources can have large effects on species composition of ecosystems (Diaz *et al.*, 2004). Orthogonal trait axes are thought to maximise the ability to understand community assembly processes due to these differences, since they provide more accurate discrimination of species in functional trait space (Laughlin, 2014). Therefore, for these analyses, I used the three independent functional trait axes described in Chapter 2 (section 2.4.2).

### 5.2.1 Null models

Observed FD values of the three trait axes were compared to corresponding values of random assemblies generated using a null model approach. For each field plot, the random simulations generated null distributions by randomly selecting, without replacement, species from the pool of 65 species, irrespective of their position in trait space. The null model thus considered that all species (and all trait values) had an equal probability of occurring throughout the study area. A total of 999 simulations were performed on each plot, with the species richness of each simulated plot kept the same as



**Fig. 5.1:** Location of Calthorpe and Wheatfen and the sampling plots within them. Data from the plots in the dry woodland (D) were not used in this study. Extracted from Waller *et al.* (2005).

in the observed data. The size axis was  $\log_{10}$ -transformed prior to analysis and all trait axes were standardised to mean zero and unit standard deviation. Plots with fewer than four species encountered were dropped from the simulations, leaving 276 plots across the four sites. Simulations were performed using functions written in R 3.2.4 (R Development Core Team, 2016).

### 5.2.2 Successional stages and management intensity

Sampling plots were classified into successional stages based on community species composition and were placed on a wetter-to-drier scale following species clustering methods. Counts of the 150 species encountered were converted into relative abundances per site (site profiles) using the chord transformation (Euclidean distance computed on site vectors normalised to length 1). This type of 'double' transformation allows the use of standard linear methods of analysis with species data, and preserves the asymmetrical distances among sites (Legendre and Gallagher, 2001; Borcard *et al.*, 2011). UPGMA (unweighted pair-group method using arithmetic averages) clustering (Legendre and Legendre, 1998) was used as the clustering method since it produced the highest Pearson correlation coefficient between the Euclidean and the cophenetic distances (0.89), and the lowest Gower distance (695.7). Plots with negative silhouette widths – a measure of the degree of membership of a plot to its cluster (Borcard *et al.*, 2011) – were excluded from all subsequent analysis, as well as clusters with no discernible ecological meaning. Care was taken to keep the integrity of the field communities within the clusters, and any plot from a field community that dropped out into another cluster was excluded. That left 205 plots across the four sites, which were used in all subsequent analyses. Cluster analysis was performed using functions in the *vegan* package version 2.4.2 (Oksanen *et al.*, 2017) in R 3.2.4 (R Development Core Team, 2016).

Six successional stages were recognised from the clustering and are from here on referred to as reedswamp, mixed sedge, *Molinia*-sedge, fen carr, wet woods and oak-ash woods (Table 5.1). The first three stages on the hydrosere sequence comprised herb fen communities dominated by tall monocotyledons (grasses, sedges and rushes). The reedswamp in Upton forms the 'reedswamp' stage (wettest). The *Cladium* and *Juncus subnodulosus* fens grouped into a 'mixed sedge' cluster, alongside the glades and the *Phragmites* fen in Woodwalton. The '*Molinia*-sedge' cluster was solely formed by the plots in the sedge fen in Woodwalton. The other three clusters were communities dominated by

**Table 5.1:** Description of the successional stages derived from species clustering, arranged vertically from wetter-to-drier stages. U = Upton Fen; W = Woodwalton Fen; E = Wheatfen; C = Calthorpe. Field community names are as presented in Chapter 2 (section 2.1).

Successional stage	Field community	Main species	Management (categories 0 to 4)	No of plots
Wetter	Reedswamp	<i>Phragmites australis</i> , <i>Carex riparia</i> , <i>Calystegia sepium</i>	Cut on a 7-8 year rotation; last cut before sampling between 2006/2007 (category 3)	8
↓	Mixed sedge	<i>Cladium</i> and <i>J. subnodulosus</i> fens (U); glades (managed and unmanaged) and <i>Phragmites</i> fen (W)	<i>Cladium</i> : same as reedswamp; <i>J. subnodulosus</i> : same as reedswamp, but last cut before sampling in May 2011; uncut glades: none (category 1); cut glades: cut annually in summer (category 4); <i>Phragmites</i> fen: uncut for c. 20 years (category 2)	51 ( <i>Cladium</i> : 10; <i>Juncus</i> : 12; uncut glades: 3; cut glades: 9; <i>Phragmites</i> fen: 17)
↓	<i>Molinia</i> -sedge	<i>Carex viridula</i> , <i>Carex panicea</i> , <i>Molinia caerulea</i> , <i>Hydrocotyle vulgaris</i>	Cut annually in summer (category 4)	13
↓	Fen carr	<i>Alnus glutinosa</i> , <i>Salix cinerea</i> , <i>Fraxinus excelsior</i> , <i>Poa trivialis</i>	None (category 0)	15
↓	Wet woods	<i>A. glutinosa</i> , <i>F. excelsior</i> , <i>Betula pubescens</i> , <i>S. cinerea</i> , <i>P. trivialis</i> , <i>C. acutiformis</i> , <i>Glechoma hederacea</i> , <i>Dryopteris dilatata</i>	None (category 0)	87 (alder carr U: 11; alder carr W: 12; fen carr C: 64)
Drier	Oak-ash woods	<i>Quercus robur</i> , <i>F. excelsior</i> , <i>A. glutinosa</i> , <i>Ribes rubrum</i> , <i>Eupatorium cannabinum</i>	None (category 0)	31

woody taxa. The fen carr in Wheatfen formed the 'fen carr' cluster, while the wet woodland in Wheatfen was clustered into the 'oak-ash woods' stage. The fen carr in Calthorpe formed the 'wet woods' cluster, alongside the alder carr communities of Upton and Woodwalton. The mixed woodland in Upton Fen could not be fitted satisfactorily along a hydroseral sequence and was dropped from all analyses. See Waller *et al.* (2005) for a description of the communities in Calthorpe and Wheatfen and Table 5.1 for a summary of the stages, including their indicator species and the number of plots within them.

In order to investigate the effects of management on species assembly processes, the management intensity that the field communities are currently under (Chapter 2, section 2.4.1) was overlaid on top of the successional stages as a second categorical variable (Table 5.1).

### 5.2.3 Functional diversity (FD)

The FD metric of Petchey and Gaston (2002) was determined for each simulated plot and the observed data, using the same methods described in Chapter 3 (section 3.2.1). Assemblages with high trait complementarity (i.e., large trait divergence in trait space) are expected to yield higher FD values than assemblages with low trait complementarity (high trait convergence), which makes FD an easily and intuitively understandable measure. FD provides some other desirable properties of a dendrogram-based method over some other commonly used metrics, such as the Functional Richness (FRic), Evenness (FEve) and Divergence (FDiv) of Vileger *et al.* (2008), particularly in the context of the current analyses. As discussed in Chapter 3 (section 3.2.1), the resulting functional diversity of a plot cannot decrease if a species is added, cannot increase if a species is removed, and remains unchanged if a species that is added or lost contains identical properties to a species that is already present (Petchey and Gaston, 2006). These are useful characteristics for our null model study, as it provides unambiguous results in accordance with the expectations of the different community assembly processes. I computed the means of the 999 simulations of each plot to compare the observed and expected FDs.

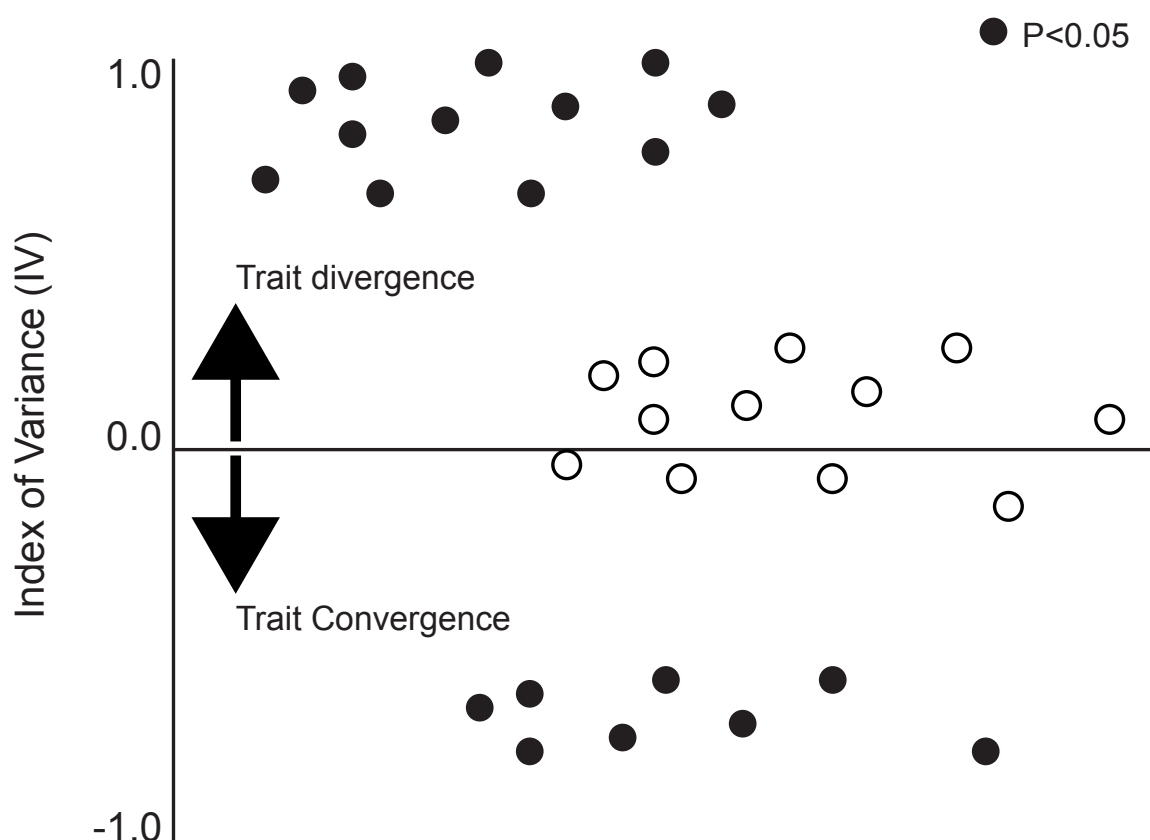
### 5.2.4 Index of variance (IV)

Shifts in the observed data from high to low FDs can be expressed as a change from one assembly process to another by comparing the observed and the mean of the expected

random distributions using a standardised measure of deviation, such as the Index of Variance (*IV*, illustrated in Fig. 5.2), adapted from the RV index of Zobel *et al.* (1993) and presented by Villeger *et al.* (2008) as:

$$IV = 2 \left[ \frac{\text{Obs}}{\text{Obs} + \text{Exp}} \right] - 1$$

where Obs and Exp are the observed and the mean expected FDs per plot, respectively. *IV* provides the ratio between observed and expected values of a test statistic and is conveniently scaled to  $-1 \leq IV \leq 1$ , making it an easier measure to work with than other indices, such as the standardised effect size (Gotelli and McCabe, 2002).



**Fig. 5.2:** Illustrative *IV* values. *IV* represents the differences between observed and mean expected (simulated) functional diversity (FD), with values farther from zero indicating higher departures from random expectation (and thus significantly different from zero under  $p < 0.05$ ) than values closer to zero. Positive *IV* values denote trait divergence (higher FD than expected by chance) and suggest limiting similarity processes, whereas negative *IV* means trait convergence (lower FD than expected by chance), indicating the predominance of habitat filtering processes.



The lower the difference between the observed and the mean expected random distribution, the closer to zero the *IV* will be. *IV* values farther from zero indicate relatively high deviation from random expectation. *IV* is a valuable statistic in showing whether the observed data is dominated by functional trait clustering (negative *IV* values showing trait distances lower than expected) or by functional trait divergence (positive *IV* values showing trait distances higher than expected) as it readily responds to changing patterns in the observed data (Fig. 5.2).

I used one-sample *t*-tests (Sokal and Rohlf, 2012) to determine whether the means of the *IV* distributions within the different categories (herbaceous and woody, successional stages and management intensity) significantly deviated from random expectations at  $p < 0.05$  (hypothesised mean = 0). Mean *IV* values significantly lower than zero indicate lower functional diversity than expected by chance and thus habitat filtering, while mean *IV* values significantly higher than zero denote higher functional diversity than expected under a null distribution, suggestive of limiting similarity processes. For simplicity, I refer to functional diversity (or FD) in the text, but all analyses involving *t*-tests were performed on *IV* values rather than observed and expected FD. Analyses were performed in R 3.2.4 (R Development Core Team, 2016).

### 5.2.5 Mean trait composition of successional stages

The dominant functional structure present in the successional stages was determined by computing plot-level trait community-weighted means (CWMs; Chapter 2, section 2.4.3) of the three trait axes (size, leaf and nutrient), as well as of the leaf traits used to calculate the PCA of the leaf axis (SLA, leaf N and leaf  $\delta^{13}\text{C}$ ). Firstly, following the methods described in section 3.2.2 (Chapter 3), I examined the effect of succession on CWMs with linear mixed effects models (LMMs), using the following formula:

$$\text{CWM} \sim \text{Successional stages, random} = \sim 1 | \text{Plot} + \varepsilon$$

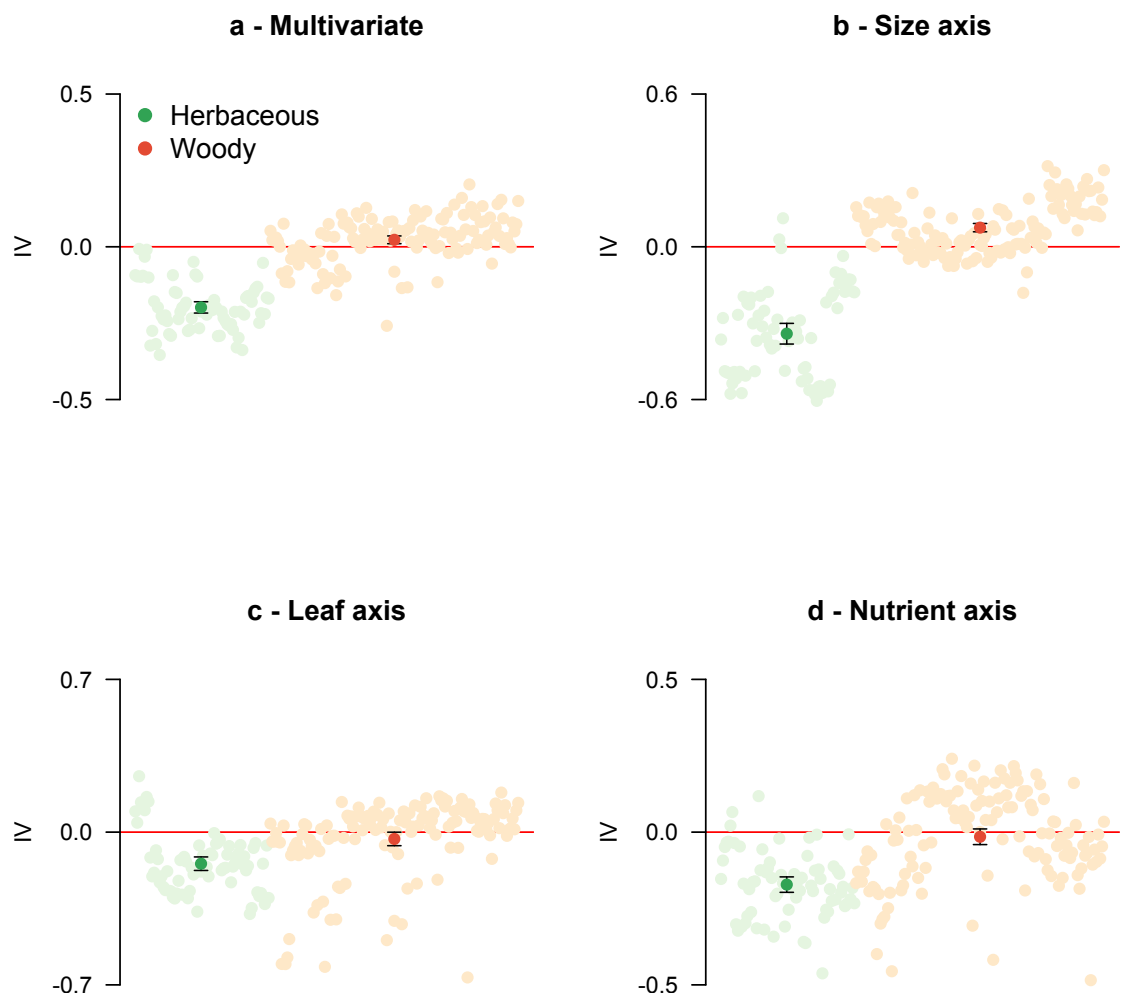
The term  $\sim 1 | \text{Plot}$  assumes an intercept that is different for each plot (see section 3.2.2).

Next, I employed multiple pairwise comparisons using Fisher's least significant differences (LSD; see section 3.2.3 in Chapter 3) on CWMs that were significantly affected ( $p < 0.05$ ) by successional development following LMM analyses. Analyses were performed in R 3.2.4 (R Development Core Team, 2016).

## 5.3 Results

### 5.3.1 Herb-dominated vs. woody communities

Overall, woodlands revealed higher *IV* values than herbaceous communities (Fig. 5.3), in both multivariate (Fig. 5.3a) and univariate (Fig. 5.3b to d) functional space, suggesting higher functional diversity in the wooded than in the herbaceous plots. On average, herb fens displayed significantly lower functional diversity (FD) than expected by chance in multivariate trait space ( $t = -21.42$ ,  $df = 71$ ,  $p < 0.001$ ; Fig. 5.3a), whereas wooded communities showed significantly higher FD than expected under a random distribution ( $t = 3.55$ ,  $df = 132$ ,  $p < 0.001$ ; Fig. 5.3a).



**Fig. 5.3:** Plot-level *IV* values (faded colours), categorised by herbaceous and wooded communities. The means of each category are highlighted. Error bars around the means are 95% confidence intervals of the *t* distribution. Panels **a** to **d** show the results of the multivariate (**a**) and univariate analyses [size (**b**), leaf (**c**) and nutrient (**d**) axes].

The size axis revealed a somewhat similar picture (Fig. 5.3b), with strong evidence of habitat filtering processes in the herb-dominated sites ( $t = -16.77$ ,  $df = 71$ ,  $p < 0.001$ ; Fig. 5.3b) and of limiting similarity patterns in the woody communities ( $t = 9.14$ ,  $df = 132$ ,  $p < 0.001$ ; Fig. 5.3b).

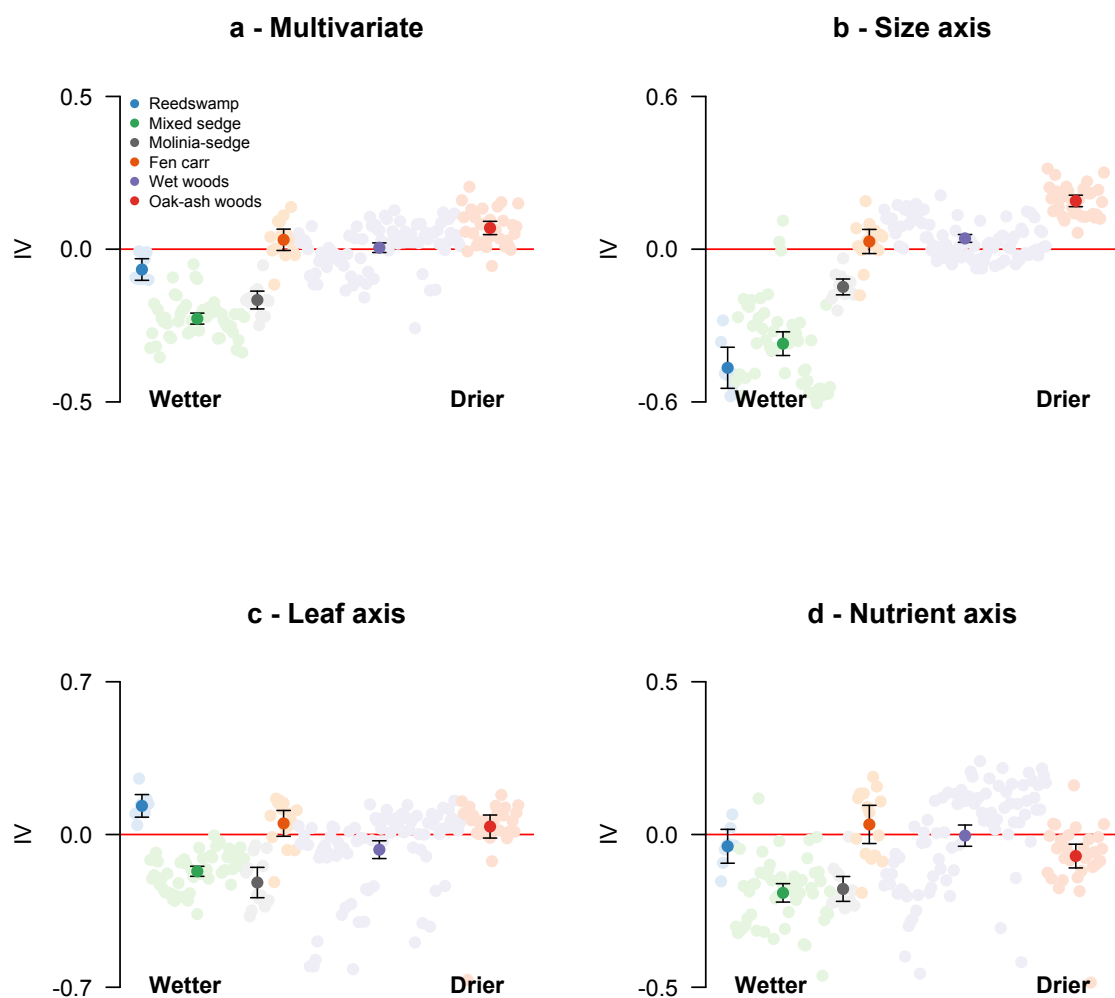
The leaf and nutrient axes (Fig. 5.3c and d) presented lower differences between the herb fens and the woodlands than the multivariate analysis (Fig. 5.3a) and the size axis (Fig. 5.3b). However, on average the herbaceous sites still revealed lower FDs than expected by chance for both the leaf ( $t = -9.32$ ,  $df = 71$ ,  $p < 0.001$ ; Fig. 5.3c) and nutrient ( $t = -13.55$ ,  $df = 71$ ,  $p < 0.001$ ; Fig. 5.3d) axes. On the other hand, the average wooded site did not deviate significantly from random expectation in neither of the two axes (leaf axis:  $t = -1.99$ ,  $df = 132$ ,  $p = 0.05$ ; Fig. 5.3c and nutrient axis:  $t = -1.17$ ,  $df = 132$ ,  $p = 0.24$ ; Fig. 5.3d).

### 5.3.2 Successional stages

Neutral- and niche-based processes seem to be acting simultaneously along a hydroseral sequence in the studied sites, from wetter reed-dominated swamp to drier oak-ash woodlands (Fig. 5.4). The early herbaceous stages in the sequence (the reedswamp and particularly the mixed sedge and *Molinia*-sedge) showed the lowest mean IVs [ $-0.07 \pm 0.04$  (95% CI,  $n = 8$ ),  $-0.23 \pm 0.02$  (95% CI,  $n = 51$ ) and  $-0.17 \pm 0.03$  (95% CI,  $n = 13$ ), respectively] and strong indication of habitat filtering processes taking place in multivariate trait space (reedswamp:  $t = -4.45$ ,  $df = 7$ ,  $p < 0.01$ ; mixed sedge:  $t = -25.44$ ,  $df = 50$ ,  $p < 0.001$  and *Molinia*-sedge:  $t = -12.45$ ,  $df = 12$ ,  $p < 0.001$ ; Fig. 5.4a). On the other hand, the later woody stages (fen carr, wet woods and oak-ash woods) displayed, on average, positive IV values [ $0.03 \pm 0.03$  (95% CI,  $n = 15$ ),  $0.005 \pm 0.02$  (95% CI,  $n = 87$ ) and  $0.07 \pm 0.02$  (95% CI,  $n = 31$ ), respectively] and shifted from the prevalence of random processes in the fen carr ( $t = 1.89$ ,  $df = 14$ ,  $p = 0.08$ ; Fig. 5.4a) and wet woods ( $t = 0.61$ ,  $df = 86$ ,  $p = 0.54$ ; Fig. 5.4a) to limiting similarity patterns in the oak-ash woods ( $t = 6.53$ ,  $df = 30$ ,  $p < 0.001$ ; Fig. 5.4a).

The size axis (Fig. 5.4b) presented generally similar results to the multivariate analysis (Fig. 5.4a). The reedswamp (wettest stage) showed the lowest mean IV ( $-0.47 \pm 0.08$ ; 95% CI,  $n = 8$ ), while the oak-ash woods (driest stage) revealed the highest ( $0.19 \pm 0.02$ ; 95% CI,  $n = 31$ ). Accordingly, the reedswamp ( $t = -13.66$ ,  $df = 7$ ,  $p < 0.001$ ; Fig. 5.4b), mixed sedge ( $t = -16.02$ ,  $df = 50$ ,  $p < 0.001$ ; Fig. 5.4b) and *Molinia*-sedge ( $t = -10.4$ ,  $df = 12$ ,  $p < 0.001$ ; Fig. 5.4b) showed evidence of strong abiotic filtering due to lower than expected mean FD, while the higher than expected mean functional diversity in the wet woods ( $t =$

5.48,  $df = 86$ ,  $p < 0.001$ ; Fig. 5.4b) and oak-ash woods ( $t = 17.18$ ,  $df = 30$ ,  $p < 0.001$ ; Fig. 5.4b) suggests biotic competition to be the main assembly process in place. The mean FD of the fen carr did not deviate significantly from random expectation ( $t = 1.37$ ,  $df = 14$ ,  $p = 0.19$ ; Fig. 5.4b).



**Fig. 5.4:** Plot-level  $IV$  values (faded colours), categorised by successional stages (see legend). The means of each category are highlighted. Error bars around the means are 95% confidence intervals of the  $t$  distribution. The  $x$  axes are arranged from left to right on a wetter-to-drier gradient, as is the legend (panel **a**) from top to bottom. Panels **a** to **d** show the results of the multivariate (**a**) and univariate analyses [size (**b**), leaf (**c**) and nutrient (**d**) axes].

The prominence of random processes in the leaf (Fig. 5.4c) and nutrient (Fig. 5.4d) axes seems to have been higher than in the size axis (Fig. 5.4b). The leaf axis was the only trait axis to reveal higher than expected mean FD for one of the herbaceous communities, namely the reedswamp ( $t = 5.99$ ,  $df = 7$ ,  $p < 0.001$ ; Fig. 5.4c). The other two herbaceous

stages still revealed lower than expected mean FD (mixed sedge:  $t = -14.73$ ,  $df = 50$ ,  $p < 0.001$  and *Molinia*-sedge:  $t = -6.90$ ,  $df = 12$ ,  $p < 0.001$ ; Fig. 5.4c). However, the mean FD of two of the woody stages did not differ significantly from random expectation (fen carr:  $t = 1.85$ ,  $df = 14$ ,  $p = 0.09$  and oak-ash woods:  $t = 1.41$ ,  $df = 30$ ,  $p = 0.17$ ; Fig. 5.4c), while the wet woods showed some indication of environmental filtering ( $t = -3.39$ ,  $df = 86$ ,  $p = 0.001$ ; Fig. 5.4c).

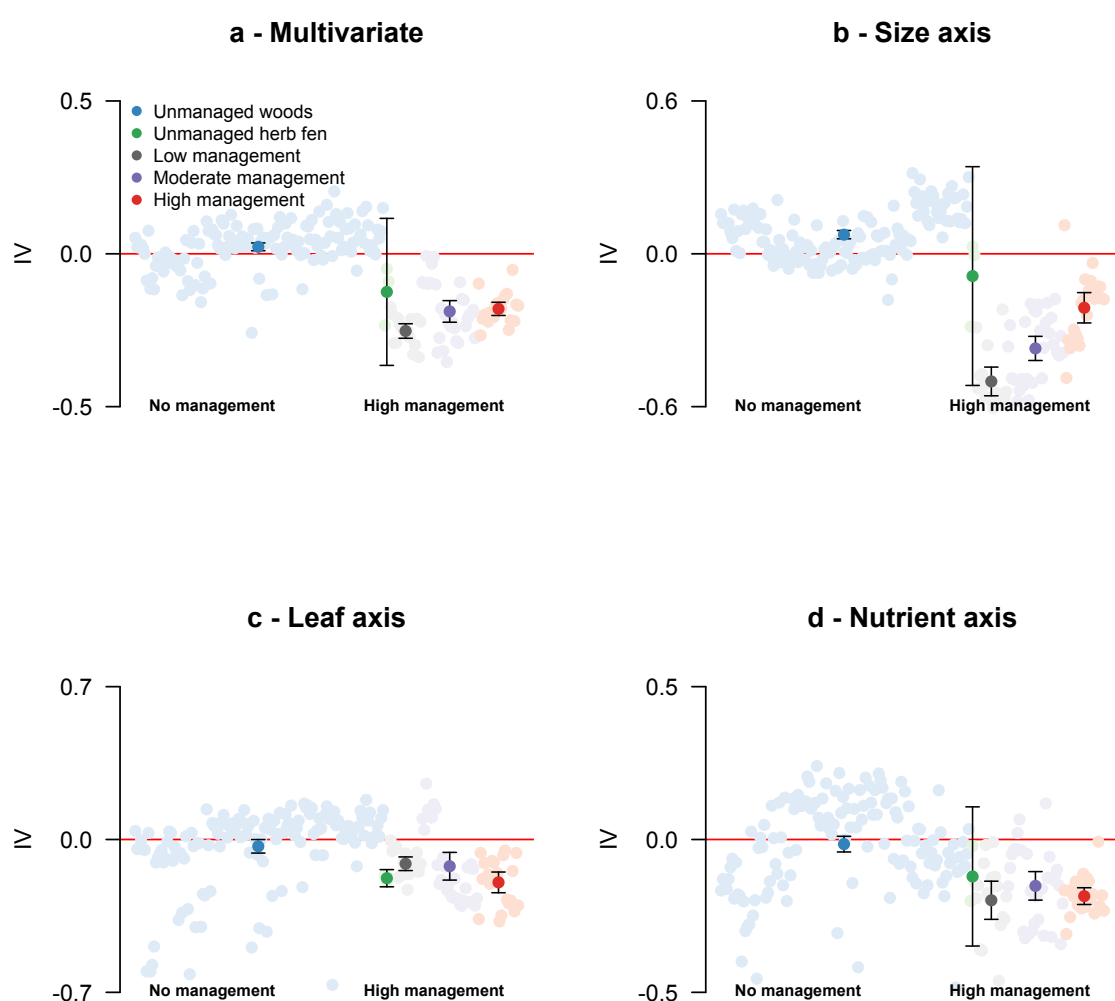
The mean FD of three successional stages did not depart from random expectation in the nutrient axis (Fig. 5.4d). These were the reedswamp ( $t = -1.65$ ,  $df = 7$ ,  $p = 0.14$ ; Fig. 5.4d), the fen carr ( $t = 1.13$ ,  $df = 14$ ,  $p = 0.28$ ; Fig. 5.4d) and the wet woods ( $t = -0.21$ ,  $df = 86$ ,  $p = 0.83$ ; Fig. 5.4d). The other three stages though revealed the predominance of habitat filtering processes, given their lower than expected mean FD (mixed sedge:  $t = -12.72$ ,  $df = 50$ ,  $p < 0.001$ ; *Molinia*-sedge:  $t = -9.53$ ,  $df = 12$ ,  $p < 0.001$  and oak-ash woods:  $t = -3.71$ ,  $df = 30$ ,  $p < 0.001$ ; Fig. 5.4d).

### 5.3.3 Management intensity

In line with results presented in Chapter 3, the multivariate and size axis analyses (Fig. 5.5a and b) revealed a decrease in observed functional diversity from unmanaged woodlands to managed herb fens, but an increasing trend in FD with increasing management intensity among the disturbed herbaceous sites. However, all managed categories exhibited functional diversity patterns associated with strong filtering effects in multivariate trait space (low management:  $t = -22.56$ ,  $df = 16$ ,  $p < 0.001$ ; moderate management:  $t = -10.91$ ,  $df = 29$ ,  $p < 0.001$  and high management:  $t = -17.36$ ,  $df = 21$ ,  $p < 0.001$ ; Fig. 5.5a) and in the size trait axis (low management:  $t = -18.86$ ,  $df = 16$ ,  $p < 0.001$ ; moderate management:  $t = -16.03$ ,  $df = 29$ ,  $p < 0.001$  and high management:  $t = -7.40$ ,  $df = 21$ ,  $p < 0.001$ ; Fig. 5.5b), likely caused by the cutting regime. The mean FD of the unmanaged herb fen did not depart from random expectation in neither the multivariate ( $t = -2.23$ ,  $df = 2$ ,  $p = 0.16$ ; Fig. 5.5a) nor in the size axis analysis ( $t = -0.88$ ,  $df = 2$ ,  $p = 0.47$ ; Fig. 5.5b), though sample size was very small ( $n = 3$ ). On the other hand, the multivariate ( $t = 3.55$ ,  $df = 132$ ,  $p < 0.001$ ; Fig. 5.5a) and the size axis results ( $t = 9.14$ ,  $df = 132$ ,  $p < 0.001$ ; Fig. 5.5b) of the unmanaged woods showed mean *IV* values suggestive of limiting similarity processes.

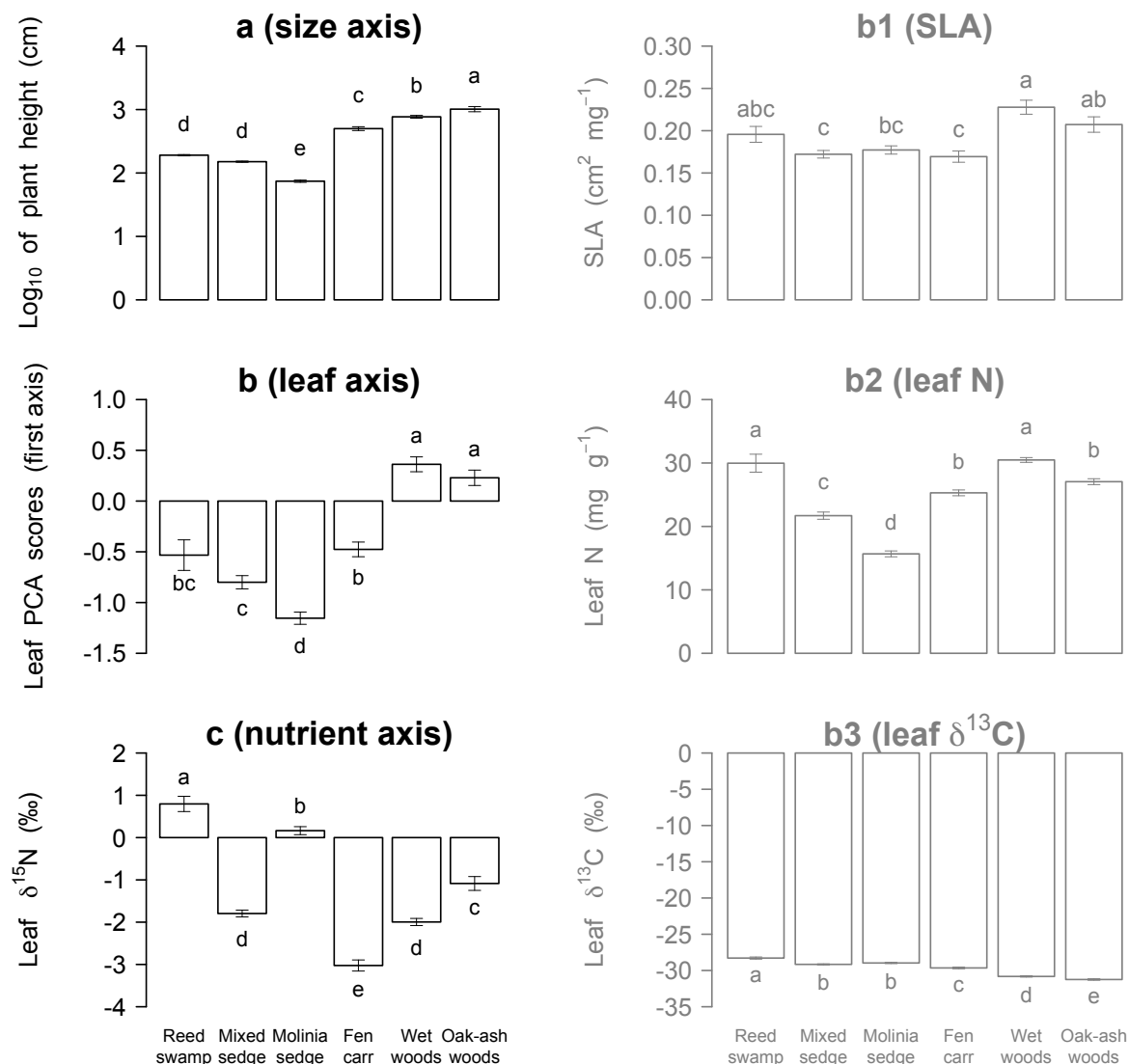
The leaf (Fig. 5.5c) and nutrient (Fig. 5.5d) axes provided a generally similar picture across management levels, though the mean FD of the unmanaged woodlands resembled

random communities in both the leaf ( $t = -1.99$ ,  $df = 132$ ,  $p = 0.05$ ; Fig. 5.5c) and the nutrient ( $t = -1.17$ ,  $df = 132$ ,  $p = 0.24$ ; Fig. 5.5d) axes, as did the unmanaged herb fen in the nutrient axis ( $t = -2.28$ ,  $df = 2$ ,  $p = 0.15$ ; Fig. 5.5d). However, the four herbaceous categories revealed evidence of habitat filtering in the leaf axis, including the unmanaged herb fen ( $t = -19.39$ ,  $df = 2$ ,  $p = 0.003$ ; Fig. 5.5c) and the low ( $t = -7.54$ ,  $df = 16$ ,  $p < 0.001$ ; Fig. 5.5c), moderate ( $t = -3.95$ ,  $df = 29$ ,  $p < 0.001$ ; Fig. 5.5c) and high ( $t = -8.61$ ,  $df = 21$ ,  $p < 0.001$ ; Fig. 5.5c) management categories. The nutrient axis results also suggest habitat filtering processes prevailing in all three managed herb fens (low management:  $t = -6.75$ ,  $df = 16$ ,  $p < 0.001$ ; moderate management:  $t = -6.65$ ,  $df = 29$ ,  $p < 0.001$  and high management:  $t = -14.06$ ,  $df = 21$ ,  $p < 0.001$ ; Fig. 5.5d).



**Fig. 5.5:** Plot-level *IV* values (faded colours), categorised by management intensity (see legend). The means of each category are highlighted. Error bars around the means are 95% confidence intervals of the *t* distribution. The *x* axes are arranged from left to right along a management gradient, from undisturbed woods to highly managed herb fens, as is the legend (panel **a**) from top to bottom. Panels **a** to **d** show the results of the multivariate (**a**) and univariate analyses [size (**b**), leaf (**c**) and nutrient (**d**) axes].

### 5.3.4 Community weighted-means (CWMs)



**Fig. 5.6:** Community weighted-means (CWMs) of the six successional stages with standard error bars. Letters above the bars indicate differences between stages according to the least significant differences (LSD) analysis (different letters indicate significant differences, and are in decreasing order from highest to lowest CWM). Panels **a** to **c** show the three trait axes used throughout, while panels **b1** to **b3** (greyed panels) present the functional traits used in the PCA analysis to generate the leaf axis (see text). The x axes are arranged from left to right on a wetter-to-drier scale.

Following LMM analyses, the different stages of successional development showed significantly different mean functional composition in the size ( $L = 371.63$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6a), leaf ( $L = 151.28$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6b) and nutrient ( $L = 178.21$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6c) axes. The early herbaceous stages had significantly lower mean vegetative

height than the later woody stages, with the *Molinia*-sedge presenting the lowest height (Fig. 5.6a;  $p < 0.05$ , LSD analysis). Moreover, the herb fens mostly revealed significantly lower mean leaf axis scores (Fig. 5.6b;  $p < 0.05$ , LSD analysis) and higher mean leaf  $\delta^{15}\text{N}$  (Fig. 5.6c;  $p < 0.05$ , LSD analysis) than the woodlands. Interestingly, a significant increase in mean vegetative height (Fig. 5.6a;  $p < 0.05$ , LSD analysis) and leaf  $\delta^{15}\text{N}$  (Fig. 5.6c;  $p < 0.05$ , LSD analysis) can be seen from wetter to drier woodlands.

Successional development also had a significant influence on SLA ( $L = 36.39$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6b1), leaf N ( $L = 214.06$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6b2) and leaf  $\delta^{13}\text{C}$  ( $L = 227.30$ ;  $df = 5$ ;  $p < 0.001$ ; Fig. 5.6b3), according to the LMM results. Mean SLA was generally even throughout the successional stages (Fig. 5.6b1), though the wet woods showed significantly higher mean SLA than the other stages (Fig. 5.6b1;  $p < 0.05$ , LSD analysis). However, mean leaf N concentration tended to be significantly higher in the woodlands than in the herb-dominated fens, though the reedswamp revealed one of the highest mean leaf N (Fig. 5.6b2;  $p < 0.05$ , LSD analysis). In addition, there was a significant decline in mean leaf N content from wetter to drier herb-fen sites, with the *Molinia*-sedge showing the lowest mean leaf N concentration of all stages (Fig. 5.6b2;  $p < 0.05$ , LSD analysis). That, coupled with one of the highest mean leaf  $\delta^{13}\text{C}$  (Fig. 5.6b3;  $p < 0.05$ , LSD analysis), suggests the intensive management regime the *Molinia*-sedge is subjected to has resulted in the filtering out of species with relatively high leaf N content and low water use efficiency. Accordingly, there was a significant reduction in leaf  $\delta^{13}\text{C}$  from wetter to drier stages of succession overall, suggesting higher leaf  $^{13}\text{C}/^{12}\text{C}$  ratios among herbaceous species compared to woody taxa (Fig. 5.6b3;  $p < 0.05$ , LSD analysis).

## 5.4 Discussion

The present study determined the importance of equalising, trait-neutral processes and stabilising, trait-driven mechanisms in the assembly of lowland fen plant communities, to help answer one of the modern-day central questions in community ecology: how the functional diversity and relatedness of species influence the assemblage of plant communities (Sutherland *et al.*, 2013). The analyses presented here have provided some key evidence that multiple assembly processes operate within and across herbaceous and woody fen communities at different levels of succession and management intensity. Both stochastic and mechanistic processes thus seem to be making simultaneous contributions to the functional composition of these plant assemblages. These results validate previous



suggestions that neutral and niche mechanisms might alternate throughout the different stages of successional change (Schleicher *et al.*, 2011) and that different levels of management intensity may result in contrasting niche-based processes operating within the same ecosystem (Mason *et al.*, 2011). Moreover, my results showed that trait-neutral mechanisms remained relatively important through the different stages of succession and management intensity, particularly when considering the leaf and nutrient axes separately, even though niche-based processes tended to prevail in multivariate trait space, probably driven by the results of the size trait axis.

Despite these somewhat diverse results emerging from the simultaneous and individual use of different trait axes, the successional gradient revealed a broad pattern of shifting community functional composition from wetter-to-drier stages, or from herb-dominated to woody communities. Habitat filtering processes appeared to be the most important assembly mechanism at the early stages of succession overall, while increasing competitive interactions among species seemed to exert stronger influence on the functional structure of later woody stages. The functional patterns revealed by the analysis therefore mostly met the expectations previously set out. Firstly, the observed functional diversity of the initial, herb-dominated stages of succession were largely lower than expected by chance (expectation I). The moderate-to-intensive levels of disturbance seems to be the main driver of filtering processes in these communities, confirming previous hypotheses that disturbance stress tends to favour species with a set of traits adapted to cope with such conditions (Weiher and Keddy, 1995b). The strong trait convergence patterns of these communities reflected the predominance of low-statured, thick-leaved monocotyledons well suited to colonise frequently disturbed ground. Interestingly, increasing management resulted in increasing trait divergence among the managed herb fens, confirming the results presented in Chapter 3. This was particularly noticeable in the size axis (Fig. 5.5b) and, to some extent, in the multivariate analysis (Fig. 5.5a).

Secondly, the functional structure of the late woody stages mostly revealed trait divergence patterns (II), suggesting the prevalence of limiting similarity processes. This is certainly a result of the relatively high diversity of life forms in the wooded communities, with an abundant understorey and containing a significant ground flora component made up of graminoids and forbs (Appendix 1). The variability in plant height seems to be the main driving force behind these multivariate functional patterns, since the latter displayed a broadly similar FD structure to the size axis. Limiting similarity is usually interpreted as a sign of interspecific competition for resources (Stubbs and Wilson, 2004; Schwilk and

Ackerly, 2005; Götzenberger *et al.*, 2012). The mean FD of the wooded communities might thus be reflecting niche differentiation in light and resource capture strategies among species in the woody communities, such as distinct emergence times and leaf traits. Evidence of limiting similarity processes has also been demonstrated in a number of other vegetation and habitat types, ranging from sand dunes (Stubbs and Wilson, 2004) and successional riverbed grasslands (Holdaway and Sparrow, 2006) in New Zealand, to dune slacks in Wales (Wilson and Gitay, 1995) and experimental grassland communities in Central Europe (Mason *et al.*, 2011). Species with similar functional characters in these communities were found to coexist less often than expected by chance.

Thirdly, both neutral- and niche-based processes seem to be alternating (III) along a successional development gradient in the leaf and nutrient axes, revealing the high variability in plant traits like SLA and leaf  $\delta^{15}\text{N}$  between monocot and dicot species (Appendix 3). Finally, differences in mean functional composition between different successional stages was confirmed by the CWM analyses, with the herb fens being mostly characterised by species producing recalcitrant leaves with relatively low leaf N and, to some extent, low SLA compared to the wooded sites, but with high leaf  $\delta^{13}\text{C}$  (IV), given their potential ability to recycle  $^{13}\text{C}$ -enriched soil respired  $\text{CO}_2$  (Farquhar *et al.*, 1989).

The present study contributes to answering questions pertinent to community assembly processes. Considering the functional attributes of species, rather than their taxonomic identity, assumes that communities are a result of biotic and abiotic filters, which exclude those phenotypes without the appropriate attributes to respond to local conditions (Garnier *et al.*, 2016). This functional approach is now widely considered to more accurately explain and predict community assemblages (Laughlin *et al.*, 2011; Mason and de Bello, 2013; Laughlin, 2014; Garnier *et al.*, 2016), since measures that quantify functional diversity have the potential to reveal data structures that elucidate the processes behind species coexistence, and to show the relevance of functional traits for these processes (Mouchet *et al.*, 2010). Moreover, though using null models has been suggested to provide inadequate means to disentangle the relative importance of different community assembly processes (van der Plas *et al.*, 2015), the importance of considering neutral patterns is still justified for they identify a set of structures that interact with mechanisms of niche differentiation (Leibold and McPeck, 2006). For instance, Fukami *et al.* (2005) propose that the simultaneous operation of trait-based assembly rules and species-level priority effects may drive community assembly in many ecosystems, making them both deterministic and stochastic at different levels of community organisation. Here,

the use of null models to elucidate the prevalence of different assembly processes allowed for a detailed, plot-level picture of community assembly to emerge, since it recognised the potential effects of both niche and neutral processes, and captured the statistical signature of opposing assembly mechanisms taking place simultaneously across orthogonal functional trait axes. Despite multiple recent attempts to elucidate the concurrent effects of neutral and niche processes (Swenson and Enquist, 2009; Mason *et al.*, 2011; Laliberté *et al.*, 2013; van der Plas *et al.*, 2015), it remained unclear whether it was possible to establish if one assembly process tended to prevail, or if contrasting mechanisms exerted cancelling effects within and across gradients that are influential to species recruitment. It is hoped the current set of analyses goes a step closer in clarifying those questions.

Another strength of the present study was the fact that observed field data was used to constrain the range of trait values used in the random simulations, which gave credibility to the artificial communities generated using different niche axes. Using real data rather than artificially generated data thus provides a promising approach in detecting the competing assembly processes in play. In addition, this study showed that community assembly results are highly dependent on the choice of functional trait axes used, and whether they are used in conjunction or separately. This may be related to Chesson's (2000) proposition that coexistence mechanisms produce density-dependent interactions that change along environmental gradients, and that differences in species' responses along these gradients are what promote their coexistence (Leibold and McPeck, 2006). I suggest that not only species behave differently along environmental gradients, but independent trait axes within species also respond in different ways to disturbance and changing conditions, as evidenced by the somewhat varied results obtained from the three niche axes used in the present study.

## 5.5 Conclusions

Understanding the mechanisms allowing species to assemble into communities remains important in attempts to maintain (or increase) biodiversity. Results showed that it is possible to distinguish between opposing assembly processes occurring simultaneously in different functional trait axes and along environmental gradients.

However, one limitation of the present work is the limited number of plant organs used to construct trait axes. Traits from multiple organs, including belowground traits, are considered increasingly important to explain community assembly (Laughlin, 2014). Due to

logistical constraints, it was not possible to include a below-ground dimension to the present study. Including such traits in future studies would provide a more detailed picture of functional trait structure in fen communities, especially considering these are habitats subjected to seasonal fluctuations in the water table and to varying degrees of peat depth and organic content in the substrata, and hence constantly changing belowground conditions. Another question of interest stems from the relative functional role rare and abundant species play in assembly processes, since their level of relatedness may differ between them, as exemplified elsewhere (Kraft *et al.*, 2007).

Taken together, these results support a mostly niche-based view of managed fen plant communities in which habitat specialisation, adaptation to disturbance and strategy differentiation allow species coexistence. An important point to make is that the successional sequence used here, and the stages these plant communities are currently found at, are a direct consequence of past and present management practices. Therefore, these analyses have arguably not revealed habitat filtering processes *per se* in the herbaceous fen communities studied, but rather a management filtering exerting strong controls on the recruitment of species and functional traits.

The type of analysis presented here was previously lacking for protected fen habitats managed for conservation purposes, despite the ecological importance of understanding the variability of community assembly processes along management and successional gradients in plant communities. Filling this gap is particularly crucial at a time of rapid global environmental change and the increasing human impact on plant community composition and function (Vitousek *et al.*, 1997; Cardinale *et al.*, 2012; Naeem *et al.*, 2012).

## Chapter 6

# Determining trait composition of mid- to late-Holocene lowland plant fen communities using fossil pollen assemblages: revealing past ecosystem processes

### 6.1 Introduction

Peat deposits represent natural environmental archives, recording changes in the peatland flora through the preservation of pollen grains and spores. Under conducive conditions, these deposits develop in a stratified sequence, incorporating pollen into the horizons as the peat accumulates (Waller, 1994). Therefore, a vertical section through layers of peat should provide samples in temporal succession, though issues with sediment erosion and redeposition need to be considered (Waller, 1994). Pollen analysis can thus be used to reconstruct, with some accuracy, the local environment during periods of peat formation. Generally, pollen assemblages are selected to provide a signal of the regional vegetation (Sugita, 1994). Indeed, peat deposits have been extensively used to provide records of past plant associations and vegetational history (Waller, 1993, 1994; Waller and Marlow, 1994; Waller and Hamilton, 2000), including records of structural and functional alterations due to anthropogenic disturbances (Ireland and Booth, 2012) and ecological changes (Waller, 2013). Godwin and Clifford (1938) used pollen analyses in the 1930s, for instance, to infer periods of wetness and dryness in the Fenland region of East Anglia based on the abundances of arboreal taxa, recognising from an early stage that both regional and local components of the vegetation could be represented in pollen diagrams. In addition, Waller *et al.* (1999) were able to assess the processes controlling the development of coastal peat vegetation in southern England throughout the mid- to late-Holocene through the use of multi-proxy investigations (using pollen, plant macrofossil and diatom analyses coupled with radiocarbon dating).

Despite the extensive use of pollen assemblages to reconstruct past taxonomic history and the developmental processes of vegetation, there have been comparatively few studies adopting a functional approach to reconstruct vegetation patterns (Prentice *et al.*, 1996; Prentice *et al.*, 2000; Lacourse, 2009). However, the occurrence and abundance of a species at a given site is likely to be driven by its interactions with other species and

the match between its traits and local environmental conditions (Weiher and Keddy, 1999). An assemblage of species in a given habitat thus represents a selection of ecological strategies and functions best suited to persist under local restraints. In this context, the identity of species is unimportant. Instead, species' traits, or combination of traits, become more useful in explaining the persistence and abundance of taxa over time under changing conditions. Moreover, there is growing consensus that ecosystem processes depend more on the functional characteristics of species than on their number or identity (Cadotte *et al.*, 2011; Lavorel, 2013; Garnier *et al.*, 2016). The type, range and abundance of functional traits are particularly important in exerting controlling effects on ecosystems across a range of environmental conditions (de Bello *et al.*, 2010). If the goal of pollen analysis research is to reconstruct past vegetation and environments, it could then positively benefit from the use of trait expressions known to be associated with environmental conditions and to have influential effects on ecosystem processes. To that end, Lacourse (2009) used pollen records from western Canada to determine relationships between species traits and environmental conditions over long ecological timescales. Significant correlations between plant traits and palaeoenvironmental variables were established, demonstrating that environmental conditions interact significantly with life-history and stress tolerance traits on a temporal scale to determine vegetation composition. However, the use of fossil pollen records coupled with plant functional data to infer past ecosystem processes has seldom featured in the literature. Moreover, the extent to which pollen data can be used as a primary source of quantitative information on functional vegetation dynamics over long timescales is still poorly understood.

The tendency to overlook the role of plant traits in palaeoecological studies may be related to the limitations normally associated with conventional pollen analysis (see Discussion section below). A disadvantage, for instance, of relying on pollen data to construct the mean trait composition of plant communities is that the taxonomic resolution to which pollen can be identified is limited, which hinders the ability to capture interspecific functional differences within and across communities. There are also difficulties concerning the pollen-plant abundance relationship and pollen source area and representation (Sugita, 1994), which are pertinent for abundance-weighted measures to describe the functional structure of a community. Pollen data should nevertheless offer unparalleled opportunities to examine broad patterns that outweigh taxonomic and other limitations (Barboni *et al.*, 2004; Lacourse, 2009), even though most pollen can only be identified to genus level and some types are only diagnostic to families.

The aim of this chapter is to demonstrate the potential for using fossil pollen records to reconstruct the functional characteristics of past fen vegetation, as well as to discuss the possible ways to overcome the limitations imposed by conventional pollen analysis on the use of weighted trait means to characterise pollen assemblages over time and to potentially infer past environmental conditions. Fossil pollen data available from previous studies (Waller, 1994; Waller *et al.*, 1999), representing assemblages from southern and eastern England, are used to characterise the mean functional composition of mid- to late-Holocene vegetation.

## 6.2 Materials and methods

Plant vegetative height ( $\log_{10}$ -transformed) and the nine leaf traits presented in Chapter 2 (see Table 2.2 for trait descriptions) were used to characterise the mean trait composition of contemporary fen plant communities and of modern pollen assemblages from apparently equivalent communities. However, the taxonomic resolution to which pollen can be identified is limited, since it is not generally possible to identify pollen to species level, with most pollen types being diagnostic to genus and family levels (e.g. *Salix*, *Potentilla*-type, Poaceae, Cyperaceae). Therefore, it is necessary to map pollen taxa (or 'types', with several species/genera included) to the species recorded in the contemporary vegetation. The pollen types are then the 'palynological equivalents' of the vegetation. The different pollen types recorded in the modern pollen assemblages from Upton and Woodwalton were thus firstly classified as palynological equivalents of the contemporary fen vegetation recorded in these two sites (Chapter 2, section 2.1 and Appendix 1). The palynological equivalent list, with the complete trait data measured from vegetation equivalent species, were then used in all analyses involving the pollen data (see below). Secondly, plot-level community weighted means (CWMs; Chapter 2, section 2.4.3) of plant traits were computed for the modern vegetation (weighted by species relative abundances) and the modern pollen assemblages (weighted by grain count of pollen types) to account for the dominant effects of the most abundant taxa present in the vegetation and the pollen samples. The next step was to determine whether mean trait values found in contemporary fen vegetation could be recognised from the average trait composition of modern pollen assemblages. The objective was to establish whether mean traits of fossil pollen assemblages from eastern and southern England, where data were available, could be reliably used to infer the mean trait composition of past fen vegetation. The fossil pollen

taxa were then characterised by the CWMs (weighted by grain count of pollen types) of the traits showing the highest degrees of association (highest  $r^2$ ) between the contemporary vegetation and the modern pollen taxa. Finally, age-depth models of the fossil pollen sites were constructed to determine changes in mean trait composition of past fen communities through time and to compare them with average conditions of contemporary fen communities, with the potential to infer past ecosystem processes through the changing functional composition of the vegetation.

### 6.2.1 Modern pollen assemblages

Pollen samples of 2 cm<sup>3</sup> were collected from the green parts of mosses comprising mostly *Kindbergia praelonga*, *Brachythecium rutabulum*, *Calliergonella cuspidata* and *Rhytidiadelphus squarrosus*. Mosses were collected from as close as possible to the centre point of the sampling plots at Upton and Woodwalton (Chapter 2, section 2.2) at the end of the flowering season (September/October 2012 and 2013, respectively). Samples of surface litter (top 1 cm) were collected from the reedswamp at Upton due to the local scarcity of mosses. Standard palynological preparation methods were used (Moore *et al.*, 1991), including acetolysis. Residues were suspended in silicon oil with a minimum pollen sum threshold of 500 used (i.e., pollen count continued until a minimum total of 500 pollen grains of land plants per plot had been achieved). The pollen data are expressed as a proportion of land pollen (a 'pollen sum' of total land pollen – TLP), with the pollen of obligate aquatics and the spores of Pteridophytes added to the sum within which they are expressed. Modern pollen samples were collected from a total of 134 plots (83 plots from herbaceous and 51 from woody communities). Two plots in the *Phragmites* fen at Woodwalton (104 and 106) were omitted from the analyses as it was not possible to achieve the minimum pollen sum (500). Pollen type definitions (and therefore palynological equivalents) are based on the scheme of Bennett (1995-2007). The pollen diagrams were made using TILIA v2.0.41 (Grimm, 1993).

The pollen taxa used in all analyses were the fen taxa with plant equivalents encountered in the modern vegetation with full trait data available (taxa with asterisks in Table 6.1). As stated above, some taxa, such as species in the Poaceae and Cyperaceae families, produce undistinguishable pollen and are thus typically grouped together as one pollen type (Table 6.1). Therefore, site-level (Upton and Woodwalton) relative abundances of the equivalent plant species with trait measurements were used to calculate weighted-



**Table 6.1:** Palynological equivalents table. Taxa order follows trees, shrubs, climbers, herbs, and pteridophytes. Site-level (Upton and Woodwalton) relative abundances of the equivalent plant species encountered in the vegetation and with trait measurements were used to calculate weighted-mean trait values of pollen types with undistinguishable pollen (e.g., *Salix*, *Cirsium*-type, Poaceae, Cyperaceae). U = Upton Fen; W = Woodwalton Fen.

Vegetation species	Code	Site	Palynological equivalent <sup>1</sup>	Site	Traits used	Code	Site
-			<i>Abies</i>	U, W	-		
-			<i>Picea</i>	U, W	-		
-			<i>Pinus</i>	U, W	-		
-			<i>Ulmus</i>	U, W	-		
-			<i>Fagus sylvatica</i>	U, W	-		
-			<i>Castanea sativa</i>	U	-		
<i>Quercus robur</i>	QR	U, W	<i>Quercus</i> *	U, W	<i>Quercus robur</i>	QR	U, W
<i>Betula pubescens</i>	BP	U, W	<i>Betula</i> *	U, W	<i>Betula pubescens</i>	BP	U, W
<i>Alnus glutinosa</i>	AG	U, W	<i>Alnus glutinosa</i> *	U, W	<i>Alnus glutinosa</i>	AG	U, W
-			<i>Carpinus betulus</i>	U, W	-		
-			<i>Tilia</i>	U, W	-		
-			<i>Taxus baccata</i>	U, W	-		
<i>Ilex aquifolium</i>	Ia	U	<i>Ilex aquifolium</i> *	U	<i>Ilex aquifolium</i>	Ia	U
<i>Acer pseudoplatanus</i>	AC	U	<i>Acer</i>	U, W	-		
<i>Fraxinus excelsior</i>	FE	U	<i>Fraxinus excelsior</i> *	U, W	<i>Fraxinus excelsior</i>	FE	U
-			<i>Corylus avellana</i> -type	U, W	-		
<i>Salix caprea</i>	Sxcp	U	<i>Salix</i> *	U, W	<i>Salix caprea</i>	Sxcp	U
<i>Salix cinerea</i>	Sxcn	U, W	<i>Salix</i>	U, W	<i>Salix cinerea</i>	Sxcn	U, W
<i>Salix fragilis</i>	Sxf	U	<i>Salix</i>	U, W	-		
<i>Salix repens</i>	Sxr	U	<i>Salix</i>	U, W	<i>Salix repens</i>	Sxr	U
<i>Crataegus monogyna</i>	Cm	U, W	<i>Sorbus</i> -type*	U, W	<i>Crataegus monogyna</i>	Cm	U, W
<i>Prunus padus</i>	Ppa	U	<i>Sorbus</i> -type	U, W	-		
<i>Sorbus aucuparia</i>	SA	U	<i>Sorbus</i> -type	U, W	-		
-			<i>Cornus sanguinea</i>	U	-		
<i>Frangula alnus</i>	Fa	U	<i>Frangula alnus</i> *	U, W	<i>Frangula alnus</i>	Fa	U
<i>Rhamnus cathartica</i>	Rc	W	<i>Rhamnus cathartica</i>	U, W	<i>Rhamnus cathartica</i> †	Rc	W
-			<i>Ligustrum vulgare</i>	U, W	-		
-			<i>Sambucus nigra</i>	U, W	-		
<i>Viburnum opulus</i>	Vo	U	<i>Viburnum opulus</i> *	U, W	<i>Viburnum opulus</i>	Vo	U
<i>Lonicera periclymenum</i>	Lp	U	<i>Lonicera periclymenum</i> *	U, W	<i>Lonicera periclymenum</i>	Lp	U
<i>Hedera helix</i>	Hh	U	<i>Hedera helix</i>	U, W	-		
<i>Calystegia sepium</i>	Cs	U, W	<i>Calystegia</i> *	U	<i>Calystegia sepium</i>	Cs	U
-			<i>Convolvulus</i>	W	-		
<i>Humulus lupulus</i>	HI	U	<i>Humulus lupulus</i> *	U, W	<i>Humulus lupulus</i>	HI	U
-			<i>Bryonia dioica</i>	U	-		

<sup>1</sup> Pollen types as palynological equivalents of the contemporary vegetation. Not all pollen types recorded occur in the vegetation (dashed lines in first column) due to the pollen rain including a 'regional component'.

\* Pollen types used in the trait analyses with trait measurements available from equivalent species recorded in the contemporary vegetation at Upton and Woodwalton.

† *Rhamnus cathartica*, *Ceratocarpus claviculata* and *Galium uliginosum* did not have leaf nutrient traits available and were therefore not included in the trait analyses.

‡ Species recorded in the contemporary vegetation but not in the modern pollen data (dashed lines in fourth column). For *Juncus* and *Luzula* this is due to the fragility of their pollen grains, which also applies to the fossil pollen samples.

# Traits used to calculate the CWMs of the contemporary vegetation but not of the modern pollen assemblages due to lack of representation in the pollen record.

Table 6.1 continued

Vegetation species	Code	Site	Palynological equivalent <sup>1</sup>	Site	Traits used	Code	Site
<i>Tamus communis</i> ‡	Tc	U	-	-	-		
-			<i>Caltha palustris</i> -type	U	-		
<i>Ranunculus acris</i>	raa	U, W	<i>Ranunculus acris</i> -type*	U, W	-		
<i>Ranunculus ficaria</i>	rafi	U	<i>Ranunculus acris</i> -type	U, W	-		
<i>Ranunculus flammula</i>	rafl	W	<i>Ranunculus acris</i> -type	U, W	<i>Ranunculus flammula</i>	rafl	W
<i>Ranunculus repens</i>	rar	U, W	<i>Ranunculus acris</i> -type	U, W	-		
<i>Thalictrum flavum</i>	tf	W	<i>Thalictrum</i>	U	-		
<i>Ceratocarpus claviculata</i> ‡	Cc	U	-	-	<i>Ceratocarpus claviculata</i> †	Cc	U
<i>Urtica dioica</i>	ud	U, W	<i>Urtica</i> *	U, W	<i>Urtica dioica</i>	ud	U, W
-			Chenopodiaceae	U, W	-		
<i>Myrica gale</i>	Mg	U	<i>Myrica gale</i> *	U, W	<i>Myrica gale</i>	Mg	U
<i>Cerastium fontanum</i>	cf	W	Caryophyllaceae undiff.*	U, W	-		
<i>Lychnis flos-cuculi</i>	lfc	W	Caryophyllaceae undiff.	U, W	-		
<i>Moehringia trinervia</i>	mot	U, W	Caryophyllaceae undiff.	U, W	<i>Moehringia trinervia</i>	mot	U, W
<i>Silene dioica</i>	sid	U	Caryophyllaceae undiff.	U, W	-		
<i>Stellaria media</i>	sm	W	Caryophyllaceae undiff.	U, W	-		
<i>Stellaria palustris</i>	sp	W	Caryophyllaceae undiff.	U, W	-		
<i>Stellaria uliginosa</i>	su	U	Caryophyllaceae undiff.	U, W	-		
-			<i>Persicaria maculosa</i> -type	U, W	-		
-			<i>Polygonum</i>	U, W	-		
-			<i>Rumex acetosa</i>	U, W	-		
<i>Rumex crispus</i>	rc	W	<i>Rumex obtusifolius</i> -type	U, W	-		
<i>Rumex sanguineus</i>	rs	W	<i>Rumex sanguineus</i> -type*	U, W	<i>Rumex sanguineus</i>	rs	W
<i>Hypericum tetrapterum</i>	ht	U	<i>Hypericum perforatum</i> -type*	U	<i>Hypericum tetrapterum</i>	ht	U
<i>Viola sp</i>	viola	W	<i>Viola palustris</i> -type	U, W	-		
<i>Cardamine flexuosa</i>	cdf	U	Brassicaceae*	U, W	-		
<i>Cardamine pratensis</i>	cdp	U, W	Brassicaceae	U, W	<i>Cardamine pratensis</i>	cdp	U, W
<i>Ribes nigrum</i>	Rin	U	<i>Ribes</i>	U, W	-		
<i>Ribes rubrum</i>	Rir	U, W	<i>Ribes</i>	U, W	-		
-			<i>Calluna vulgaris</i>	U, W	-		
<i>Lysimachia vulgaris</i>	lv	U, W	<i>Lysimachia vulgaris</i> -type*	U, W	<i>Lysimachia vulgaris</i>	lv	U, W
-			<i>Chrysosplenium</i>	U	-		
<i>Filipendula ulmaria</i>	fu	U, W	<i>Filipendula</i> *	U, W	<i>Filipendula ulmaria</i>	fu	U, W
<i>Rubus fruticosus</i>	rf	U, W	<i>Rubus</i> undiff. (Rosaceae undiff.)*	U, W	<i>Rubus fruticosus</i>	rf	U, W
<i>Potentilla anserina</i>	poa	W	<i>Potentilla</i> -type	U, W	-		
<i>Potentilla erecta</i>	poe	W	<i>Potentilla</i> -type	U, W	-		
<i>Potentilla palustris</i>	pop	U, W	<i>Potentilla</i> -type	U, W	-		
<i>Geum urbanum</i> ‡	geu	U	-	-	-		
<i>Rosa sp</i>	rosa	U, W	<i>Rosa</i>	U, W	-		
-			Rosaceae undiff.	U, W	-		
<i>Lotus pedunculatus</i>	lop	U, W	<i>Lotus</i> *	U, W	<i>Lotus pedunculatus</i>	lop	U, W
-			Fabaceae undiff.	U, W	-		
<i>Vicia cracca</i>	Vc	W	<i>Vicia cracca</i> (Fabaceae undiff.)*	W	<i>Vicia cracca</i>	Vc	W
-			<i>Vicia sylvatica</i> -type (Fabaceae undiff.)	U, W	-		
-			<i>Lathyrus</i> (Fabaceae undiff.)	U	-		
<i>Trifolium repens</i>	tr	W	<i>Trifolium</i> -type (Fabaceae undiff.)	W	-		
<i>Lythrum salicaria</i>	ls	U, W	<i>Lythrum salicaria</i> -type*	U, W	<i>Lythrum salicaria</i>	ls	U, W
<i>Circaea lutetiana</i>	ccl	W	<i>Circaea</i> *	W	<i>Circaea lutetiana</i>	ccl	W
<i>Epilobium hirsutum</i> ‡	eph	U, W	-	-	<i>Epilobium hirsutum</i> #	eph	U, W
<i>Epilobium montanum</i> ‡	epm	W	-	-	-		
-			<i>Mercurialis perennis</i>	W	-		
-			<i>Euphorbia</i>	U	-		
<i>Geranium robertianum</i>	ger	U, W	<i>Geranium</i> *	U, W	<i>Geranium robertianum</i>	ger	U, W
<i>Impatiens sp.</i> ‡	impa	W	-	-	-		
<i>Hydrocotyle vulgaris</i>	hv	W	<i>Hydrocotyle vulgaris</i> *	U, W	<i>Hydrocotyle vulgaris</i>	hv	W

Table 6.1 continued

Vegetation species	Code	Site	Palynological equivalent <sup>1</sup>	Site	Traits used	Code	Site
<i>Angelica sylvestris</i>	as	U, W	Apiaceae undiff.*	U, W	<i>Angelica sylvestris</i>	as	U, W
<i>Apium nodiflorum</i>	an	U, W	Apiaceae undiff.	U, W	-		
<i>Peucedanum palustre</i>	pp	U	Apiaceae undiff.	U, W	<i>Peucedanum palustre</i>	pp	U
<i>Sium latifolium</i>	siu	U	Apiaceae undiff.	U, W	<i>Sium latifolium</i>	siu	U
<i>Solanum dulcamara</i>	sod	U, W	<i>Solanum dulcamara</i> *	U, W	<i>Solanum dulcamara</i>	sod	U, W
-			<i>Echium vulgare</i>	U	-		
<i>Symphytum officinale</i>	so	W	<i>Symphytum</i> *	U, W	<i>Symphytum officinale</i>	so	W
<i>Myosotis scorpioides</i>	ms	W	<i>Myosotis arvensis</i> -type	U	-		
<i>Lamium purpureum</i>	lap	W	Lamiaceae undiff.*	U, W	-		
<i>Stachys palustris</i>	spa	W	Lamiaceae undiff.	U, W	-		
<i>Stachys sylvatica</i>	ss	W	Lamiaceae undiff.	U, W	<i>Stachys sylvatica</i>	ss	W
<i>Glechoma hederacea</i> ‡	glh	U, W	-		<i>Glechoma hederacea</i> #	glh	U, W
<i>Prunella vulgaris</i> ‡	pv	W	-		-		
<i>Scutellaria galericulata</i> ‡	sg	U, W	-		-		
<i>Lycopus europaeus</i>	le	W	<i>Mentha</i> -type*	U, W	<i>Lycopus europaeus</i>	le	W
<i>Mentha aquatica</i>	ma	U, W	<i>Mentha</i> -type	U, W	<i>Mentha aquatica</i>	ma	U, W
-			<i>Plantago lanceolata</i>	U, W	-		
-			<i>Plantago major</i>	U, W	-		
-			<i>Scrophularia</i> -type	U, W	-		
<i>Veronica anagallis-aquatica</i>	veaa	U	<i>Veronica</i>	U, W	-		
<i>Veronica scutellata</i>	vs	W	<i>Veronica</i>	U, W	-		
<i>Odontites vernus</i> ‡	ov	W	-		-		
<i>Galium aparine</i>	ga	U, W	Rubiaceae*	U, W	<i>Galium aparine</i>	ga	U, W
<i>Galium palustre</i>	gp	W	Rubiaceae	U, W	-		
<i>Galium uliginosum</i>	gu	U, W	Rubiaceae	U, W	<i>Galium uliginosum</i> †	gu	U, W
<i>Valeriana officinalis</i>	va	U	<i>Valeriana officinalis</i> *	U, W	<i>Valeriana officinalis</i>	va	U
<i>Cirsium arvense</i>	cia	W	<i>Cirsium</i> -type*	U, W	<i>Cirsium arvense</i>	cia	W
<i>Cirsium palustre</i>	cip	U, W	<i>Cirsium</i> -type	U, W	<i>Cirsium palustre</i>	cip	U, W
<i>Cirsium vulgare</i>	civ	W	<i>Cirsium</i> -type	U, W	-		
<i>Centaurea nigra</i>	cn	W	<i>Centaurea nigra</i>	U, W	-		
<i>Lapsana communis</i>	lc	W	Lactuceae	U, W	-		
<i>Sonchus sp</i>	Son	W	Lactuceae	U, W	-		
<i>Taraxacum sp</i>	trx	W	Lactuceae	U, W	-		
<i>Eupatorium cannabinum</i>	ec	U, W	<i>Solidago virgaurea</i> -type*	U, W	<i>Eupatorium cannabinum</i>	ec	U, W
<i>Senecio sp</i>	Sen	W	<i>Solidago virgaurea</i> -type	U, W	-		
-			<i>Artemisia</i> -type	U, W	-		
<i>Achillea millefolium</i>	am	W	<i>Achillea</i> -type	U, W	-		
<i>Juncus articulatus</i> ‡	Jjar	W	-		<i>Juncus articulatus</i> #	Jjar	W
<i>Juncus bufonius</i> ‡	Jjbu	W	-		-		
<i>Juncus conglomeratus</i> ‡	Jjc	W	-		-		
<i>Juncus effusus</i> ‡	Jje	W	-		<i>Juncus effusus</i> #	Jje	W
<i>Juncus subnodulosus</i> ‡	Jjs	U, W	-		<i>Juncus subnodulosus</i> #	Jjs	U, W
<i>Luzula multiflora</i> ‡	Jlm	W	-		-		
<i>Cladium mariscus</i>	Cclm	U, W	<i>Cladium mariscus</i> * (Cyperaceae und.)	U, W	<i>Cladium mariscus</i>	Cclm	U, W
<i>Carex acutiformis</i>	Ccxa	U, W	Cyperaceae undiff.*	U, W	<i>Carex acutiformis</i>	Ccxa	U, W
<i>Carex diandra</i>	Ccxd	U	Cyperaceae undiff.	U, W	-		
<i>Carex elata</i>	Ccxe	W	Cyperaceae undiff.	U, W	<i>Carex elata</i>	Ccxe	W
<i>Carex nigra</i>	Ccxn	W	Cyperaceae undiff.	U, W	-		
<i>Carex otrubae</i>	Ccxo	W	Cyperaceae undiff.	U, W	-		
<i>Carex panicea</i>	Ccxpa	U, W	Cyperaceae undiff.	U, W	<i>Carex panicea</i>	Ccxpa	U, W
<i>Carex riparia</i>	Ccxri	U	Cyperaceae undiff.	U, W	<i>Carex riparia</i>	Ccxri	U
<i>Carex rostrata</i>	Ccxro	W	Cyperaceae undiff.	U, W	-		
<i>Carex viridula</i>	Ccxv	W	Cyperaceae undiff.	U, W	<i>Carex viridula</i>	Ccxv	W
<i>Eleocharis palustris</i>	Cep	W	Cyperaceae undiff.	U, W	-		
<i>Agrostis capillaris</i>	Pac	W	Poaceae undiff.*	U, W	-		
<i>Agrostis stolonifera</i>	Pas	U, W	Poaceae undiff.	U, W	<i>Agrostis stolonifera</i>	Pas	U, W

Table 6.1 continued

Vegetation species	Code	Site	Palynological equivalent <sup>1</sup>	Site	Traits used	Code	Site
<i>Anthoxanthum odoratum</i>	Pao	W	Poaceae undiff.	U, W	-		
<i>Brachypodium sylvaticum</i>	Pbs	W	Poaceae undiff.	U, W	-		
<i>Calamagrostis canescens</i>	Pcc	U, W	Poaceae undiff.	U, W	<i>Calamagrostis canescens</i>	Pcc	U, W
<i>Calamagrostis epigejos</i>	Pce	W	Poaceae undiff.	U, W	<i>Calamagrostis epigejos</i>	Pce	W
<i>Festuca rubra</i>	Pfr	W	Poaceae undiff.	U, W	-		
<i>Holcus lanatus</i>	Phl	W	Poaceae undiff.	U, W	<i>Holcus lanatus</i>	Phl	W
<i>Holcus mollis</i>	Phm	U	Poaceae undiff.	U, W	-		
<i>Molinia caerulea</i>	Pmc	W	Poaceae undiff.	U, W	<i>Molinia caerulea</i>	Pmc	W
<i>Phalaris arundinacea</i>	Ppha	W	Poaceae undiff.	U, W	<i>Phalaris arundinacea</i>	Ppha	W
<i>Phragmites australis</i>	Ppau	U, W	Poaceae undiff.	U, W	<i>Phragmites australis</i>	Ppau	U, W
<i>Poa pratensis</i>	Ppp	W	Poaceae undiff.	U, W	-		
<i>Poa trivialis</i>	Ppt	U, W	Poaceae undiff.	U, W	<i>Poa trivialis</i>	Ppt	U, W
<i>Glyceria fluitans</i>	Pgf	W	<i>Glyceria /Bromus</i>	U, W	-		
-			<i>Cerealia</i> -type	U, W	-		
<i>Dactylorhiza</i> sp. ‡	dac	W	-	-	-		
-			<i>Myriophyllum spicatum</i>	U	-		
-			<i>Callitriche</i>	U	-		
-			<i>Alisma</i> -type	W	-		
-			<i>Potamogeton natans</i> -type	U, W	-		
-			<i>Sparganium emersum</i> -type	U, W	-		
<i>Typha latifolia</i>	tl	U	<i>Typha latifolia</i>	U, W	-		
<i>Iris pseudacorus</i>	ip	U, W	<i>Iris</i> *	U	<i>Iris pseudacorus</i>	ip	U
<i>Equisetum palustre</i>	Tep	U	<i>Equisetum</i> *	U	<i>Equisetum palustre</i>	Tep	U
-			<i>Osmunda regalis</i>	W	-		
-			<i>Polypodium</i>	W	-		
-			<i>Pteridium aquilinum</i>	U, W	-		
<i>Athyrium filix-femina</i>	Taf	U	<i>Athyrium filix-femina</i> -type	U	-		
<i>Dryopteris dilatata</i>	Tdd	U, W	<i>Dryopteris dilatata</i> *	U, W	<i>Dryopteris dilatata</i>	Tdd	U, W
<i>Dryopteris filix-mas</i>	Tdf	U	<i>Dryopteris filix-mas</i> -type	U, W	-		
<i>Thelypteris palustris</i>	Ttp	U	<i>Thelypteris palustris</i> *	U	<i>Thelypteris palustris</i>	Ttp	U
<i>Athyrium filix-femina</i>	Taf	U	Pteropsida (monolete) indet.*	U	-		
<i>Dryopteris dilatata</i>	Tdd	U, W	Pteropsida (monolete) indet.	U, W	<i>Dryopteris dilatata</i>	Tdd	U, W
<i>Dryopteris filix-mas</i>	Tdf	U	Pteropsida (monolete) indet.	U, W	-		
<i>Thelypteris palustris</i>	Ttp	U	Pteropsida (monolete) indet.	U	<i>Thelypteris palustris</i>	Ttp	U

mean trait values of such pollen types (Table 6.1). A total of 103 species were encountered in the vegetation surveys of herbaceous and woody communities at Upton and Woodwalton for which relative abundance calculations were possible (Chapter 2, section 2.2.1), with a trait data coverage representing 62.1% of species and approximately 98% of the total species cover (Chapter 2, section 2.2.2). The modern pollen assemblages revealed 106 different pollen types, with 45 of those (42.5%) being assigned mean trait values for the ten traits listed above for the present analyses (Table 6.1). This represented approximately 93% of the total pollen count across the sampled sites (estimated by scaling the number of pollen counts with trait measurements by the total number of counts overall). Upton had 92.4% of total pollen count with trait measurements and Woodwalton 93.7%. The minimum plot-level coverage was 82.3% (one plot in the mixed woodland in Upton with relatively high count of *Pinus sylvestris* pollen, a species with no trait

measurements), while 21 out of 134 plots (15.7%) showed trait coverage < 90% (Table 6.2).

**Table 6.2:** Proportion of total modern pollen count with trait measurements for each sampled community. Proportional cover with full trait data was estimated by scaling the number of pollen counts with trait measurements by the total number of counts.

	Community	No. of plots	Plot-level % total count with trait data		No. of plots with...		
			Mean	Minimum	< 80% trait coverage	< 90% trait coverage	100% trait coverage
Upton Fen	Reedswamp	10	86.4	83.8	0	10	0
	<i>Cladium</i> fen	12	92.9	90.2	0	0	0
	<i>Juncus subnodulosus</i> fen	12	95.3	93.1	0	0	0
	Alder carr	17	92.1	86.1	0	5	0
	Mixed woodland	17	93.9	82.3	0	1	0
Woodwalton Fen	Alder carr	17	95.9	93.9	0	0	0
	Glade (unmanaged)	8	95.6	91.5	0	0	0
	Glade (managed)	9	93.1	89.5	0	1	0
	<i>Phragmites</i> fen	15*	92.6	89.1	0	1	0
	Sedge fen	17	92.0	86.2	0	3	0
Total		134			0	21	0

\* Two plots (104 and 106) were excluded from analyses due to low pollen count (see text).

### 6.2.2 Fossil pollen assemblages

Fossil pollen samples were extracted from mid- to late-Holocene peat deposits from eastern (Waller, 1994) and southern (Waller *et al.*, 1999) England (Fenland and Romney Marsh, respectively) and are inferred from pollen and macro-remains (e.g. wood) to originate from herbaceous and woody vegetation (Table 6.3). These sites were chosen due to the availability of fossil pollen data, published in Waller (1994), Long and Innes (1995) and Waller *et al.* (1999), where detailed description of the sites are given. Essentially, these

**Table 6.3:** Description of the fossil pollen sites in Romney Marsh and Fenland, with the major taxa in the local pollen assemblage zones (LPAZs) that reflect different types of vegetation at that particular locality. Derived from Waller (1994) and Waller *et al.* (1999).

LPAZs	Major taxa
<b>Romney Marsh (RM)</b>	
Brookland (BR): 50°59'N 0°50'E, 25 samples (1 - 25)	
Depth range 312-216 cm; age range c . 4800-2150 cal. yr BP	
BR-2	<i>Alnus glutinosa</i> , <i>Betula</i> , <i>Corylus avellana</i> -type, <i>Salix</i>
BR-3	Cyperaceae, <i>Corylus avellana</i> -type, <i>Osmunda regalis</i>
The Dowells (DOW): 51°02'N 0°49'E, 26 samples (26 - 51)	
Depth range 318-122 cm; age range c . 5300-2400 cal. yr BP	
DOW-4	<i>Alnus glutinosa</i> , Cyperaceae, Pteropsida (monolete) indet.
DOW-5	<i>Alnus glutinosa</i> , <i>Betula</i> , <i>Corylus avellana</i> -type
DOW-6	<i>Alnus glutinosa</i> , <i>Quercus</i> , <i>Corylus avellana</i> -type, <i>Osmunda regalis</i>
Hope Farm (HF): 51°01'N 0°50'E, 27 samples (52 - 78)	
Depth range 288-184 cm; age range c . 4900-1900 cal. yr BP	
HF-3	<i>Alnus glutinosa</i> , Cyperaceae, Pteropsida (monolete) indet.
HF-4	<i>Alnus glutinosa</i> , <i>Betula</i> , <i>Quercus</i> , <i>Osmunda regalis</i>
HF-5	Cyperaceae, Poaceae, Pteropsida (monolete) indet.
HF-6	<i>Salix</i> , <i>Betula</i> , <i>Osmunda regalis</i>
HF-7	<i>Myrica gale</i> , <i>Betula</i>
<b>Fenland (FE)</b>	
Murrow (MU): 52°38'N 0°01'E, 11 samples (91 - 101)	
Depth range 0.5-0.32 cm; age range c . 2800-2000 cal. yr BP	
MU-5	Cyperaceae, Poaceae, Rubiaceae, <i>Sparganium emersum</i> -type
MU-6	Cyperaceae, Poaceae, <i>Salix</i> , <i>Betula</i> , <i>Alnus</i> , Pteropsida (monolete) indet.
Redmere (RM): 52°26'N 0°26'E, 33 samples (102 - 134)	
Depth range 128-35 cm; age range c . 4200-1700 cal. yr BP	
RM-1	<i>Quercus</i> , Poaceae, <i>Corylus</i> -type, <i>Alnus</i> , Cyperaceae, Chenopodiaceae
RM-2	<i>Salix</i> , <i>Alnus</i> , Brassicaceae, Cyperaceae, Poaceae
RM-3	Cyperaceae, Poaceae, Rubiaceae, Brassicaceae, Pteropsida (monolete) indet.
RM-4a	Poaceae, Cyperaceae, Brassicaceae, Lactuceae, <i>Glyceria /Bromus</i> , Pteropsida (monolete) indet.
Swineshead (SH): 52°56'N 0°09'W, 6 samples (135 - 140)	
Depth range 0.35-0.3 cm; age range c . 1800-1500 cal. yr BP	
SH-2	Poaceae, Cyperaceae, Lactuceae
Welney Washes 3rd peat (WW3): 52°30'N 0°15'E, 27 samples (141 - 167)	
Depth range 325-223 cm; age range c . 4200-2200 cal. yr BP	
WW-10	<i>Alnus</i> , <i>Quercus</i> , <i>Salix</i> , Poaceae
WW-11	Cyperaceae, Brassicaceae, <i>Salix</i> , Poaceae, Pteropsida (monolete) indet.
WW-12	Poaceae, Cyperaceae, Apiaceae, Pteropsida (monolete) indet., <i>Sparganium emersum</i> -type
Welney Washes 4th peat (WW4): 52°30'N 0°15'E, 14 samples (168 - 181)	
Depth range 137-89 cm; age range c . 1650-700 cal. yr BP	
WW-14	Poaceae, Cyperaceae, <i>Sparganium emersum</i> -type
WW-15	Poaceae, Cyperaceae, <i>Glyceria /Bromus</i> , Pteropsida (monolete) indet.

Holocene assemblages derived from large sedimentary systems deposited during periods of widespread peat formation, with most of the peats intercalated between marine-brackish sediments. The selected locations were more than 1 km distant from contemporary dry land, so that the fossil pollen assemblages were likely to be dominated by wetland taxa.

The three Romney Marsh sites (Brookland, The Dowells and Hope Farm; Table 6.3) originate from the same peat layer that extended out from the upland edge from c. 5000 cal. yr BP onwards. They revealed initial sequences indicative of short periods of open vegetation, though this phase was more extended at The Dowells, the site closest to dry land. An extended period of tree pollen abundance followed at all three sites. The pollen assemblages in the upper half of the peat are more variable, though they are largely dominated by herbaceous pollen.

Four Fenland sites were selected (Murrow, Redmere, Welney Washes and Swineshead; Table 6.3), including two peat profiles (the 3<sup>rd</sup> and 4<sup>th</sup> peats in stratigraphic sequence from the base upwards) at Welney Washes. At Welney Washes 3<sup>rd</sup> peat and at Redmere, where the peat is overlain by freshwater marls rather than marine/brackish clays like the other sites, high pollen values of woody taxa were followed by assemblages dominated by herbaceous pollen. The opposite is true for Murrow. The Swineshead and the Welney Washes 4<sup>th</sup> peat profiles were taken from the most recent stage of peat formation in Fenland and were probably deposited close to major rivers (the Witham and the Great Ouse). At both sites, the fossil pollen assemblages were dominated by herbaceous taxa, with the presence within the peat of horizontally bedded *Phragmites* a strong indication of *in situ* reedswamp at Swineshead.

Fossil pollen samples were classified as deriving from predominantly herbaceous or woody vegetation according to the relative abundances of herbaceous or woody taxa in the fossil pollen record, respectively. A threshold of > 30% TLP from herbaceous taxa (classified as herb-dominated) and > 70% TLP from woody taxa (classified as wooded) was based on the over-representation of tree pollen in these environments (see Waller *et al.*, 2005 and Bunting *et al.*, 2005). The different pollen types present in the fossil record (only the fen taxa recorded in the modern vegetation are reported here) were assigned mean (unweighted) trait values following a similar approach to the one used for the modern pollen data; matching equivalent species encountered in the contemporary vegetation at Upton and Woodwalton with full trait data available to palynological equivalents (Table 6.4). There were 39 fen pollen types in the fossil record (Table 6.4), of which 32 (or 82.1%)

**Table 6.4:** Equivalent species with trait measurements recorded in the vegetation at Upton and Woodwalton used to characterise the fossil pollen types (fen taxa only) from Romney Marsh and Fenland. Taxa order follows trees, shrubs, climbers, herbs, and pteridophytes. BR = Brookland; DOW = The Dowells; HF = Hope Farm; MU = Murrow; RM = Redmere; SH = Swineshead; WW3 = Welney Washes 3<sup>rd</sup> peat; WW4 = Welney Washes 4<sup>th</sup> peat.

Pollen type	Site	Traits used	Code
<i>Quercus</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Quercus robur</i>	QR
<i>Betula</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Betula pubescens</i>	BP
<i>Alnus glutinosa</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Alnus glutinosa</i>	AG
<i>Fraxinus excelsior</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Fraxinus excelsior</i>	FE
<i>Salix</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Salix caprea</i>	Sxcp
<i>Salix</i>	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Salix cinerea</i>	Sxcn
<i>Salix</i>	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Salix repens</i>	Sxr
<i>Sorbus</i> -type*	DOW, MU, RM, WW3, WW4	<i>Crataegus monogyna</i>	Cm
<i>Rhamnus cathartica</i>	BR, DOW, HF, WW4	<i>Rhamnus cathartica</i> †	Rc
<i>Viburnum opulus</i> *	BR, DOW, HF, RM, SH, WW3, WW4	<i>Viburnum opulus</i>	Vo
<i>Lonicera periclymenum</i> *	DOW, HF	<i>Lonicera periclymenum</i>	Lp
<i>Hedera helix</i>	BR, DOW, HF, RM, WW3, WW4	-	
<i>Humulus lupulus</i> *	RM, WW3, WW4	<i>Humulus lupulus</i>	HI
<i>Ranunculus acris</i> -type*	DOW, HF, MU, RM, WW3, WW4	<i>Ranunculus flammula</i>	rafl
<i>Urtica</i> *	DOW, HF, MU, RM, SH, WW3, WW4	<i>Urtica dioica</i>	ud
<i>Myrica gale</i> *	BR, DOW, HF	<i>Myrica gale</i>	Mg
Caryophyllaceae undiff.*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Moehringia trinervia</i>	mot
<i>Rumex obtusifolius</i> -type	BR, DOW, HF, RM	-	
<i>Rumex sanguineus</i> -type*	BR, DOW, HF, RM, WW3, WW4	<i>Rumex sanguineus</i>	rs
Brassicaceae*	DOW, HF, MU, RM, SH, WW3, WW4	<i>Cardamine pratensis</i>	cdp
<i>Lysimachia vulgaris</i> -type*	BR, DOW, HF, RM, WW4	<i>Lysimachia vulgaris</i>	lv
<i>Filipendula</i> *	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Filipendula ulmaria</i>	fu
<i>Rubus</i> undiff. (Rosaceae undiff.)*	DOW, HF, WW3, WW4	<i>Rubus fruticosus</i>	rf
<i>Potentilla</i> -type	BR, DOW, HF, MU, WW4	-	
Rosaceae undiff.	BR, DOW, HF, RM, WW3, WW4	-	
<i>Lotus</i> *	RM, WW3	<i>Lotus pedunculatus</i>	lop
<i>Lythrum salicaria</i> -type*	DOW, HF, RM, SH, WW3, WW4	<i>Lythrum salicaria</i>	ls
<i>Hydrocotyle vulgaris</i> *	DOW, HF, WW4	<i>Hydrocotyle vulgaris</i>	hv
Apiaceae undiff.*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Angelica sylvestris</i>	as
Apiaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Peucedanum palustre</i>	pp
Apiaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Sium latifolium</i>	siu
<i>Solanum dulcamara</i> *	HF, WW3, WW4	<i>Solanum dulcamara</i>	sod
Lamiaceae undiff.*	RM, SH, WW3, WW4	<i>Stachys sylvatica</i>	ss
<i>Mentha</i> -type*	BR, HF, RM, WW3	<i>Lycopus europaeus</i>	le
<i>Mentha</i> -type	BR, HF, RM, WW3	<i>Mentha aquatica</i>	ma
Rubiaceae*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Galium aparine</i>	ga
Rubiaceae	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Galium uliginosum</i> †	gu
<i>Cirsium</i> -type*	BR, DOW, RM	<i>Cirsium arvense</i>	cia
<i>Cirsium</i> -type	BR, DOW, RM	<i>Cirsium palustre</i>	cip
<i>Solidago virgaurea</i> -type*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Eupatorium cannabinum</i>	ec
<i>Achillea</i> -type	RM, WW4	-	
Cyperaceae undiff.*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Cladium mariscus</i>	Cclm
Cyperaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Carex acutiformis</i>	Ccxa
Cyperaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Carex elata</i>	Ccxe

\* Pollen types used in the trait analyses with trait data available from equivalent species recorded in the contemporary vegetation at Upton and Woodwalton

† *Rhamnus cathartica* and *Galium uliginosum* did not have leaf nutrient traits available and were therefore not included in the analyses



Table 6.4 continued

Pollen type	Site	Traits used	Code
Cyperaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Carex panicea</i>	Ccxpa
Cyperaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Carex riparia</i>	Ccxri
Cyperaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Carex viridula</i>	Ccxv
Poaceae undiff.*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Agrostis stolonifera</i>	Pas
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Calamagrostis canescens</i>	Pcc
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Calamagrostis epigejos</i>	Pce
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Holcus lanatus</i>	Phl
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Molinia caerulea</i>	Pmc
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Phalaris arundinacea</i>	Ppha
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Phragmites australis</i>	Ppau
Poaceae undiff.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Poa trivialis</i>	Ppt
<i>Glyceria /Bromus</i>	DOW, HF, RM, SH, WW3, WW4	-	
<i>Equisetum</i> *	BR, WW3, WW4	<i>Equisetum palustre</i>	Tep
Pteropsida (monolete) indet.*	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Thelypteris palustris</i>	Ttp
Pteropsida (monolete) indet.	BR, DOW, HF, MU, RM, SH, WW3, WW4	<i>Dryopteris dilatata</i>	Tdd

were assigned trait values measured from the contemporary vegetation (taxa with asterisks in Table 6.4). This represented approximately 99.4% of the total pollen count across the sampled sites (estimated by scaling the number of pollen counts with trait measurements by the total number of counts overall). Romney Marsh sites had 99.4% of total pollen count with trait measurements on average, while Fenland had 99.5%. The minimum sample-level coverage was 95.1%, while 58 out of 169 samples (34.3%) showed 100% trait coverage (Table 6.5).

A comparative approach to the interpretation of fossil pollen records has been shown (using the same data presented here) to be broadly applicable where fen communities are suspected (Waller *et al.*, 2017), since most of the fossil samples were found, through the use of PCA, to correspond to groupings produced by the modern pollen samples (Waller *et al.*, 2017).

Age chronologies were constructed for each fossil site using the radiocarbon dates of selected samples published in Waller (1994) and Waller *et al.* (1999). To correct for variations in atmospheric  $^{14}\text{C}$  concentration through time, the IntCal09 calibration curve (Reimer *et al.*, 2009) within the software CLAM (Blaauw, 2010) was used to 'calibrate' the dates, which are expressed in calendar (calibrated) years before present (cal. yr BP; Table 6.3). Age-depth models were then created using linear interpolation between the weighted means of the samples with calibrated dates, as follows:

$$A_i = \left[ \left( \frac{A_2 - A_1}{D_2 - D_1} \right) * (D_i - D_j) \right] + A_j$$

**Table 6.5:** Proportion of total fossil pollen count with trait measurements for each sampled community. Proportional cover with full trait data was estimated by scaling the number of pollen counts with trait measurements by the total number of counts.

	Site	No. of samples	% total count with trait data		No. of samples with...		
			Mean	Minimum	< 80% trait coverage	< 90% trait coverage	100% trait coverage
Romney Marsh	Brookland	25	99.4	98.5	0	0	5
	The Dowells	26	99.6	98.3	0	0	12
	Hope Farm	27	99.1	95.1	0	0	4
Fenland	Murrow	11	99.97	99.7	0	0	10
	Redmere	33	99.5	97.0	0	0	13
	Swineshead	6	99.7	99.6	0	0	2
	Welney Washes 3rd peat	27	99.6	97.7	0	0	10
	Welney Washes 4th peat	14	98.6	96.0	0	0	2
Total		169			0	0	58

where  $A_i$  is the interpolated age of undated sample  $i$ ,  $A_1$  and  $A_2$  are the radiocarbon dated ages of samples 1 and 2,  $D_1$  and  $D_2$  are the depths of the respective dated samples,  $D_i$  is the depth of the sample for which age is to be estimated, and  $D_j$  and  $A_j$  are the depth and age of the sample immediately preceding sample  $i$ . See Waller (1994) and Waller *et al.* (1999) for a more detailed description of the methods used and the data obtained at these sites.

### 6.2.3 Statistical analysis

Linear mixed effects models (LMMs; see section 3.2.2 in Chapter 3) were fitted with the following formula:

$$\text{CWM of contemporary vegetation} \sim \text{CWM of modern pollen, random} = \sim 1 | \text{Plot} + \varepsilon$$

The term  $\sim 1|\text{Plot}$  assumes a different intercept for each plot (see section 3.2.2). LMMs were used to determine how well plot-level mean trait composition of the contemporary fen vegetation reflected that of the modern pollen taxa, in order to establish if mean trait values of fossil pollen assemblages could be reliably used to infer mean trait composition of past fen vegetation from apparent equivalent communities. The traits with the highest correspondence (highest  $r^2$ ) between the modern pollen and the modern vegetation were then used to characterise the fossil pollen assemblages. Following the methods proposed by Nakagawa and Schielzeth (2013), I used the marginal  $r^2$  to describe the proportion of variance explained by the fixed factor (CWM of modern pollen), where the fixed-effect variance is divided by the total variance explained by the model, including the fixed-effects variance and the random variance. I used the *piecewiseSEM* package (Lefcheck, 2016) in R 3.2.4 (R Development Core Team, 2016) to estimate the marginal  $r^2$  of each fitted model.

Means and 95% confidence intervals (using two-tailed Student's  $t$  at  $\alpha = 0.025$ ) of the CWMs of the herbaceous and woody modern vegetation at Upton and Woodwalton were calculated to characterise average conditions expected to be found in contemporary fen communities, against which past mean trait composition revealed by the fossil pollen assemblages [i.e., the mean trait composition (CWM) of each fossil sample] were compared by means of one-observation  $t$ -tests (Sokal and Rohlf, 2012). This technique – appropriate when independent observations cannot be grouped together (as in this case with fossil samples of different ages) – tests whether a single observation could belong to a given population whose parameters were estimated from sample data. The one-observation  $t$ -test is thus calculated as:

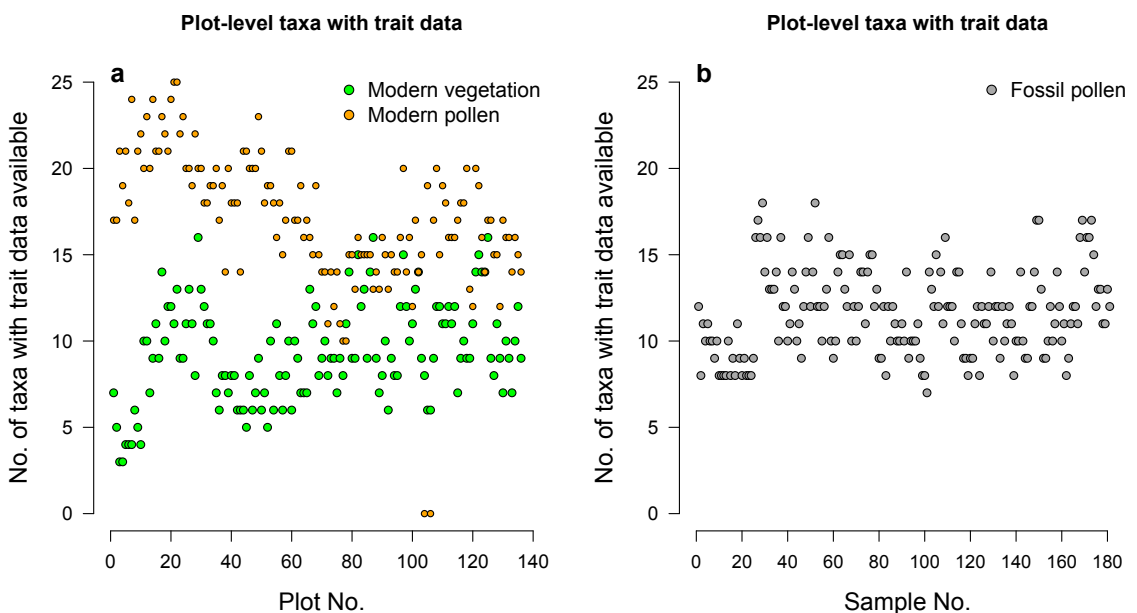
$$t_s = \frac{Y_1 - \bar{Y}_2}{S_2 \sqrt{\frac{n_2 + 1}{n_2}}}$$

where  $Y_1$  is the value of the single observation (the CWM of a given fossil pollen sample) and  $\bar{Y}_2, S_2$  and  $n_2$  are, respectively the mean, standard deviation and size of the sample (the sample being the CWMs of the modern herbaceous and woody fen vegetation). The fossil pollen sample was considered significantly different from the modern herbaceous and/or woody vegetation if  $p < 0.05$  for a given  $t$ -statistic, with 82 and 51 degrees of freedom for herbaceous and wooded modern fen communities, respectively.

## 6.3 Results

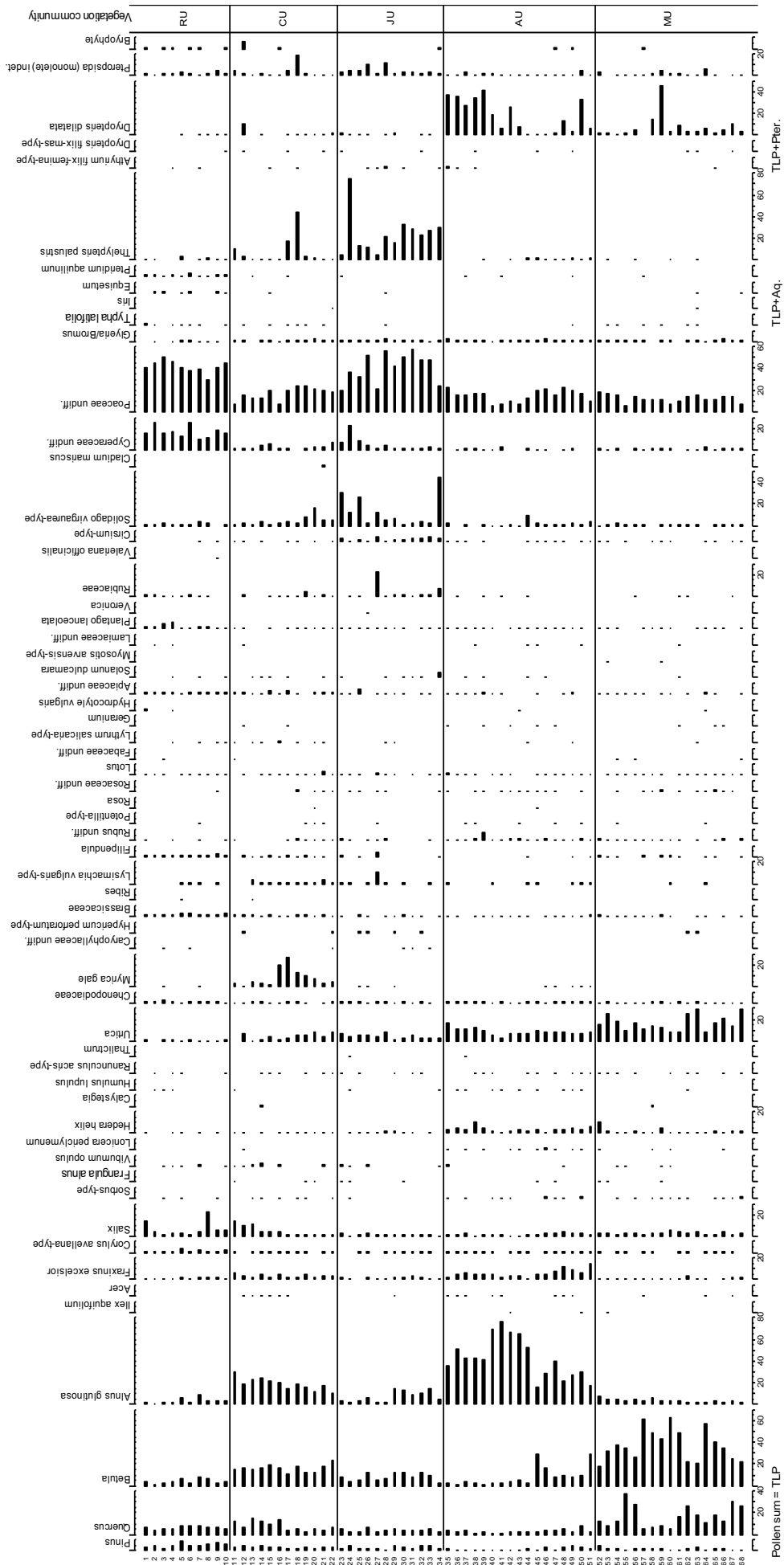
### 6.3.1 The modern pollen and vegetation datasets

The modern pollen assemblages revealed consistently higher numbers of plot-level taxa with trait data available than the contemporary vegetation and the fossil pollen samples (Fig. 6.1), ranging from 10 to 25 different pollen types per plot (median = 17; Fig. 6.1a). The plot-level species richness of the modern vegetation with full trait data varied from 3 to 16 (median = 9; Fig. 6.1a), while fen taxa composition in the fossil pollen samples varied between 7 and 18 pollen types per plot (median = 12; Fig. 6.1b).

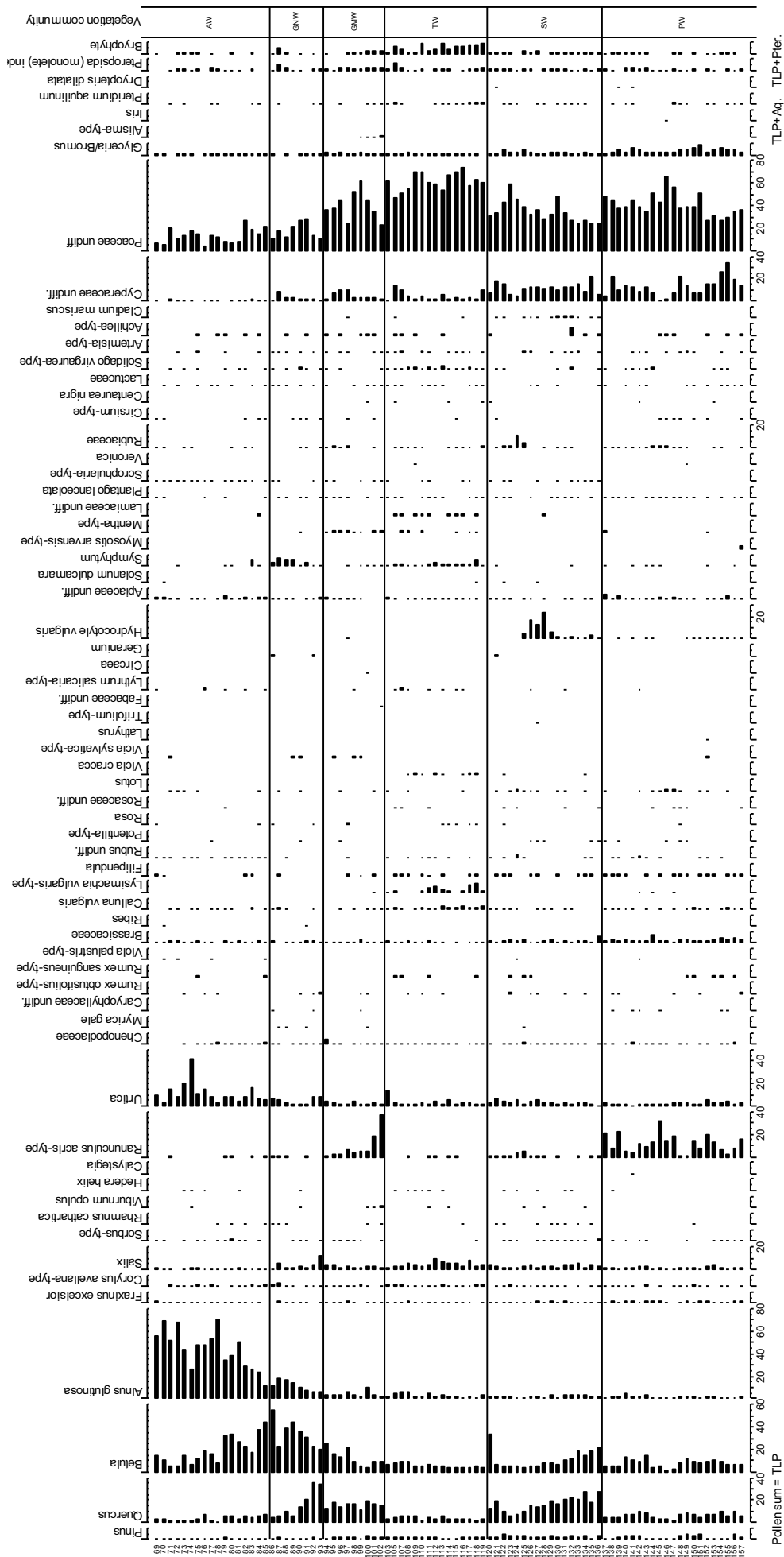


**Fig. 6.1:** Number of taxa recorded in the standing vegetation and in the pollen assemblages for which complete trait data were available. Plots 104 and 106 (panel a) did not achieve the minimum pollen count (500) and were excluded from the analyses. Fossil pollen samples 79 – 90 (panel b) were not included in the current analyses. See Table 6.3 for sample numbers of the fossil pollen.

The modern pollen assemblages from the herbaceous fens in Upton, reedswamp (plots 1 to 10), *Cladium* fen (11 to 22) and *Juncus subnodulosus* fen (23 to 34), presented relatively high Poaceae values, with c. 20% TLP or higher consistently recorded (Fig. 6.2). Cyperaceae pollen was also high (c. 20% TLP) in the reedswamp, while *Thelypteris palustris* (sum for Pteridophytes is TLP + Pteridophytes) and *Solidago virgaurea*-type often showed



**Fig. 6.2:** Modern pollen data from Upton Fen. All taxa occurring at >2% TLP plus the palynological equivalents of taxa recorded in the site vegetation surveys. Only the fen taxa are considered in this study. Plot numbers (1 to 68) are shown on the left, and community abbreviations on the right. Pollen diagram produced by Martyn Waller.



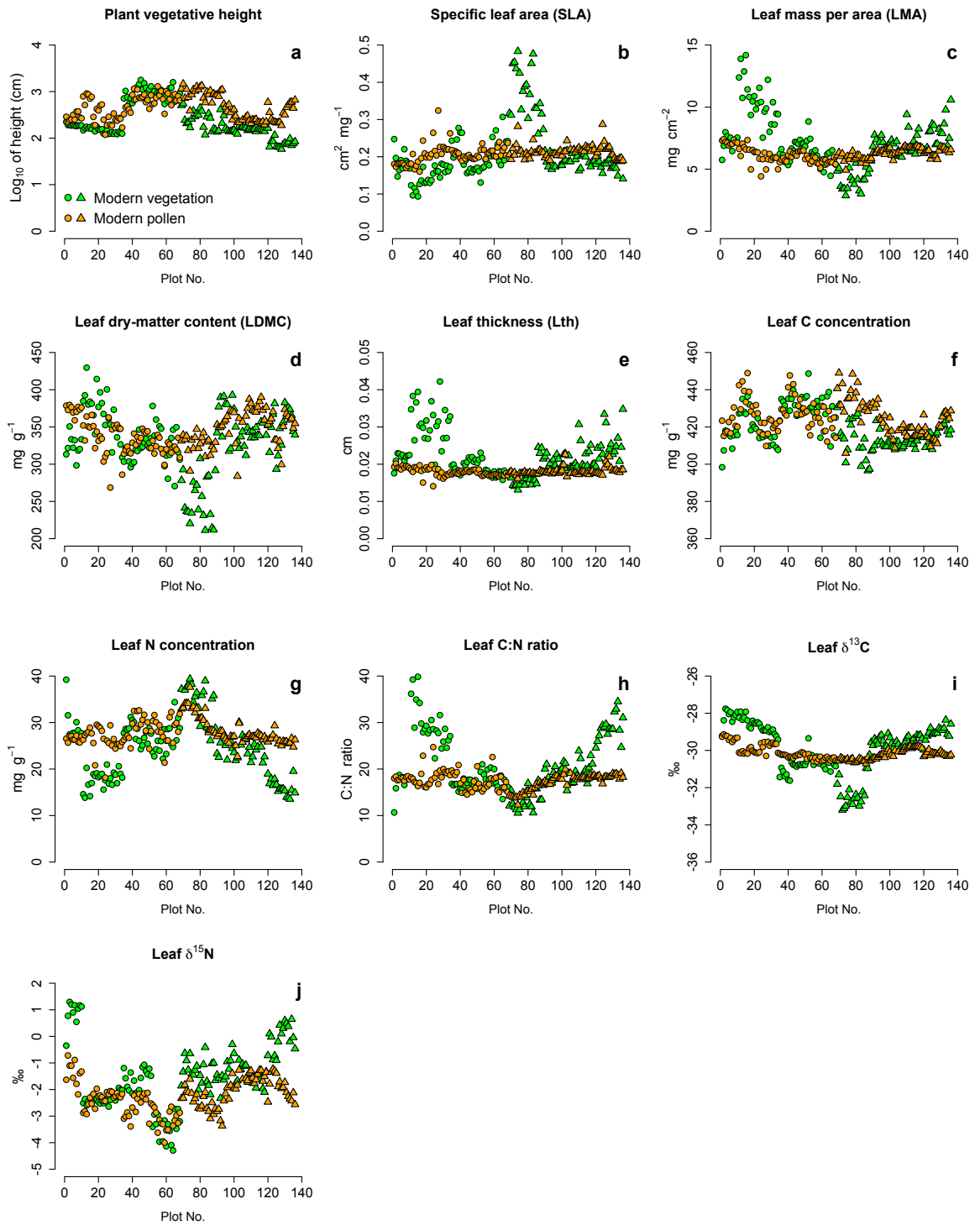
**Fig. 6.3:** Modern pollen data from Woodwalton. All taxa occurring at >2% TLP plus the palynological equivalents of taxa recorded in the site vegetation surveys. The *Juncus* pasture (plots 137 to 157; PW) is not considered here. Only the fen taxa are considered in this study. Plot numbers (69 to 136) are shown on the left, and community abbreviations on the right. Pollen diagram produced by Martyn Waller.

> 20% and > 10% TLP + Pterid. and TLP, respectively in the *J. subnodulosus* fen (Fig. 6.2). The pollen of woody taxa was scarce in the reedswamp, while the *Cladium* and *J. subnodulosus* fens revealed relatively high values of *Alnus glutinosa* and *Betula* pollen, as evidenced by values commonly higher than 10% TLP in both communities, particularly in the *Cladium* fen (Fig. 6.2). The alder carr (plots 36 to 51) and mixed woodland (52 to 68) pollen assemblages were dominated by tree taxa, especially *Alnus glutinosa* (mostly > c. 30% TLP) in the former and *Betula* (typically > c. 20% TLP) in the latter, with values of *Quercus* pollen also remaining largely above 10% TLP in the mixed woodland plots (Fig. 6.2). Moreover, values for *Urtica*, Poaceae and *Dryopteris dilatata* were consistently above 10% TLP and TLP + Pterid. throughout (Fig. 6.2).

Poaceae pollen values were generally higher at Woodwalton (> c. 20% TLP), particularly in the annually-cut glades (plots 94 to 102), *Phragmites* fen (103 to 119) and sedge fen (120 to 136) communities (Fig. 6.3). *Alnus glutinosa* and *Betula* pollen were notably high in the alder carr (plots 69 to 85), with values as high as 70% and 40% TLP, respectively (Fig. 6.3). In addition, *Urtica* and *Ranunculus acris*-type pollen frequently exceeded 10% TLP in the uncut and annually-cut glades, respectively (Fig. 6.3). The intensively managed sedge fen presented high pollen counts of tree taxa (*Betula* and *Quercus* typically > 10% TLP) and Cyperaceae (> 10% TLP; Fig. 6.3). See Chapter 2 (section 2.1) for a description of the modern vegetation at Upton and Woodwalton.

### 6.3.2 CWMs of the modern pollen and vegetation

Overall, the modern pollen taxa showed lower variability in community weighted means (CWMs) of plant traits in Upton and Woodwalton than the modern vegetation, which displayed large variations between some of the herb-dominated sites (plots 1 to 34 and 86 to 136) and one of the woody communities, the alder carr in Woodwalton (plots 69 to 85), particularly in leaf mass/area traits (Fig. 6.4). The difference in height between herbaceous and woody assemblages of the modern pollen data was lower than the one seen in the vegetation (Fig. 6.4a), probably due to the presence of arboreal pollen in the herb fens. However, pollen data from the *J. subnodulosus* fen in Upton (plots 23 to 34) and the *Phragmites* fen in Woodwalton (plots 103 to 119) revealed taxa with the lowest heights (Fig. 6.4a). As expected, plant height of the modern vegetation was higher in the woodlands (plots 35 to 85) than in the herb fens (Fig. 6.4a). Moreover, the vegetation of the intensively managed sedge fen site in Woodwalton showed the lowest heights (plots 120 to 136).



**Fig. 6.4:** Plot-level CWMs of modern vegetation (green symbols) and modern pollen (brown symbols). Plots 1 to 68 are Upton Fen (circles) and plots 69 to 136 are Woodwalton Fen (triangles). See Table 2.1 in Chapter 2 for community plot numbers and description.

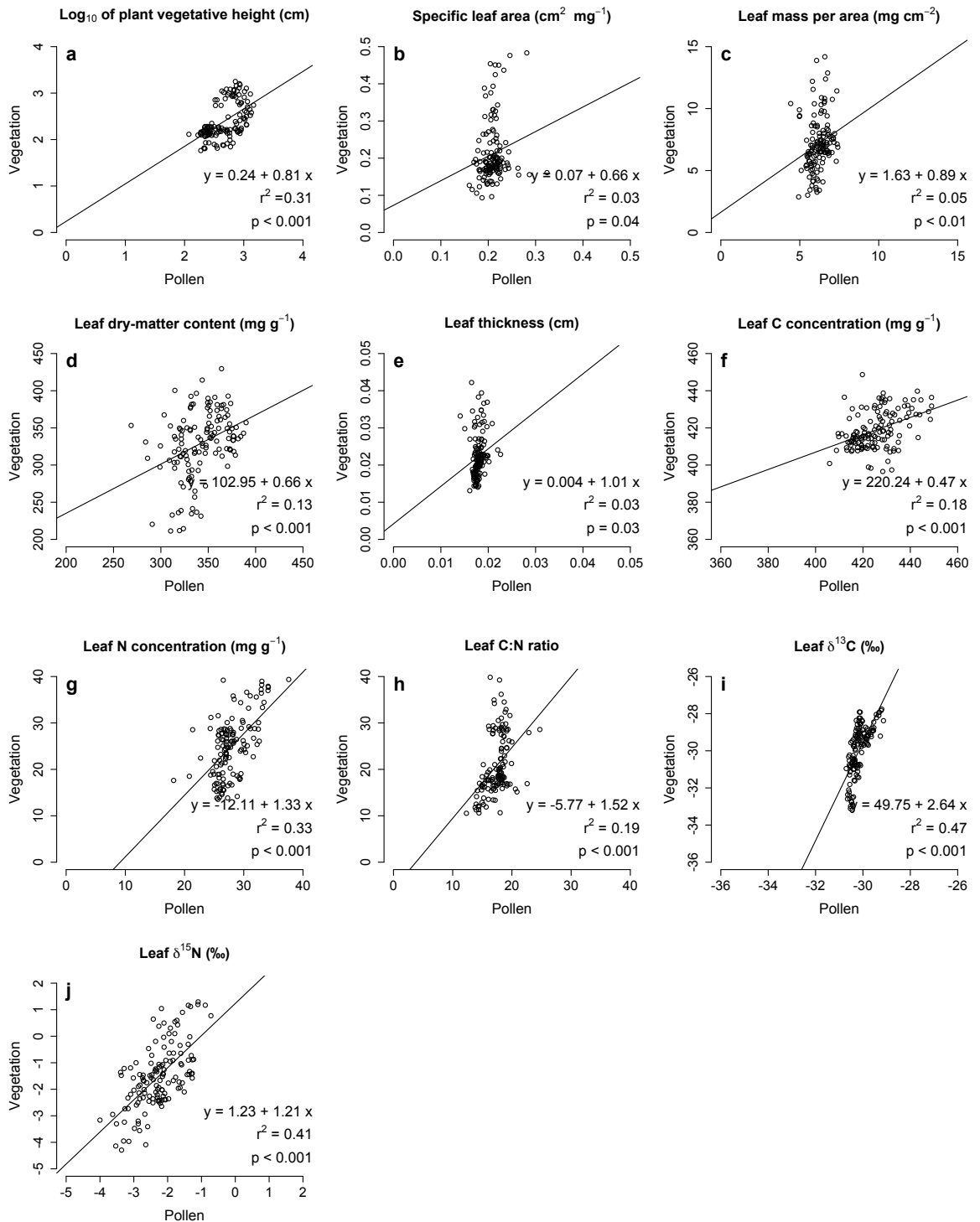
The leaf mass/area traits (SLA, LMA, LDMC and Lth) of the modern pollen taxa did not vary markedly between woody and herbaceous assemblages (Fig. 6.4b-e), though LDMC showed some variability between plots (Fig. 6.4d). The vegetation taxa, however,



exhibited some marked differences between wooded and herb fens, particularly between the alder carr in Woodwalton (plots 69 to 85) and the *Cladium* (plots 11 to 22) and *Juncus subnodulosus* (plots 23 to 34) fens in Upton (Fig. 6.4b-e). The alder carr in Woodwalton was mostly characterised by species with relatively high SLA and low LDMC and Lth (Fig. 6.4b-e), whereas the *Cladium* and *J. subnodulosus* fens in Upton presented the lowest SLA and highest LDMC and Lth of all communities (Fig. 6.4b-e). The other communities mostly showed values in between, though the intensively managed sedge fen in Woodwalton (plots 120 to 136) revealed species with relatively high LMA (Fig. 6.4c) and Lth (Fig. 6.4e).

The contemporary pollen flora generally exhibited slightly higher values of leaf C concentration than the modern vegetation throughout the sites (Fig. 6.4f), except for the alder carr (plots 35 to 51) and the mixed woodland (plots 52 to 68) in Upton, where there were no noticeable differences between them. The modern pollen taxa did not display the same degree of variability between herbaceous and woody assemblages as the vegetation taxa, but the alder carr in Woodwalton (*A. glutinosa*-dominated) showed the highest leaf N content (Fig. 6.4g) and the lowest leaf C:N ratio (Fig. 6.4h) when compared to the other sites. Leaf N concentration (Fig. 6.4g) and leaf C:N ratio (Fig. 6.4h) of the modern vegetation presented some noticeable differences between herbaceous and wooded sites. Similar to the leaf mass/area traits, the *Cladium* and the *J. subnodulosus* fens in Upton and the sedge fen in Woodwalton (low leaf N and high leaf C:N ratio) markedly contrasted the alder carr in Woodwalton (high leaf N and low leaf C:N ratio), while the other communities showed moderate leaf nutrient values in between (Fig. 6.4f-h).

Leaf  $\delta^{13}\text{C}$  (Fig. 6.4i) of the modern pollen assemblages presented very low variability throughout the sites, but there was some contrast between woody and herbaceous assemblages in leaf  $\delta^{15}\text{N}$  (Fig. 6.4j). The mixed woodland in Upton (plots 52 to 68) displayed the lowest values of leaf  $\delta^{15}\text{N}$ , while the *Phragmites* fen in Woodwalton (plots 103 to 119) revealed the highest (Fig. 6.4j). Moreover, the pollen data of the reedswamp in Upton (plots 1 to 10) showed the highest isotope results overall. The contemporary herb fens largely revealed higher leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$  than the woody sites, particularly in the reedswamp in Upton. The alder carr in Woodwalton (plots 69 to 85) and the mixed woodland in Upton presented the lowest leaf  $\delta^{13}\text{C}$  (Fig. 6.4i) and leaf  $\delta^{15}\text{N}$  (Fig. 6.4j), respectively. The implications of these results for the modern vegetation communities were discussed in Chapter 3.



**Fig. 6.5:** Linear relationship between the CWMs of the modern pollen and the modern vegetation. Coefficients (mean of the random intercepts and the fixed slope) and marginal  $r^2$  (see text) of linear mixed effects models (LMMs) of the standing vegetation as a function of the modern pollen data are shown in each panel. LMMs and marginal  $r^2$  were used to determine how well plot-level mean trait composition of modern pollen assemblages can predict mean trait values of the modern fen vegetation.

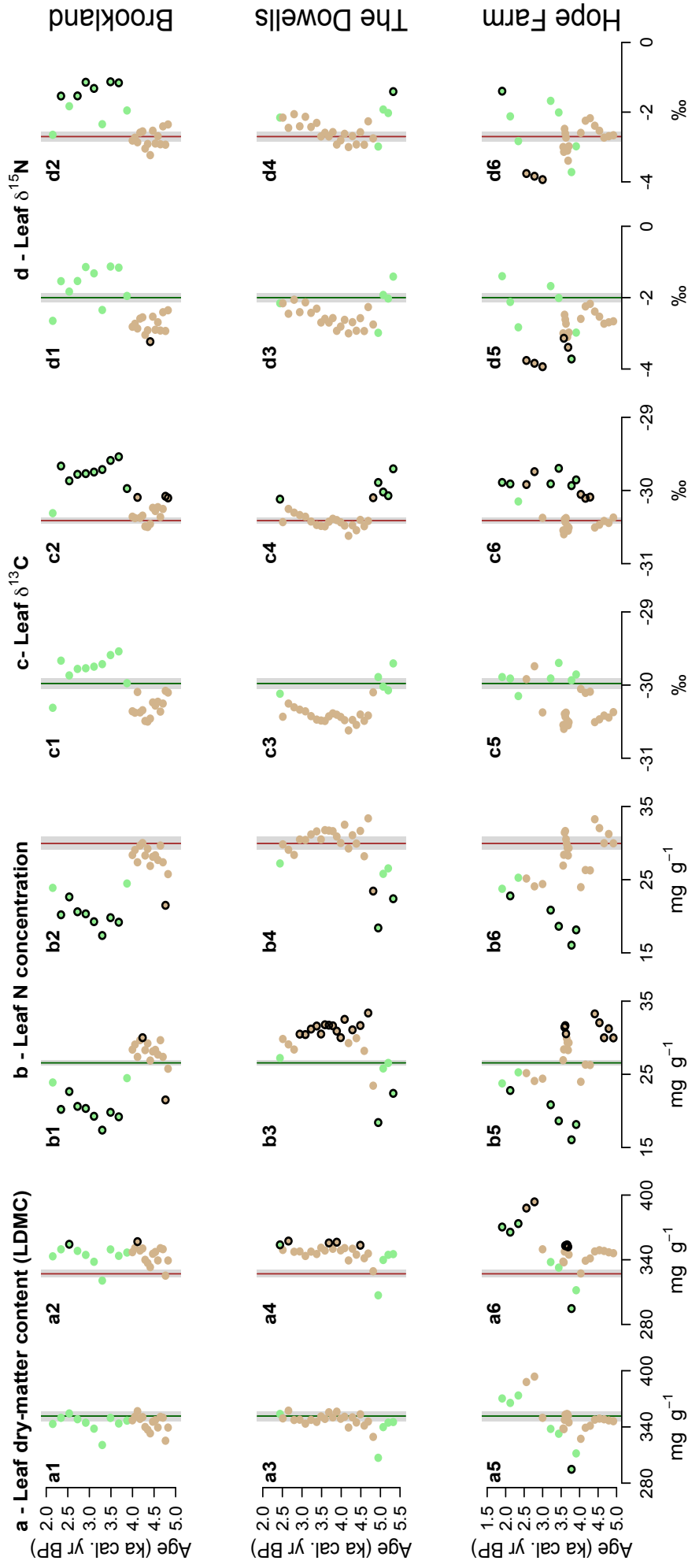
### 6.3.3 Relationship between the modern pollen and vegetation

Linear mixed effects models confirmed that leaf traits of the modern vegetation generally showed higher variability than the contemporary pollen taxa (Fig. 6.5). Plant height clearly revealed two distinct populations of herbaceous and woody species, particularly within the modern vegetation (Fig. 6.5a).

The traits with the highest proportion of variance explained by the fixed factor in mixed models fitting the CWMs of the modern vegetation varying as a function of the CWMs of modern pollen assemblages were leaf  $\delta^{13}\text{C}$  ( $r^2 = 0.47$ ; Fig. 6.5i), leaf  $\delta^{15}\text{N}$  ( $r^2 = 0.41$ ; Fig. 6.5j), leaf N concentration ( $r^2 = 0.33$ ; Fig. 6.5g) and plant vegetative height ( $r^2 = 0.31$ ; Fig. 6.5a), whereas the lowest marginal  $r^2$  were those of Lth ( $r^2 = 0.03$ ; Fig. 6.5e), SLA ( $r^2 = 0.03$ ; Fig. 6.5b) and LMA ( $r^2 = 0.05$ ; Fig. 6.5c). Among the leaf mass/area traits, LDMC presented the highest amount of variance explained by the fixed factor ( $r^2 = 0.13$ ; Fig. 6.5d), showing a similar marginal  $r^2$  value to those of leaf C concentration ( $r^2 = 0.18$ ; Fig. 6.5f) and leaf C:N ratio ( $r^2 = 0.19$ ; Fig. 6.5h).

### 6.3.4 The fossil pollen datasets

The fossil record indicates wooded conditions largely prevailed in the Romney Marsh area between c. 4800 and 2500 cal. yr BP (Fig. 6.6), notably at The Dowells and Hope Farm, though in Brookland herbaceous taxa dominated from c. 3900 to 2200 cal. yr BP (Fig. 6.6). The Fenland sites were mostly under herbaceous taxa from c. 3700 to 700 cal. yr BP (Fig. 6.7), following a short earlier period of woodland dominance between c. 4200 and 3700 cal. yr BP at Redmere and the Welney Washes 3<sup>rd</sup> peat (Fig. 6.7). The phases dominated by woodland were mainly characterised by an abundance of *Alnus glutinosa* pollen, with *Quercus* and *Betula* also prominent in some periods. *Fraxinus excelsior* was less prominent, though likely to be under-represented in the fossil record (Bunting *et al.*, 2005; Waller *et al.*, 2005). *Salix* was an important component, particularly between c. 4200 and 3200 cal. yr BP in Fenland and from c. 3000 to 2400 cal. yr BP in Romney Marsh. *Viburnum opulus* and *Myrica gale* were other main shrubs present in the Romney Marsh area, especially between c. 4900 and 2900 cal. yr BP and from c. 3500 to 1900 cal. yr BP, respectively. Moreover, *Rhamnus cathartica* only occurred at Hope Farm from c. 4900 to 3900 cal. yr BP.



**Fig. 6.6:** Changes in CWMs through time (in calendar years before present) of the fossil pollen taxa from Romney Marsh (site names shown on the right). Green and brown circles indicate the predominance of herbaceous and woody taxa in the fossil record, respectively. The means of the modern vegetation are shown for herb (green vertical lines) and woody (brown vertical lines) fens. Greyed areas around the modern means depict their 95% confidence intervals. Circles highlighted in black show fossil samples significantly different from modern vegetation means at  $p < 0.05$  (one-observation  $t$ -tests). Circles to the left of the modern means indicate that lower than expected trait values for contemporary fen vegetation prevailed in the fossil record, while circles to the right show the opposite. See section 6.2.3 for calculation methods. Uncertainty associated with estimates of pollen trait values may be caused by issues related to pollen taxonomic resolution, source area and pollen representation (see section 6.4.1 for a discussion).

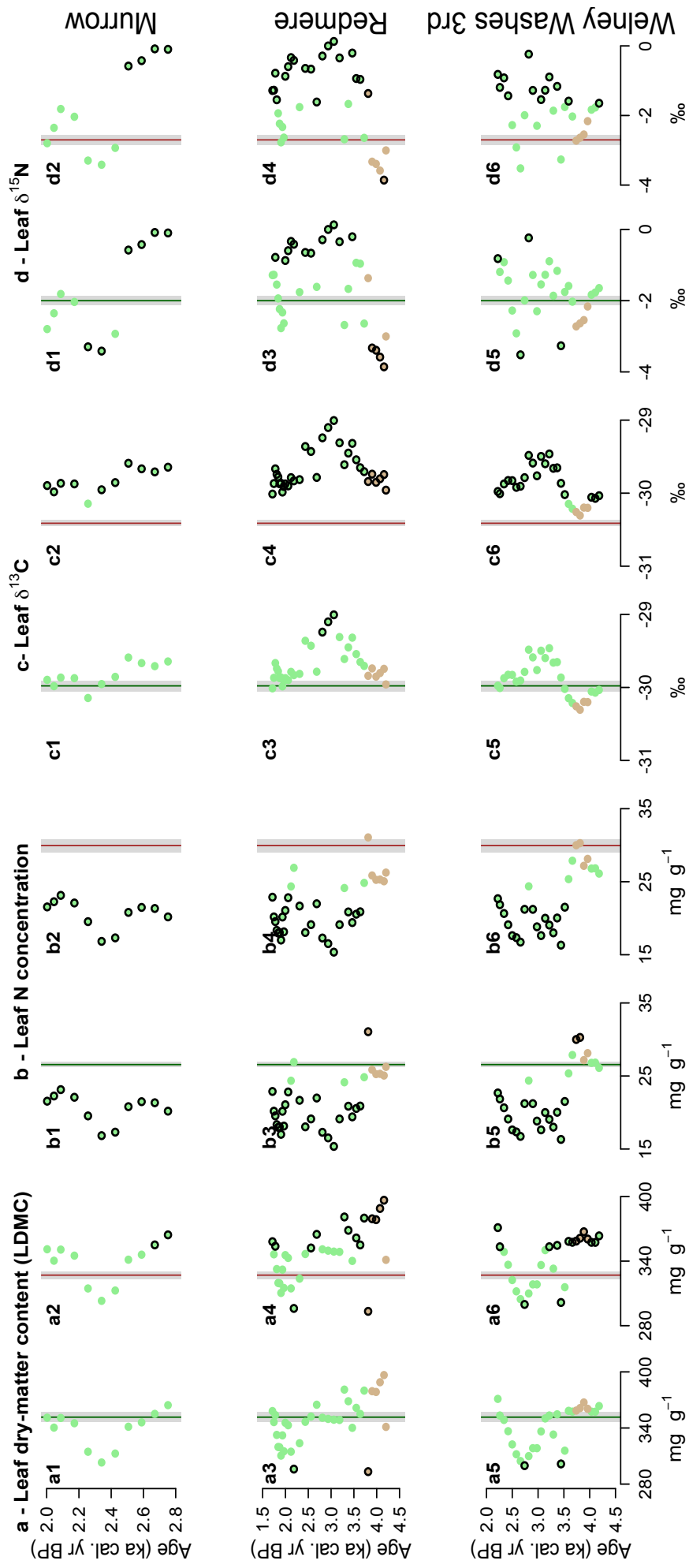
During the periods dominated by herbaceous pollen, grasses (Poaceae pollen) and sedges (Cyperaceae pollen) alternated in abundance. Ferns were also a common component of the ground flora, with most fern spores lacking the diagnostic features required for further taxonomic resolution and classified as Pteropsida monolet spores. Other notable presences in the fossil pollen record were Apiaceae, Rubiaceae and *Solidago virgaurea*-type throughout, but more locally *Filipendula* and *Lysimachia vulgaris*-type at The Dowells and *Ranunculus acris*-type in Redmere, Welney Washes and The Dowells. *Potentilla*-type pollen was constant albeit scarce, while *Urtica* was virtually absent throughout.

### 6.3.5 Changes in trait composition of the fossil pollen taxa through time

Leaf  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , N content and LDMC were selected to characterise the fossil pollen taxa through time since these traits revealed the highest proportion of variance in the vegetation explained by the modern pollen assemblages (see section 6.3.3 above). LDMC was selected for it showed the highest marginal  $r^2$  among the leaf mass/area traits. Plant height was not considered due to lack of variability within and between herbaceous fens.

Overall, leaf nutrient traits (leaf N, leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$ ) showed higher variability throughout the mid- to late-Holocene than LDMC, particularly in Fenland (Fig. 6.6 and 6.7). Shifts in vegetation (between wooded and herb-dominated taxa) largely resulted in changes in trait composition, with declines in leaf N and increases in leaf carbon and nitrogen isotopes generally caused by the replacement of *Alnus glutinosa*-dominated assemblages for taxa where grasses and sedges prevailed (and vice-versa; Fig. 6.6 and 6.7). Moreover, changes in mean trait values, particularly LDMC, also happened following changes in taxa composition within the herb-dominated flora (shifts in predominance between grasses and sedges mostly), especially in Fenland (Fig. 6.7).

Herb-dominated fossil taxa displayed, for the most part, lower leaf N content than the average contemporary herbaceous and woody fens in both regions (Fig. 6.6 and 6.7). However, wooded fossil assemblages in Romney Marsh (with *A. glutinosa* dominance) broadly revealed higher leaf N than modern expectations (Fig. 6.6), whereas the woody taxa in Fenland (where *Quercus* and *Betula* were more prominent) did not differ significantly from contemporary fen communities (Fig. 6.7). In addition, leaf  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the fossil flora in Fenland (particularly the herbaceous taxa) were usually higher than the



**Fig. 6.7:** Changes in CWMs through time (in calendar years before present) of the fossil pollen taxa from Fenland (site names shown on the right). Green and brown circles indicate the predominance of herbaceous and woody taxa in the fossil record, respectively. The means of the modern vegetation are shown for herb (green vertical lines) and woody (brown vertical lines) fens. Greyed areas around the modern means depict their 95% confidence intervals. Circles highlighted in black show fossil samples significantly different from modern vegetation means at  $p < 0.05$  (one-observation  $t$ -tests). Circles to the left of the modern means indicate that lower than expected trait values for contemporary fen vegetation prevailed in the fossil record, while circles to the right show the opposite. See section 6.2.3 for calculation methods. Uncertainty associated with estimates of pollen trait values may be caused by issues related to pollen taxonomic resolution, source area and pollen representation (see section 6.4.1 for a discussion).

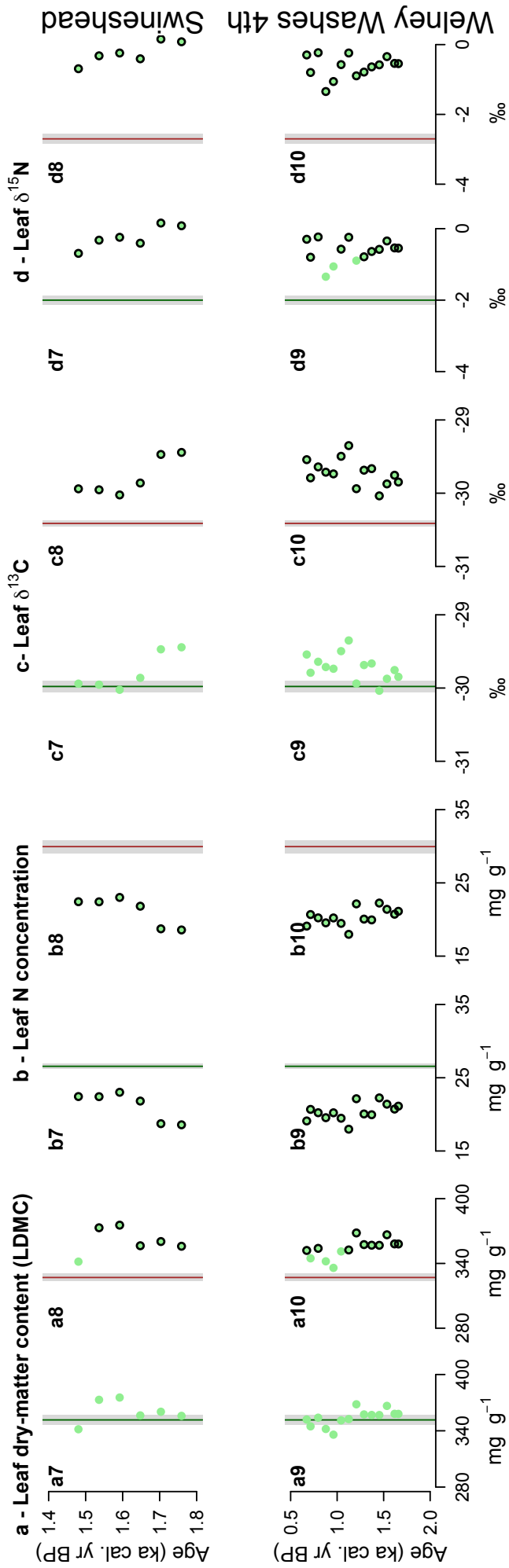


Fig. 6.7 continued.

contemporary fen average (Fig. 6.7), but at the Romney Marsh sites they were largely similar to the modern data (Fig. 6.6).

### 6.3.5-a Romney Marsh

The Romney Marsh (Brookland, The Dowells and Hope Farm) fossil pollen assemblages derived from herbaceous vegetation generally revealed higher variability in leaf traits through time than the pollen assemblages dominated by woody taxa (Fig. 6.6). Significant departures from present-day fen averages were mostly evident in leaf N concentration (Fig. 6.6b) and leaf  $\delta^{13}\text{C}$  (Fig. 6.6c). LDMC remained fairly constant in Brookland and The Dowells from c. 5500 to 2000 cal. yr BP under both herbaceous and wooded vegetation (Fig. 6.6a1-4), but varied more markedly at Hope Farm, particularly between c. 4500 and 3500 cal. yr BP and between c. 3000 and 2000 cal. yr BP, during which shifts from wooded (*A. glutinosa*-dominated) to herbaceous (mainly grasses and ferns with *Myrica gale* in the latter period) conditions led to noticeable decreases in LDMC (Fig. 6.6a5-6). The only significant departure from the contemporary LDMC herbaceous mean of  $351.6 \pm 5.4 \text{ mg g}^{-1}$  (95% CI,  $n = 83$ ;  $p < 0.05$ ; one-observation  $t$ -test) was recorded at c. 3800 cal. yr BP at Hope Farm (Fig. 6.6a5; Table 6.6), when pollen taxa (mostly sedges and ferns, with *A. glutinosa* and *Quercus* also present) with LDMC values lower than modern average conditions seem to have prevailed in the fossil record. Significant departures from mean LDMC of contemporary woody vegetation ( $327 \pm 3.4 \text{ mg g}^{-1}$ , 95% CI,  $n = 51$ ;  $p < 0.05$ ; one-observation  $t$ -test) also occurred throughout the same period, but most noticeably at Hope Farm at approximately 3500 cal. yr BP and between c. 3000 and 2000 cal. yr BP (Fig. 6.6a6, Table 6.6), when taxa (mainly grasses and sedges with *M. gale* and *Betula*) with higher LDMC than expected at present were more prominent in the fossil pollen record.

Leaf N concentration of the fossil flora departed significantly from modern herbaceous ( $26.6 \pm 0.4 \text{ mg g}^{-1}$ , 95% CI,  $n = 83$ ;  $p < 0.05$ ; one-observation  $t$ -test) and woody ( $30 \pm 0.9 \text{ mg g}^{-1}$ , 95% CI,  $n = 51$ ;  $p < 0.05$ ; one-observation  $t$ -test) community means (Fig. 6.6b), particularly in the period from approximately 4500 to 2500 cal. yr BP. The herb-dominated fossil samples in Brookland and Hope Farm (grasses, sedges and ferns with *A. glutinosa*, *Betula* and *Salix*) and the wooded fossil assemblages of The Dowells and Hope Farm (*A. glutinosa* dominance with *Betula*, *Quercus* and *Salix*) largely presented lower (Fig. 6.6b1-2 and b5-6) and higher (Fig. 6.6b3) values than expected at present, respectively (Table 6.6). There was a marked decrease in leaf N concentration in the Brookland fossil



flora at c. 3700 cal. yr BP, when a shift from wooded to predominantly herbaceous conditions (from *A. glutinosa*-dominated to sedge-dominated vegetation) seems to have occurred (Fig. 6.6b1-2). The opposite is true at The Dowells, where the transition from herbaceous to wooded conditions at around 4900 cal. yr BP (from mostly ferns and sedges to *A. glutinosa* dominance with *Betula*, *Quercus* and *Salix*) led to an overall increase in leaf N concentration (Fig. 6.6b3-4). The Hope Farm samples showed higher variability in leaf N, but broadly presented the same scenario of higher values under wooded (*A. glutinosa*, *Betula* and *Quercus* with *M. gale*) than herbaceous (mostly ferns and sedges) assemblages, with shifts in vegetation from woody to herbaceous at c. 3900 cal. yr BP and c. 3400 cal. yr BP leading to reduced leaf N content (Fig. 6.6b5-6).

Herb-dominated fossil assemblages in Romney Marsh mostly exhibited higher values of leaf  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than their wooded equivalents (Fig. 6.6c and d). The Brookland pollen samples representing herbaceous vegetation (grasses, sedges and ferns with *Betula* and *Quercus*) displayed significantly higher values of leaf  $\delta^{13}\text{C}$  ( $-30.4 \pm 0.04$  ‰, 95% CI,  $n = 51$ ;  $p < 0.05$ ; one-observation  $t$ -test) and leaf  $\delta^{15}\text{N}$  ( $-2.7 \pm 0.1$  ‰, 95% CI,  $n = 51$ ;  $p < 0.05$ ; one-observation  $t$ -test) than average contemporary woody fen communities between c. 3700 and 2300 cal. yr BP (Fig. 6.6c2 and d2; Table 6.6). The woody fossil assemblages (*A. glutinosa*, *Betula*, *Quercus* and *Salix* with a substantial fern component) were largely similar to present conditions though (Fig. 6.6c2 and d2). Interestingly, there was a gradual increase in leaf C and N isotopes under wooded conditions at The Dowells from c. 4800 to 2500 cal. yr BP (*A. glutinosa*, *Betula* and *Quercus* with *Salix*), even though no apparent shift to herbaceous vegetation happened during this period (Fig. 6.6c3-4 and d3-4). The herbaceous assemblages prevalent between c. 5300 and 4900 cal. yr BP (mainly ferns and sedges with *A. glutinosa* and *Quercus* present) had significantly higher leaf  $\delta^{13}\text{C}$  ( $p < 0.05$ ; one-observation  $t$ -test) than average modern woody fen communities (Fig. 6.6c4). Herb-dominated fossil assemblages in Hope Farm (ferns and sedges) largely revealed significantly higher values of leaf  $\delta^{13}\text{C}$  ( $p < 0.05$ ; one-observation  $t$ -test) than contemporary fen woodlands (Fig. 6.6c6; Table 6.6), but were similar to modern herbaceous sites (Fig. 6.6c5). On the other hand, woody pollen assemblages in Hope Farm at around 3700 cal. yr BP and from c. 3000 to 2600 cal. yr BP (*A. glutinosa*, *Betula* and *Quercus* with *M. gale*) presented significantly lower leaf  $\delta^{15}\text{N}$  than that of average present-day herbaceous ( $-2 \pm 0.1$  ‰, 95% CI,  $n = 51$ ;  $p < 0.05$ ; one-observation  $t$ -test) and woody fen communities (Fig. 6.6d5-6; Table 6.6).

**Table 6.6:** Site-level results of one-observation *t*-tests (*t*; depicted in Fig. 6.6 and 6.7), comparing the CWMs of selected leaf traits of the fossil pollen data (traits with the highest marginal  $r^2$  between the modern vegetation and modern pollen; see Fig. 6.5 above) with the mean trait composition of the modern herb and woody fens (and associated *p* values). Significant results ( $p < 0.05$ ) are highlighted in bold. LDMC = leaf dry-matter content.

	Type <sup>†</sup>	Age* <sup>*</sup>	LDMC				Leaf N concentration				Leaf $\delta^{13}\text{C}$				Leaf $\delta^{15}\text{N}$			
			herbaceous <sup>a</sup>		woody <sup>b</sup>		herbaceous <sup>c</sup>		woody <sup>d</sup>		herbaceous <sup>e</sup>		woody <sup>f</sup>		herbaceous <sup>g</sup>		woody <sup>h</sup>	
			<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Brookland	h	2.2	-0.3	0.74	1.3	0.19	-1.6	0.12	-2.0	0.06	-1.0	0.34	0.7	0.48	-1.2	0.25	0.1	0.92
	h	2.3	-0.1	0.94	1.9	0.07	-3.7	<b>&lt; 0.001</b>	-3.1	<b>0.003</b>	0.9	0.37	5.2	<b>&lt; 0.001</b>	0.8	0.42	2.2	<b>0.03</b>
	h	2.5	0.1	0.91	2.3	<b>0.03</b>	-2.3	<b>0.02</b>	-2.4	<b>0.02</b>	0.3	0.75	3.8	<b>&lt; 0.001</b>	0.3	0.76	1.7	0.10
	h	2.7	-0.1	0.89	1.8	0.08	-3.5	<b>0.001</b>	-3.0	<b>0.004</b>	0.6	0.57	4.4	<b>&lt; 0.001</b>	0.8	0.41	2.3	<b>0.03</b>
	h	2.9	-0.3	0.78	1.5	0.15	-3.6	<b>&lt; 0.001</b>	-3.1	<b>0.003</b>	0.6	0.55	4.5	<b>&lt; 0.001</b>	1.5	0.13	3.0	<b>0.004</b>
	h	3.1	-0.5	0.59	0.9	0.36	-4.3	<b>&lt; 0.001</b>	-3.4	<b>0.001</b>	0.7	0.51	4.6	<b>&lt; 0.001</b>	1.2	0.23	2.7	<b>0.01</b>
	h	3.3	-1.2	0.22	-0.5	0.61	-5.4	<b>&lt; 0.001</b>	-4.1	<b>&lt; 0.001</b>	0.8	0.45	4.8	<b>&lt; 0.001</b>	-0.6	0.54	0.7	0.50
	h	3.5	-0.1	0.94	1.9	0.07	-4.0	<b>&lt; 0.001</b>	-3.3	<b>0.002</b>	1.1	0.27	5.7	<b>&lt; 0.001</b>	1.5	0.13	3.0	<b>0.004</b>
	h	3.7	-0.3	0.75	1.4	0.17	-4.3	<b>&lt; 0.001</b>	-3.5	<b>0.001</b>	1.3	0.21	6.1	<b>&lt; 0.001</b>	1.5	0.14	3.0	<b>0.004</b>
	h	3.9	-0.2	0.84	1.6	0.11	-1.2	0.23	-1.8	0.08	0.0	0.99	3.0	<b>0.004</b>	0.1	0.93	1.4	0.16
	w	4.0	-0.2	0.86	1.7	0.10	1.1	0.29	-0.5	0.61	-1.1	0.28	0.4	0.71	-1.4	0.15	-0.2	0.83
	w	4.1	0.0	0.98	2.0	0.05	1.5	0.15	-0.3	0.78	-1.2	0.25	0.2	0.81	-1.3	0.20	-0.1	0.95
	w	4.1	0.2	0.83	2.5	<b>0.02</b>	0.5	0.63	-0.8	0.41	-0.3	0.74	2.2	<b>0.03</b>	-1.5	0.13	-0.3	0.75
	w	4.2	-0.1	0.90	1.8	0.08	1.8	0.07	-0.1	0.93	-1.1	0.26	0.3	0.79	-1.0	0.30	0.2	0.83
	w	4.2	0.0	0.96	1.9	0.06	2.0	<b>0.05</b>	0.0	0.99	-1.1	0.30	0.5	0.64	-1.0	0.33	0.3	0.78
	w	4.3	-0.5	0.64	1.1	0.29	1.0	0.31	-0.5	0.60	-1.5	0.14	-0.5	0.59	-1.9	0.07	-0.7	0.51
	w	4.4	-0.6	0.56	0.8	0.41	1.6	0.12	-0.2	0.82	-1.5	0.14	-0.6	0.55	-1.6	0.11	-0.4	0.68
	w	4.4	-0.7	0.46	0.5	0.61	0.2	0.85	-1.0	0.33	-1.4	0.17	-0.3	0.75	-2.2	<b>0.03</b>	-1.0	0.31
	w	4.5	-0.2	0.81	1.5	0.13	0.9	0.36	-0.6	0.56	-0.7	0.46	1.2	0.23	-0.9	0.35	0.3	0.75
	w	4.5	-0.2	0.86	1.7	0.10	1.0	0.30	-0.5	0.60	-0.9	0.39	0.9	0.37	-1.6	0.11	-0.4	0.70
w	4.6	-0.5	0.62	1.0	0.31	0.7	0.51	-0.7	0.47	-0.7	0.47	1.3	0.21	-1.2	0.23	0.0	0.98	
w	4.6	0.0	0.97	2.0	0.05	1.8	0.07	-0.1	0.93	-1.1	0.27	0.3	0.73	-1.6	0.11	-0.4	0.67	
w	4.7	-0.1	0.94	1.9	0.06	0.5	0.63	-0.8	0.41	-0.8	0.43	1.1	0.27	-0.7	0.47	0.6	0.58	
w	4.8	-1.1	0.29	-0.1	0.89	-3.0	<b>0.004</b>	-2.7	<b>0.01</b>	-0.3	0.77	2.3	<b>0.03</b>	-1.7	0.10	-0.4	0.66	
w	4.8	-0.5	0.62	1.0	0.31	-0.5	0.64	-1.4	0.18	-0.4	0.72	2.2	<b>0.04</b>	-0.6	0.53	0.7	0.51	
The Dowells	h	2.4	0.1	0.93	2.2	<b>0.03</b>	0.4	0.70	-0.9	0.38	-0.4	0.69	2.0	<b>0.05</b>	-0.3	0.78	1.1	0.30
	w	2.5	-0.1	0.92	1.8	0.07	1.9	0.06	0.0	0.97	-1.3	0.19	-0.1	0.89	-0.3	0.78	1.0	0.30
	w	2.7	0.2	0.82	2.5	<b>0.02</b>	1.5	0.14	-0.3	0.78	-0.8	0.43	1.1	0.27	-0.8	0.43	0.5	0.63
	w	2.8	-0.2	0.87	1.7	0.10	1.1	0.29	-0.5	0.62	-0.9	0.35	0.8	0.45	-0.1	0.92	1.2	0.22
	w	2.9	-0.2	0.88	1.7	0.09	2.3	<b>0.02</b>	0.2	0.86	-1.0	0.31	0.5	0.60	-0.7	0.47	0.6	0.57
	w	3.1	-0.3	0.75	1.4	0.18	2.3	<b>0.03</b>	0.2	0.88	-1.1	0.28	0.4	0.71	-0.2	0.81	1.1	0.28
	w	3.2	-0.2	0.87	1.7	0.09	2.7	<b>0.01</b>	0.4	0.69	-1.3	0.20	-0.1	0.94	-0.8	0.45	0.5	0.60
	w	3.4	-0.3	0.80	1.5	0.13	3.0	<b>0.004</b>	0.5	0.60	-1.4	0.16	-0.4	0.68	-0.5	0.59	0.8	0.45
	w	3.5	0.0	0.99	2.0	0.05	2.3	<b>0.02</b>	0.2	0.86	-1.5	0.15	-0.5	0.62	-1.2	0.22	0.0	0.99
	w	3.6	-0.1	0.90	1.8	0.08	3.1	<b>0.003</b>	0.6	0.56	-1.5	0.14	-0.5	0.59	-1.0	0.30	0.2	0.83
	w	3.7	0.2	0.87	2.4	<b>0.02</b>	3.0	<b>0.003</b>	0.6	0.57	-1.3	0.20	-0.1	0.92	-1.2	0.22	0.0	1.00
	w	3.8	-0.1	0.95	1.9	0.06	3.0	<b>0.004</b>	0.5	0.59	-1.2	0.24	0.2	0.86	-1.0	0.31	0.2	0.81
	w	3.9	0.2	0.85	2.4	<b>0.02</b>	2.5	<b>0.01</b>	0.3	0.76	-1.2	0.22	0.1	0.96	-1.6	0.10	-0.4	0.66
	w	4.0	-0.1	0.91	1.8	0.08	2.0	<b>0.05</b>	0.0	0.99	-1.3	0.19	-0.2	0.87	-1.4	0.16	-0.2	0.83
	w	4.1	0.0	0.98	2.0	0.05	3.5	<b>0.001</b>	0.8	0.41	-1.4	0.15	-0.5	0.64	-1.1	0.27	0.2	0.88
	w	4.2	-0.5	0.62	1.0	0.31	1.6	0.12	-0.2	0.83	-1.8	0.07	-1.4	0.16	-1.8	0.08	-0.6	0.57
	w	4.3	-0.1	0.96	1.9	0.06	2.6	<b>0.01</b>	0.4	0.72	-1.4	0.15	-0.4	0.66	-1.2	0.23	0.0	0.98
	w	4.4	-0.3	0.78	1.5	0.15	2.0	0.05	0.0	1.00	-1.6	0.11	-0.9	0.36	-1.6	0.10	-0.4	0.66
	w	4.5	0.1	0.94	2.2	<b>0.03</b>	3.0	<b>0.004</b>	0.6	0.58	-1.2	0.23	0.1	0.95	-1.0	0.31	0.2	0.81
	w	4.6	-0.4	0.68	1.2	0.24	1.0	0.34	-0.6	0.58	-1.5	0.15	-0.5	0.60	-1.7	0.10	-0.5	0.65
	w	4.7	-0.2	0.82	1.6	0.13	4.0	<b>&lt; 0.001</b>	1.1	0.28	-1.3	0.21	0.0	0.98	-0.5	0.64	0.8	0.40
	w	4.8	-0.9	0.37	0.2	0.84	-1.8	0.07	-2.1	<b>0.04</b>	-0.3	0.73	2.2	<b>0.04</b>	-1.3	0.19	-0.1	0.92
	h	4.9	-1.8	0.08	-1.7	0.10	-4.8	<b>&lt; 0.001</b>	-3.7	<b>0.001</b>	0.3	0.80	3.6	<b>0.001</b>	-1.7	0.08	-0.6	0.59
h	5.1	-0.5	0.64	1.1	0.29	-0.4	0.66	-1.3	0.19	-0.1	0.90	2.7	<b>0.01</b>	0.1	0.89	1.5	0.14	
h	5.2	-0.3	0.78	1.5	0.15	0.0	0.99	-1.1	0.28	-0.3	0.79	2.4	<b>0.02</b>	0.0	0.97	1.3	0.20	
h	5.3	-0.3	0.80	1.5	0.14	-2.4	<b>0.02</b>	-2.4	<b>0.02</b>	0.8	0.43	4.9	<b>&lt; 0.001</b>	1.0	0.30	2.5	<b>0.02</b>	

<sup>†</sup> Type of vegetation prevalent in the fossil pollen sample (h = herbaceous; w = woody)

\* Age of fossil pollen sample in thousands of calendar years before present (see text)

<sup>a</sup> LDMC herb fen modern vegetation mean =  $351.60 \pm 24.66 \text{ mg g}^{-1}$  ( $S; n = 83$ )

<sup>b</sup> LDMC woody fen modern vegetation mean =  $326.97 \pm 11.94 \text{ mg g}^{-1}$  ( $S; n = 51$ )

<sup>c</sup> Leaf N herb fen modern vegetation mean =  $26.56 \pm 1.7 \text{ mg g}^{-1}$  ( $S; n = 83$ )

<sup>d</sup> Leaf N woody fen modern vegetation mean =  $29.96 \pm 3.07 \text{ mg g}^{-1}$  ( $S; n = 51$ )

<sup>e</sup> Leaf  $\delta^{13}\text{C}$  herb fen modern vegetation mean =  $-29.98 \pm 0.34 \text{ ‰}$  ( $S; n = 83$ )

<sup>f</sup> Leaf  $\delta^{13}\text{C}$  woody fen modern vegetation mean =  $-30.41 \pm 0.14 \text{ ‰}$  ( $S; n = 51$ )

<sup>g</sup> Leaf  $\delta^{15}\text{N}$  herb fen modern vegetation mean =  $-2.0 \pm 0.56 \text{ ‰}$  ( $S; n = 83$ )

<sup>h</sup> Leaf  $\delta^{15}\text{N}$  woody fen modern vegetation mean =  $-2.7 \pm 0.51 \text{ ‰}$  ( $S; n = 51$ )

Table 6.6 continued

	Type <sup>†</sup>	Age <sup>*</sup>	LDMC				Leaf N concentration				Leaf δ <sup>13</sup> C				Leaf δ <sup>15</sup> N			
			herbaceous <sup>a</sup>		wooded <sup>b</sup>		herbaceous <sup>c</sup>		wooded <sup>d</sup>		herbaceous <sup>e</sup>		wooded <sup>f</sup>		herbaceous <sup>g</sup>		wooded <sup>h</sup>	
			t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p
Hope Farm	h	1.9	0.8	0.45	3.6	<b>0.001</b>	-1.6	0.10	-2.0	0.05	0.3	0.80	3.6	<b>0.001</b>	1.1	0.29	2.5	<b>0.02</b>
	h	2.1	0.6	0.57	3.2	<b>0.002</b>	-2.2	<b>0.03</b>	-2.3	<b>0.03</b>	0.2	0.85	3.5	<b>0.001</b>	-0.2	0.83	1.1	0.27
	h	2.3	0.9	0.38	3.9	<b>&lt; 0.001</b>	-0.8	0.45	-1.5	0.14	-0.5	0.62	1.8	0.08	-1.5	0.15	-0.3	0.80
	w	2.6	1.5	0.15	5.1	<b>&lt; 0.001</b>	-0.8	0.42	-1.5	0.13	0.2	0.86	3.4	<b>0.001</b>	-3.1	<b>0.002</b>	-2.0	<b>0.05</b>
	w	2.8	1.7	0.09	5.5	<b>&lt; 0.001</b>	-1.4	0.15	-1.9	0.07	0.7	0.50	4.6	<b>&lt; 0.001</b>	-3.3	<b>0.002</b>	-2.2	<b>0.03</b>
	w	3.0	-0.1	0.94	1.9	0.07	-1.3	0.21	-1.8	0.08	-1.1	0.26	0.3	0.79	-3.4	<b>0.001</b>	-2.4	<b>0.02</b>
	h	3.2	-0.6	0.58	0.9	0.37	-3.4	<b>0.001</b>	-2.9	<b>0.01</b>	0.2	0.84	3.5	<b>0.001</b>	0.6	0.57	2.0	0.05
	h	3.4	-0.8	0.45	0.5	0.64	-4.6	<b>&lt; 0.001</b>	-3.6	<b>0.001</b>	0.8	0.42	5.0	<b>&lt; 0.001</b>	0.0	0.99	1.3	0.19
	w	3.6	-0.5	0.59	0.9	0.35	0.2	0.83	-1.0	0.33	-1.6	0.11	-0.9	0.36	-1.8	0.08	-0.6	0.57
	w	3.6	-0.6	0.58	0.9	0.38	1.1	0.29	-0.5	0.62	-1.8	0.08	-1.3	0.20	-2.0	<b>0.05</b>	-0.8	0.40
	w	3.6	-0.2	0.87	1.7	0.09	2.9	<b>0.01</b>	0.5	0.63	-1.2	0.23	0.1	0.90	-0.8	0.40	0.4	0.67
	w	3.6	0.1	0.95	2.2	<b>0.04</b>	3.0	<b>0.004</b>	0.5	0.59	-1.3	0.19	-0.1	0.89	-1.1	0.28	0.2	0.87
	w	3.6	0.1	0.95	2.2	<b>0.04</b>	2.3	<b>0.02</b>	0.2	0.85	-1.1	0.25	0.2	0.81	-1.3	0.20	-0.1	0.95
	w	3.7	0.1	0.93	2.2	<b>0.03</b>	2.0	0.05	0.0	0.99	-1.6	0.12	-0.7	0.47	-1.9	0.07	-0.7	0.50
	w	3.7	0.1	0.93	2.2	<b>0.03</b>	1.6	0.11	-0.2	0.84	-1.5	0.15	-0.5	0.60	-2.0	0.05	-0.8	0.44
	w	3.7	0.0	0.99	2.1	<b>0.04</b>	1.0	0.31	-0.5	0.60	-1.6	0.10	-1.0	0.34	-2.5	<b>0.02</b>	-1.3	0.19
	w	3.7	-0.3	0.79	1.5	0.15	1.6	0.11	-0.2	0.84	-1.5	0.13	-0.7	0.51	-1.7	0.09	-0.5	0.59
	h	3.8	-2.3	<b>0.02</b>	-2.7	<b>0.01</b>	-6.2	<b>&lt; 0.001</b>	-4.5	<b>&lt; 0.001</b>	0.1	0.90	3.3	<b>0.002</b>	-3.0	<b>0.003</b>	-2.0	0.06
	h	3.9	-1.6	0.11	-1.3	0.21	-4.9	<b>&lt; 0.001</b>	-3.8	<b>&lt; 0.001</b>	0.4	0.72	3.9	<b>&lt; 0.001</b>	-1.7	0.09	-0.5	0.59
	w	4.0	-1.0	0.33	0.0	0.98	-1.5	0.13	-1.9	0.06	-0.2	0.83	2.5	<b>0.02</b>	-1.1	0.30	0.2	0.84
	w	4.2	-0.5	0.62	1.0	0.32	-0.1	0.89	-1.2	0.25	-0.4	0.71	2.1	<b>0.04</b>	-0.4	0.66	0.9	0.38
w	4.3	-0.4	0.68	1.2	0.24	-0.2	0.87	-1.2	0.24	-0.3	0.75	2.2	<b>0.03</b>	-0.3	0.76	1.0	0.31	
w	4.4	-0.2	0.88	1.7	0.09	3.9	<b>&lt; 0.001</b>	1.1	0.29	-1.5	0.13	-0.7	0.52	-0.7	0.49	0.6	0.55	
w	4.5	-0.1	0.91	1.8	0.08	3.2	<b>0.002</b>	0.7	0.50	-1.4	0.16	-0.4	0.70	-0.9	0.35	0.3	0.75	
w	4.7	-0.1	0.89	1.8	0.09	2.0	<b>0.05</b>	0.0	0.99	-1.3	0.21	0.0	0.98	-1.3	0.20	-0.1	0.96	
w	4.8	-0.2	0.85	1.7	0.10	2.7	<b>0.01</b>	0.4	0.68	-1.3	0.18	-0.2	0.83	-1.2	0.22	0.0	0.99	
w	4.9	-0.2	0.83	1.6	0.12	2.0	<b>0.05</b>	0.0	1.00	-1.1	0.26	0.3	0.77	-1.2	0.24	0.1	0.94	
Murrrow	h	2.0	0.0	0.98	2.0	0.05	-2.9	<b>0.004</b>	-2.7	<b>0.01</b>	0.2	0.81	3.6	<b>0.001</b>	-1.4	0.16	-0.2	0.85
	h	2.0	-0.5	0.65	1.1	0.27	-2.5	<b>0.01</b>	-2.5	<b>0.02</b>	0.0	0.99	3.0	<b>0.004</b>	-0.6	0.53	0.7	0.51
	h	2.1	0.0	0.97	2.0	0.05	-2.0	<b>0.05</b>	-2.2	<b>0.03</b>	0.3	0.75	3.8	<b>&lt; 0.001</b>	0.3	0.74	1.7	0.09
	h	2.2	-0.3	0.79	1.5	0.14	-2.6	<b>0.01</b>	-2.5	<b>0.01</b>	0.3	0.76	3.7	<b>&lt; 0.001</b>	-0.1	0.95	1.3	0.21
	h	2.3	-1.5	0.14	-1.0	0.31	-4.1	<b>&lt; 0.001</b>	-3.4	<b>0.002</b>	-0.5	0.63	1.9	0.07	-2.3	<b>0.02</b>	-1.1	0.26
	h	2.3	-2.0	0.05	-2.0	0.05	-5.7	<b>&lt; 0.001</b>	-4.2	<b>&lt; 0.001</b>	0.1	0.94	3.2	<b>0.003</b>	-2.5	<b>0.01</b>	-1.4	0.17
	h	2.4	-1.6	0.12	-1.2	0.24	-5.4	<b>&lt; 0.001</b>	-4.1	<b>&lt; 0.001</b>	0.4	0.72	3.9	<b>&lt; 0.001</b>	-1.6	0.10	-0.4	0.66
	h	2.5	-0.4	0.68	1.2	0.24	-3.4	<b>0.001</b>	-2.9	<b>0.01</b>	1.1	0.27	5.7	<b>&lt; 0.001</b>	2.5	<b>0.01</b>	4.1	<b>&lt; 0.001</b>
	h	2.6	-0.2	0.82	1.6	0.12	-3.0	<b>0.004</b>	-2.7	<b>0.01</b>	0.9	0.37	5.2	<b>&lt; 0.001</b>	2.8	<b>0.01</b>	4.4	<b>&lt; 0.001</b>
	h	2.7	0.1	0.89	2.3	<b>0.02</b>	-3.1	<b>0.003</b>	-2.8	<b>0.01</b>	0.8	0.44	4.9	<b>&lt; 0.001</b>	3.4	<b>0.001</b>	5.1	<b>&lt; 0.001</b>
h	2.8	0.5	0.61	3.1	<b>0.003</b>	-3.7	<b>&lt; 0.001</b>	-3.1	<b>0.003</b>	1.0	0.34	5.3	<b>&lt; 0.001</b>	3.4	<b>0.001</b>	5.0	<b>&lt; 0.001</b>	
Redmere	h	1.7	0.3	0.79	2.6	<b>0.01</b>	-2.2	<b>0.03</b>	-2.3	<b>0.03</b>	-0.1	0.92	2.8	<b>0.01</b>	1.3	0.21	2.7	<b>0.01</b>
	h	1.7	-0.2	0.83	1.6	0.12	-3.7	<b>&lt; 0.001</b>	-3.1	<b>0.003</b>	0.3	0.75	3.8	<b>&lt; 0.001</b>	1.3	0.20	2.8	<b>0.01</b>
	h	1.8	0.1	0.93	2.2	<b>0.03</b>	-4.1	<b>&lt; 0.001</b>	-3.4	<b>0.002</b>	0.9	0.37	5.2	<b>&lt; 0.001</b>	2.2	<b>0.03</b>	3.7	<b>0.001</b>
	h	1.8	-0.8	0.45	0.5	0.64	-4.8	<b>&lt; 0.001</b>	-3.7	<b>&lt; 0.001</b>	0.7	0.50	4.7	<b>&lt; 0.001</b>	0.8	0.43	2.2	<b>0.03</b>
	h	1.8	-1.3	0.20	-0.6	0.55	-5.0	<b>&lt; 0.001</b>	-3.9	<b>&lt; 0.001</b>	0.6	0.57	4.4	<b>&lt; 0.001</b>	0.1	0.91	1.5	0.15
	h	1.9	-1.3	0.20	-0.6	0.53	-5.0	<b>&lt; 0.001</b>	-3.8	<b>&lt; 0.001</b>	0.3	0.76	3.8	<b>&lt; 0.001</b>	-0.4	0.68	0.9	0.37
	h	1.9	-1.7	0.10	-1.4	0.18	-5.6	<b>&lt; 0.001</b>	-4.2	<b>&lt; 0.001</b>	0.3	0.74	3.8	<b>&lt; 0.001</b>	-1.4	0.18	-0.1	0.89
	h	1.9	-0.8	0.43	0.4	0.67	-3.7	<b>&lt; 0.001</b>	-3.2	<b>0.003</b>	0.0	0.99	3.0	<b>0.01</b>	-0.6	0.56	0.7	0.48
	h	2.0	-1.5	0.15	-1.0	0.33	-4.9	<b>&lt; 0.001</b>	-3.8	<b>&lt; 0.001</b>	0.2	0.84	3.5	<b>0.001</b>	-1.1	0.26	0.1	0.90
	h	2.0	-0.2	0.81	1.5	0.13	-3.2	<b>0.002</b>	-2.9	<b>0.01</b>	0.3	0.76	3.7	<b>&lt; 0.001</b>	2.0	<b>0.05</b>	3.5	<b>0.001</b>
	h	2.1	-0.3	0.73	1.3	0.19	-2.2	<b>0.03</b>	-2.3	<b>0.03</b>	0.2	0.82	3.5	<b>0.001</b>	2.5	<b>0.02</b>	4.1	<b>&lt; 0.001</b>
	h	2.1	-1.5	0.14	-1.0	0.31	-1.3	0.20	-1.8	0.08	0.6	0.58	4.3	<b>&lt; 0.001</b>	3.0	<b>0.004</b>	4.6	<b>&lt; 0.001</b>
	h	2.2	-2.2	<b>0.03</b>	-2.6	<b>0.01</b>	0.2	0.84	-1.0	0.33	0.4	0.67	4.0	<b>&lt; 0.001</b>	2.8	<b>0.01</b>	4.4	<b>&lt; 0.001</b>
	h	2.3	-1.1	0.26	-0.3	0.79	-2.9	<b>0.01</b>	-2.7	<b>0.01</b>	0.5	0.64	4.1	<b>&lt; 0.001</b>	0.4	0.67	1.8	0.08
	h	2.4	-0.2	0.84	1.6	0.11	-5.0	<b>&lt; 0.001</b>	-3.8	<b>&lt; 0.001</b>	1.8	0.08	7.3	<b>&lt; 0.001</b>	2.4	<b>0.02</b>	4.0	<b>&lt; 0.001</b>
	h	2.6	0.0	0.98	2.1	<b>0.04</b>	-4.4	<b>&lt; 0.001</b>	-3.5	<b>0.001</b>	1.6	0.12	6.8	<b>&lt; 0.001</b>	2.4	<b>0.02</b>	3.9	<b>&lt; 0.001</b>
	h	2.7	0.5	0.59	3.1	<b>0.003</b>	-2.7	<b>0.01</b>	-2.6	<b>0.01</b>	0.6	0.58	4.4	<b>&lt; 0.001</b>	0.7	0.49	2.1	<b>0.04</b>
	h	2.8	0.0	0.98	2.0	0.05	-5.4	<b>&lt; 0.001</b>	-4.1	<b>&lt; 0.001</b>	2.1	<b>0.04</b>	8.1	<b>&lt; 0.001</b>	3.0	<b>0.003</b>	4.7	<b>&lt; 0.001</b>
	h	2.9	-0.1	0.94	1.9	0.07	-5.9	<b>&lt; 0.001</b>	-4.3	<b>&lt; 0.001</b>	2.5	<b>0.01</b>	9.1	<b>&lt; 0.001</b>	3.5	<b>0.001</b>	5.2	<b>&lt; 0.001</b>
	h	3.1	-0.1	0.91	1.8	0.08	-6.6	<b>&lt; 0.001</b>	-4.7	<b>&lt; 0.001</b>	2.8	<b>0.01</b>	9.8	<b>&lt; 0.001</b>	3.8	<b>&lt; 0.001</b>	5.5	<b>&lt; 0.001</b>
	h	3.2	-0.1	0.90	1.8	0.08	-4.4	<b>&lt; 0.001</b>	-3.5	<b>0.001</b>	1.9	0.06	7.6	<b>&lt; 0.001</b>	2.9	<b>0.004</b>	4.5	<b>&lt; 0.001</b>
	h	3.3	1.2	0.24	4.5	<b>&lt; 0.001</b>	-1.4	0.16	-1.9	0.07	1.1	0.29	5.6	<b>&lt; 0.001</b>	-1.2	0.23	0.0	0.97
	h	3.4	0.7	0.50	3.5	<b>0.001</b>	-3.3	<b>0.001</b>	-2.9	<b>0.01</b>	1.5	0.13	6.7	<b>&lt; 0.001</b>	0.6	0.56	2.0	0.05
	h	3.5	-0.5	0.65	1.1	0.28	-4.2	<b>&lt; 0.001</b>	-3.4	<b>0.001</b>								

Table 6.6 continued

	Type <sup>†</sup>	Age <sup>*</sup>	LDMC				Leaf N concentration				Leaf $\delta^{13}\text{C}$				Leaf $\delta^{15}\text{N}$			
			herbaceous <sup>a</sup>		wooded <sup>b</sup>		herbaceous <sup>c</sup>		wooded <sup>d</sup>		herbaceous <sup>e</sup>		wooded <sup>f</sup>		herbaceous <sup>g</sup>		wooded <sup>h</sup>	
			t	p	t	p	t	p	t	p	t	p	t	p	t	p	t	p
Welney Washes 3rd peat	h	2.2	0.8	0.43	3.7	<b>0.001</b>	-2.3	<b>0.03</b>	-2.3	<b>0.02</b>	0.0	1.00	3.0	<b>0.004</b>	2.1	<b>0.04</b>	3.6	<b>0.001</b>
	h	2.3	0.1	0.94	2.2	<b>0.03</b>	-2.8	<b>0.01</b>	-2.6	<b>0.01</b>	-0.1	0.93	2.8	<b>&lt;0.001</b>	1.4	0.16	2.9	<b>0.01</b>
	h	2.3	-0.1	0.91	1.8	0.08	-3.5	<b>&lt;0.001</b>	-3.0	<b>0.004</b>	0.3	0.76	3.7	<b>&lt;0.001</b>	1.9	0.06	3.4	<b>0.001</b>
	h	2.4	-0.6	0.55	0.8	0.43	-4.4	<b>&lt;0.001</b>	-3.5	<b>0.001</b>	0.4	0.66	4.1	<b>&lt;0.001</b>	1.0	0.32	2.4	<b>0.02</b>
	h	2.5	-1.2	0.24	-0.4	0.71	-5.2	<b>&lt;0.001</b>	-4.0	<b>&lt;0.001</b>	0.4	0.67	4.0	<b>&lt;0.001</b>	-0.5	0.63	0.8	0.42
	h	2.6	-1.6	0.11	-1.3	0.22	-5.4	<b>&lt;0.001</b>	-4.1	<b>&lt;0.001</b>	0.2	0.87	3.4	<b>0.001</b>	-1.6	0.11	-0.4	0.68
	h	2.7	-1.9	0.06	-1.9	0.07	-5.8	<b>&lt;0.001</b>	-4.3	<b>&lt;0.001</b>	0.2	0.83	3.5	<b>0.001</b>	-2.7	<b>0.01</b>	-1.6	0.12
	h	2.7	-2.1	<b>0.04</b>	-2.3	<b>0.03</b>	-3.1	<b>0.002</b>	-2.8	<b>0.01</b>	0.6	0.58	4.3	<b>&lt;0.001</b>	0.0	0.99	1.4	0.18
	h	2.8	-1.7	0.10	-1.4	0.16	-1.3	0.20	-1.8	0.08	1.4	0.16	6.4	<b>&lt;0.001</b>	3.1	<b>0.002</b>	4.8	<b>&lt;0.001</b>
	h	2.9	-1.3	0.18	-0.7	0.48	-3.1	<b>0.002</b>	-2.8	<b>0.01</b>	1.1	0.26	5.7	<b>&lt;0.001</b>	1.3	0.20	2.7	<b>0.01</b>
	h	3.0	-1.3	0.18	-0.7	0.48	-4.5	<b>&lt;0.001</b>	-3.6	<b>0.001</b>	0.6	0.54	4.5	<b>&lt;0.001</b>	-0.5	0.60	0.8	0.44
	h	3.1	-0.6	0.54	0.8	0.44	-5.2	<b>&lt;0.001</b>	-4.0	<b>&lt;0.001</b>	1.4	0.17	6.3	<b>&lt;0.001</b>	0.8	0.42	2.2	<b>0.03</b>
	h	3.1	-0.1	0.96	1.9	0.06	-3.8	<b>&lt;0.001</b>	-3.2	<b>0.002</b>	1.1	0.28	5.7	<b>&lt;0.001</b>	1.3	0.20	2.8	<b>0.01</b>
	h	3.2	0.1	0.94	2.2	<b>0.03</b>	-4.4	<b>&lt;0.001</b>	-3.5	<b>0.001</b>	1.5	0.14	6.6	<b>&lt;0.001</b>	2.0	0.05	3.5	<b>0.001</b>
	h	3.3	-0.7	0.46	0.5	0.62	-5.0	<b>&lt;0.001</b>	-3.9	<b>&lt;0.001</b>	0.9	0.36	5.2	<b>&lt;0.001</b>	0.2	0.81	1.6	0.11
	h	3.4	0.1	0.90	2.3	<b>0.03</b>	-3.8	<b>&lt;0.001</b>	-3.2	<b>0.002</b>	0.9	0.35	5.3	<b>&lt;0.001</b>	1.5	0.14	3.0	<b>0.01</b>
	h	3.4	-2.0	<b>0.05</b>	-2.1	<b>0.04</b>	-6.0	<b>&lt;0.001</b>	-4.4	<b>&lt;0.001</b>	0.3	0.74	3.8	<b>&lt;0.001</b>	-2.2	<b>0.03</b>	-1.1	0.28
	h	3.5	-1.4	0.15	-0.9	0.36	-3.0	<b>0.004</b>	-2.7	<b>0.01</b>	-0.1	0.91	2.7	<b>0.01</b>	0.4	0.67	1.8	0.07
	h	3.6	0.3	0.79	2.6	<b>0.01</b>	-0.7	0.48	-1.5	0.15	-0.5	0.63	1.8	0.07	0.7	0.47	2.2	<b>0.04</b>
	h	3.7	0.2	0.81	2.5	<b>0.01</b>	0.8	0.44	-0.7	0.51	-0.7	0.50	1.4	0.17	-0.1	0.96	1.3	0.20
w	3.7	0.3	0.78	2.6	<b>0.01</b>	2.0	<b>0.05</b>	0.0	0.99	-0.8	0.42	1.1	0.29	-1.3	0.20	0.0	0.97	
w	3.8	0.4	0.70	2.8	<b>0.01</b>	2.2	<b>0.03</b>	0.1	0.92	-0.9	0.35	0.7	0.46	-1.1	0.26	0.1	0.90	
w	3.9	0.6	0.53	3.3	<b>0.002</b>	0.4	0.72	-0.9	0.38	-0.6	0.53	1.5	0.14	-1.0	0.34	0.3	0.77	
w	4.0	0.4	0.72	2.8	<b>0.01</b>	0.9	0.36	-0.6	0.56	-0.6	0.52	1.5	0.15	-0.3	0.77	1.0	0.30	
h	4.0	0.2	0.81	2.5	<b>0.02</b>	0.1	0.89	-1.0	0.31	-0.2	0.82	2.5	<b>0.02</b>	0.3	0.77	1.7	0.10	
h	4.1	0.2	0.82	2.5	<b>0.02</b>	0.2	0.88	-1.0	0.32	-0.3	0.79	2.4	<b>0.02</b>	0.4	0.68	1.8	0.08	
h	4.2	0.5	0.63	3.0	<b>0.004</b>	-0.3	0.79	-1.2	0.22	-0.2	0.87	2.6	<b>0.01</b>	0.6	0.53	2.0	<b>0.05</b>	
Swineshead	h	1.5	-0.4	0.69	1.2	0.23	-2.4	<b>0.02</b>	-2.4	<b>0.02</b>	0.1	0.91	3.3	<b>0.002</b>	2.3	<b>0.02</b>	3.9	<b>&lt;0.001</b>
	h	1.5	0.9	0.39	3.8	<b>&lt;0.001</b>	-2.4	<b>0.02</b>	-2.4	<b>0.02</b>	0.1	0.94	3.2	<b>0.003</b>	3.0	<b>0.004</b>	4.6	<b>&lt;0.001</b>
	h	1.6	1.0	0.34	4.0	<b>&lt;0.001</b>	-2.1	<b>0.04</b>	-2.2	<b>0.03</b>	-0.1	0.90	2.7	<b>0.01</b>	3.1	<b>0.003</b>	4.8	<b>&lt;0.001</b>
	h	1.6	0.2	0.85	2.4	<b>0.02</b>	-2.8	<b>0.01</b>	-2.6	<b>0.01</b>	0.3	0.74	3.8	<b>&lt;0.001</b>	2.8	<b>0.01</b>	4.4	<b>&lt;0.001</b>
	h	1.7	0.4	0.73	2.8	<b>0.01</b>	-4.6	<b>&lt;0.001</b>	-3.6	<b>0.001</b>	1.5	0.15	6.5	<b>&lt;0.001</b>	3.8	<b>&lt;0.001</b>	5.5	<b>&lt;0.001</b>
	h	1.8	0.2	0.86	2.4	<b>0.02</b>	-4.7	<b>&lt;0.001</b>	-3.7	<b>0.001</b>	1.5	0.13	6.7	<b>&lt;0.001</b>	3.7	<b>&lt;0.001</b>	5.4	<b>&lt;0.001</b>
Welney Washes 4th peat	h	0.7	0.0	0.99	2.1	<b>0.04</b>	-4.4	<b>&lt;0.001</b>	-3.5	<b>0.001</b>	1.3	0.21	6.0	<b>&lt;0.001</b>	3.0	<b>0.003</b>	4.6	<b>&lt;0.001</b>
	h	0.7	-0.3	0.78	1.5	0.15	-3.4	<b>0.001</b>	-3.0	<b>0.004</b>	0.5	0.59	4.3	<b>&lt;0.001</b>	2.1	<b>0.04</b>	3.7	<b>0.001</b>
	h	0.8	0.1	0.92	2.2	<b>0.03</b>	-3.7	<b>&lt;0.001</b>	-3.1	<b>0.003</b>	1.0	0.33	5.3	<b>&lt;0.001</b>	3.1	<b>0.002</b>	4.8	<b>&lt;0.001</b>
	h	0.9	-0.4	0.70	1.2	0.22	-4.1	<b>&lt;0.001</b>	-3.4	<b>0.002</b>	0.8	0.45	4.8	<b>&lt;0.001</b>	1.2	0.25	2.6	<b>0.01</b>
	h	1.0	-0.6	0.53	0.7	0.46	-3.7	<b>&lt;0.001</b>	-3.1	<b>0.003</b>	0.7	0.49	4.7	<b>&lt;0.001</b>	1.7	0.10	3.2	<b>0.003</b>
	h	1.0	0.0	0.99	2.0	0.05	-4.2	<b>&lt;0.001</b>	-3.4	<b>0.001</b>	1.4	0.17	6.4	<b>&lt;0.001</b>	2.5	<b>0.01</b>	4.1	<b>&lt;0.001</b>
	h	1.1	0.0	0.97	2.1	<b>0.04</b>	-5.0	<b>&lt;0.001</b>	-3.9	<b>&lt;0.001</b>	1.8	0.07	7.4	<b>&lt;0.001</b>	3.1	<b>0.002</b>	4.8	<b>&lt;0.001</b>
	h	1.2	0.7	0.50	3.4	<b>0.001</b>	-2.6	<b>0.01</b>	-2.5	<b>0.02</b>	0.1	0.91	3.3	<b>0.002</b>	2.0	0.05	3.5	<b>0.001</b>
	h	1.3	0.2	0.81	2.5	<b>0.02</b>	-3.8	<b>&lt;0.001</b>	-3.2	<b>0.002</b>	0.8	0.40	5.0	<b>&lt;0.001</b>	2.2	<b>0.03</b>	3.7	<b>0.001</b>
	h	1.4	0.2	0.83	2.5	<b>0.02</b>	-3.9	<b>&lt;0.001</b>	-3.2	<b>0.002</b>	0.9	0.37	5.2	<b>&lt;0.001</b>	2.4	<b>0.02</b>	4.0	<b>&lt;0.001</b>
	h	1.5	0.2	0.84	2.5	<b>0.02</b>	-2.5	<b>0.01</b>	-2.5	<b>0.02</b>	-0.2	0.87	2.6	<b>0.01</b>	2.5	<b>0.01</b>	4.1	<b>&lt;0.001</b>
	h	1.5	0.6	0.55	3.3	<b>0.002</b>	-3.0	<b>0.003</b>	-2.8	<b>0.01</b>	0.3	0.76	3.7	<b>&lt;0.001</b>	2.9	<b>0.004</b>	4.6	<b>&lt;0.001</b>
	h	1.6	0.3	0.79	2.6	<b>0.01</b>	-3.4	<b>0.001</b>	-3.0	<b>0.01</b>	0.6	0.52	4.6	<b>&lt;0.001</b>	2.6	<b>0.01</b>	4.2	<b>&lt;0.001</b>
	h	1.7	0.3	0.80	2.6	<b>0.01</b>	-3.2	<b>0.002</b>	-2.8	<b>0.01</b>	0.4	0.71	3.9	<b>&lt;0.001</b>	2.6	<b>0.01</b>	4.2	<b>&lt;0.001</b>

## 6.3.5-b Fenland

Overall, Fenland fossil assemblages showed higher variability in leaf traits than Romney Marsh assemblages from c. 4200 to 1500 cal. yr BP (Fig. 6.7). They also revealed greater differences to the trait values of modern fen communities from c. 4200 to 700 cal. yr BP (Fig. 6.7; Table 6.6). Marked reductions in LDMC occurred under herb-dominated vegetation in Murrow (c. 2500-2200 cal. yr BP; Fig. 6.7a1-2), Redmere (c. 2300-1700 cal. yr BP; Fig. 6.7a3-4) and the Welney Washes 3<sup>rd</sup> peat (c. 3400-2700 cal. yr BP; Fig. 6.7a5-6), when fern frequencies exceeded those of grasses and sedges. The shift from woody (mostly *Salix*, *Betula* and ferns) to herbaceous (mainly ferns, grasses and sedges, with *Quercus*,

*Betula* and *Salix* also present) assemblages at approximately 3700 cal. yr BP in Redmere also led to a decrease in LDMC until about 2000 cal. yr BP (Fig. 6.7a3-4). Furthermore, the woody pollen assemblages from c. 4200 to 3800 cal. yr BP had significantly higher LDMC than modern woody communities ( $p < 0.05$ ; one-observation  $t$ -test), as did the herb-dominated assemblages between c. 3700 and 3300 cal. yr BP (Fig. 6.7a4; Table 6.6). The Welney Washes 3<sup>rd</sup> peat also exhibited a decline in LDMC following a shift from wooded to herbaceous conditions at c. 3600 cal. yr BP (from *A. glutinosa* dominance with *Quercus* and *Salix* to mostly sedges, ferns and grasses; Fig. 6.7a5-6). Similar to Redmere, the woody assemblages prevalent at the Welney Washes 3<sup>rd</sup> peat from c. 4000 to 3700 cal. yr BP (*A. glutinosa* with *Quercus* and *Salix*) showed significantly higher LDMC ( $p < 0.05$ ; one-observation  $t$ -test) than average modern fen carr communities (Fig. 6.7a6; Table 6.6). On the other hand, the predominance of herbaceous conditions at Swineshead (mostly grasses, sedges and Apiaceae, with *Quercus* present) and Welney Washes 4<sup>th</sup> peat (mainly sedges, grasses and ferns with *Quercus* and *Salix*) during the period between c. 1800 to 700 cal. yr BP resulted in lower variability in LDMC overall (Fig. 6.7a7 to a10), though they showed significant departures from the modern woodland mean ( $p < 0.05$ ; one-observation  $t$ -test) throughout most of this period (Fig. 6.7a8 and a10; Table 6.6).

Leaf N concentration of the fossil taxa in Fenland differed significantly from that of modern fen vegetation (both woody and herbaceous;  $p < 0.05$ ; one-observation  $t$ -test) during most of the recorded period (Fig. 6.7b; Table 6.6). Leaf N of pollen assemblages remained consistently lower than present mean values during times when herb-dominated vegetation prevailed at all sites (Fig. 6.7b; Table 6.6). Moreover, the woody fossil samples in Redmere and the Welney Washes 3<sup>rd</sup> peat (largely dominated by *A. glutinosa*) showed generally higher leaf N content than the herbaceous fossil assemblages (dominated by grasses, sedges and ferns), with declining leaf N following apparent shifts in the vegetation (from woody to herbaceous; Fig. 6.7b3 to b6).

Leaf  $\delta^{13}\text{C}$  showed opposite results of leaf N, with Fenland fossil assemblages presenting significantly higher values than contemporary woody communities ( $p < 0.05$ ; one-observation  $t$ -test), particularly during periods when herbaceous vegetation was prominent in the fossil pollen record (Fig. 6.7c; Table 6.6). The pollen assemblages from Redmere dominated by woody taxa between c. 4200 and 3800 cal. yr BP (mostly *Salix* with *A. glutinosa* and *Quercus*) also displayed significantly higher values of leaf  $\delta^{13}\text{C}$  ( $p < 0.05$ ; one-observation  $t$ -test) than expected at present in wooded fens (Fig. 6.7c4; Table 6.6), which may reflect the presence of relatively open woodland with herb-rich ground layer,

as values for grasses, sedges and ferns were relatively high (typically > 10% TLP and > 5% TLP + Pterid.). In addition, the herb-dominated pollen samples from Redmere and Welney Washes 3<sup>rd</sup> peat between c. 3500 and 1700 cal. yr BP (mainly sedges with *Quercus*) presented consistently higher values of leaf  $\delta^{13}\text{C}$  than wooded fossil assemblages (Fig. 6.7c3 to c6), but were largely similar to average modern herbaceous conditions ( $-29 \pm 0.08$  ‰, 95% CI,  $n = 83$ ;  $p > 0.05$ ; one-observation  $t$ -test; Fig. 6.7c3 and c5).

Leaf  $\delta^{15}\text{N}$  results of the fossil flora displayed greater variability than leaf  $\delta^{13}\text{C}$  (Fig. 6.7d), particularly in Murrow (Fig. 6.7d1-2), Redmere (Fig. 6.7d3-4) and Welney Washes 3<sup>rd</sup> peat (Fig. 6.7d5-6). Herbaceous fossil assemblages largely revealed higher leaf  $\delta^{15}\text{N}$  than the woody-dominated fossil taxa (Fig. 6.7d1 to d6). There was a marked decline in leaf  $\delta^{15}\text{N}$  in Murrow at around 2300 cal. yr BP (when ferns and *Betula* pollen values increased, possibly indicating some woodland locally), rising again from about 2200 to 2000 cal. yr BP (following increases in *A. glutinosa* and *Salix*) to more closely resemble average contemporary conditions (Fig. 6.7d1-2). Earlier herbaceous assemblages present at this site between c. 2800 and 2500 cal. yr BP (dominated by sedges and grasses) displayed significantly higher leaf  $\delta^{15}\text{N}$  ( $p < 0.05$ ; one-observation  $t$ -test) than the mean recorded for modern fen communities (both herbaceous and woody; Fig. 6.7d1-2; Table 6.6). The apparent shift from wooded to herb-dominated vegetation at Redmere at c. 3700 cal. yr BP (indicated by an increase in Poaceae pollen) resulted in a sharp rise in leaf  $\delta^{15}\text{N}$  (Fig. 6.7d3-4). These herb-dominated fossil assemblages also showed significantly higher N isotope values than the modern herbaceous and woody means ( $p < 0.05$ ; one-observation  $t$ -test) throughout most of the period between c. 3600 and 2000 cal. yr BP (Fig. 6.7d3-4). However, earlier wooded assemblages present from c. 4200 to 3900 cal. yr BP (mostly *Salix* with *A. glutinosa*) revealed significantly lower leaf  $\delta^{15}\text{N}$  ( $p < 0.05$ ; one-observation  $t$ -test) than expected for contemporary herb fens (Fig. 6.7d3; Table 6.6). The herbaceous and wooded pollen assemblages from Welney Washes 3<sup>rd</sup> peat exhibited lower dissimilarities between them, but the herb-dominated vegetation prevalent between c. 3600 and 2200 cal. yr BP (with high fern values) displayed, for the most part, significantly higher leaf  $\delta^{15}\text{N}$  ( $p < 0.05$ ; one-observation  $t$ -test) than the modern woody average (Fig. 6.7d6; Table 6.6). The earlier wooded vegetation recorded between c. 4000 and 3700 cal. yr BP (mostly *A. glutinosa* with *Salix*) did not differ significantly ( $p > 0.05$ ; one-observation  $t$ -test) from modern conditions though (Fig. 6.7d5-6). Lastly, the herbaceous fossil assemblages of Swineshead and Welney Washes 4<sup>th</sup> peat showed less variability in leaf  $\delta^{15}\text{N}$  than the other sites between c. 1800 and 1200 cal. yr BP (with high grass and sedge pollen values), and

had mostly significantly higher isotope values ( $p < 0.05$ ; one-observation  $t$ -test) than contemporary herbaceous and woody fen communities (Fig. 6.7d7 to d10; Table 6.6). However, from c. 1100 to 700 cal. yr BP the herb-dominated fossil fens of the Welney Washes 4<sup>th</sup> peat revealed higher variability in leaf  $\delta^{15}\text{N}$  when other taxa (notably *Ranunculus acris*-type, *Hydrocotyle vulgaris*, Apiaceae, Rubiaceae and Brassicaceae) became slightly more prominent in the fossil record.

## 6.4 Discussion

### 6.4.1 Functional differences between the modern pollen taxa and the contemporary vegetation

The modern pollen assemblages suggested lower variability in functional traits between herb-dominated and woody communities than the modern vegetation (Fig. 6.4), particularly in leaf mass/area traits. The higher variability exhibited by the modern vegetation (mostly as a result of the differences between herbaceous and wooded sites) can be explained by differences in taxa abundance and composition between the two types of assemblages, likely caused by issues related to taxonomic resolution, pollen source area and pollen representation (see Faegri *et al.*, 1989 and Moore *et al.*, 1991 for a detailed discussion of these issues).

Firstly, the issue of taxonomic precision in pollen identification (caused by species that produce morphologically indistinguishable pollen, most notably in the Poaceae and Cyperaceae families in fen systems; Table 6.1) is one of the major constraints of conventional pollen analysis (Waller, 1994) and influenced the calculation of functional trait means of the pollen assemblages. In fact, only slightly over half of the taxa recorded in the vegetation of some herbaceous communities where Poaceae and Cyperaceae dominate (Appendix 1) were palynologically distinguishable (Waller *et al.*, 2017). Consequently, the relatively low variability in mean trait composition shown by the modern pollen assemblages across communities (Fig. 6.4) was possibly due, in part, to the averaging of trait values to characterise taxa with undistinguishable pollen, especially the highly abundant Poaceae and Cyperaceae (Fig. 6.2 and 6.3). For example, the particularly high SLA and LMA values exhibited by *Poa trivialis* (Appendix 3, 2.2e) and *Cladium mariscus* (Appendix 3, 2.3f), respectively were likely offset by the lower trait values presented by the other Poaceae and Cyperaceae taxa when calculating means. These two species were

particularly prominent in the alder carr in Woodwalton (plots 69 to 85) and the *Cladium* fen in Upton (plots 11 to 22), respectively and probably influenced the correspondingly higher SLA and LMA presented by the vegetation taxa of these two communities compared to the equivalent pollen assemblages (Fig. 6.4b and c).

Secondly, pollen is likely to be derived from a wider area (largely due to wind pollination) than that covered by the plant communities from which pollen samples were derived. As a result, the pollen signal from the *in situ* herb-dominated or woody vegetation gets 'diluted' by pollen from species of varied life forms from external sources, evidenced by the presence of arboreal pollen (the pollen of which, due to their height, has a greater dispersal potential than herb pollen) in herb-dominated communities (particularly *Alnus glutinosa*, *Betula* and *Quercus*; Fig. 6.2 and 6.3) and, to a much lesser extent, the relatively high herbaceous pollen (notably Poaceae) in wooded sites (Fig. 6.2 and 6.3). For instance, the *Cladium* fen in Upton revealed relatively high counts of *A. glutinosa* and *Betula* pollen (typically > 20% TLP; Fig. 6.2), even though these taxa were not recorded in the standing vegetation (Appendix 1). Consequently, the weighted-mean trait composition of the vegetation – which only accounts for the species present within a community – emphasises the characteristics of the dominant life form (herbaceous or woody), whereas the palynologically diverse taxa of the pollen assemblages (especially in the herbaceous sites; Fig. 6.2 and 6.3) probably leverages any extreme trait values presented by the dominant flora of the standing vegetation. That would explain the rather low variability in vegetative height between herbaceous and woody communities exhibited by the pollen taxa compared to the vegetation flora (Fig. 6.4a). Accordingly, the comparatively low height presented by the pollen samples of the *Juncus subnodulosus* fen in Upton and the *Phragmites* fen in Woodwalton (Fig. 6.4a) is due to the relatively low arboreal pollen count in these two communities (Fig. 6.2 and 6.3).

Thirdly, relative representation in the pollen record, due to production and dispersal bias, is likely another reason for the differences seen in trait composition between the modern pollen assemblages and the vegetation, given that mean trait values were abundance-weighted. Some taxa attain higher pollen frequencies than their abundance in the vegetation would suggest (and are hence over-represented), while other taxa, prominent in the vegetation, may be scarce, or even absent from the pollen record (under-represented). For instance, *Salix* spp. and *Viburnum opulus*, somewhat locally prominent in the recorded vegetation, and the occasionally present *Frangula alnus* (Appendix 1) are all entomophilous species (insect pollinated and low pollen producers) and tend to be heavily



under-represented in the pollen record compared with the anemophilous (wind pollinated and high pollen producer) *Alnus glutinosa* (Waller, 1994). Moreover, the pollen of some other prominent genera in fen systems, like *Luzula* and more notably *Juncus*, are not preserved and are hence typically absent from pollen records. In fact, the vegetation species of the *Cladium* fen in Upton (plots 11 to 22; Fig. 6.4), where *Juncus* and occasionally *Salix* were relatively abundant (Appendix 1) and showed comparatively high leaf C tissue and low leaf N (Appendix 3, 2.6c and g and 2.7c and g), exhibited lower SLA and leaf N and higher LDMC, Lth and leaf C:N ratio than the equivalent pollen assemblages, from which these taxa were under-represented or absent (Fig. 6.2). Other notable examples of discrepancy in taxa representation and abundance between the pollen and vegetation data causing differences in trait composition include *Fraxinus excelsior* in the woodlands in Upton, which was common in the alder carr and fairly prominent in the mixed woodland (Appendix 1), but scarce in the pollen samples (Fig. 6.2), and *Glechoma hederacea* (a species with relatively high SLA and leaf N and low LDMC; Appendix 3, 2.2a, 2.4a and 2.7a), which was abundant in the alder carr and recorded in the glades in Woodwalton (Appendix 1), but absent from the modern pollen record. Moreover, tree taxa such as *Alnus glutinosa*, *Betula* and *Quercus*, all species with relatively high leaf C concentration (Appendix 3, 2.6b), were relatively abundant in the pollen record throughout Upton and Woodwalton (Fig. 6.2 and 6.3), including in the herb-dominated communities, and supposedly caused the pollen assemblages to generally display slightly higher leaf C content than the modern vegetation (Fig. 6.4f).

Even though many pollen types can only be identified to genus level and some are only diagnostic to family level (Table 6.1), pollen assemblages should offer significant opportunities to examine functional patterns in vegetation that outweigh this taxonomic limitation (Barboni *et al.*, 2004). In fact, despite the limitations discussed above, it has been shown elsewhere (using Indices of Association and the same data presented here) that any loss of taxonomic precision in pollen identifications should not preclude the identification of fen communities in the pollen record, including tall-herbaceous vegetation (Waller *et al.*, 2017). The taxonomic detail was found to remain sufficiently high in the palynological equivalents data for the areas sampled to be effectively separated, by examining variations in the proportions of Poaceae and Cyperaceae pollen and the presence of diagnostic herbs associated with particular habitats (Waller *et al.*, 2017). Results such as these thus imply pollen presence can be interpreted as indicative of the local presence of some fen taxa. The satisfactory degree of association found for four functional traits (LDMC, leaf N, leaf  $\delta^{13}\text{C}$

and leaf  $\delta^{15}\text{N}$ ; Fig. 6.5) linking the modern pollen and vegetation taxa should, therefore, allow for the interpretation of fossil pollen records to infer the functional characteristics of past vegetation.

#### 6.4.2 Trait composition of the fossil pollen taxa

The use of palaeoecological records generally allows for the reconstruction of ecosystem dynamics over space and time (Jeffers *et al.*, 2015), with fossil pollen records representing major sources for reconstructing and understanding vegetation dynamics on long timescales (Lacourse, 2009) such as the Holocene (Marquer *et al.*, 2014). The current analyses using fossil pollen assemblages from Romney Marsh and Fenland clearly establish that temporal shifts in the functional composition of fen vegetation, generally accompanied by shifts between herb-dominated and woody taxa, are closely linked to interspecific trait differences between the diverse life forms alternating in prominence over time. Crucially, interspecific differences in plant functional traits provide the means through which changing environmental conditions control vegetation dynamics (Lacourse, 2009). The variety of individual leaf or plant level traits amongst life forms underpins a functional hierarchy of plant traits (Pillar, 1999), in which life form is the fundamental characteristic of a plant, followed by leaf type and phenology and finally leaf and plant traits (Lavorel *et al.*, 1997). The functional differentiation resulting from shifts in the relative abundance of co-existing groups (deciduous trees and shrubs and perennial grasses, sedges, ferns and forbs) not only influence the mean trait composition of communities, but can also lead to large and consistent 'afterlife' effects on ecosystem processes, such as decomposition rates and nutrient cycling (Cornwell *et al.*, 2008). The fundamental role of life forms in the functional composition of plant communities is central to the results presented here. For instance, it is apparent that pollen assemblages dominated by woody taxa are more reliable when attempting to reconstruct the functional composition of past vegetation than herb-dominated assemblages, given the intrusion of arboreal pollen in the latter, weakening the signal of the dominant herbaceous *in situ* vegetation and affecting weighted-mean trait calculations. On the other hand, intrusion of herbaceous pollen on woody-dominated samples seems to be much less pronounced. The wooded assemblages were generally better at reflecting the mean functional composition of contemporary fen communities than the herb-dominated assemblages, which constantly revealed significant departures from the modern means throughout the mid- to

late-Holocene (Fig 6.6 and 6.7), particularly in Fenland (Fig. 6.7). Once again, that may reflect, to some extent, the relatively high tree pollen among herbaceous fossil assemblages and the virtual absence of tree taxa from modern herb-dominated communities.

Romney Marsh sites generally presented fossil assemblages more closely resembling the modern fen vegetation than the Fenland sites (Fig. 6.6). Leaf nutrient traits (N content,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) broadly revealed higher variability between fossil samples and greater differences to contemporary fen communities than LDMC (Fig. 6.6 and 6.7). Differences in taxa composition between the fossil records and the modern communities probably explain the instances where the two types of assemblage (pollen and vegetation) differed significantly. The virtual absence from the pollen record of taxa with nitrogen-rich leaves that were notably present in the modern vegetation, such as *Urtica dioica*, *Solanum dulcamara*, *Glechoma hederacea* and *Vicia cracca* (Appendix 3, 2.7a and d) may explain the significantly lower leaf N content of the fossil pollen assemblages in relation to the modern herbaceous and woody vegetation means, particularly in Fenland (Fig. 6.7). However, the particularly high pollen values of *A. glutinosa* (a N-fixing species) throughout most of the woody fossil records of Hope Farm and The Dowells were likely responsible for their higher leaf N content than the modern herbaceous mean (Fig. 6.6). The predominance of sedges and grasses in the pollen record with relatively high mean values of leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$  compared to trees, shrubs and herbs (Appendix 3, 1i and j) would justify the significantly higher values of C and N isotopes in the herb-dominated fossil assemblages in relation to the modern vegetation, most notably in Fenland (Fig. 6.7). In fact, the predominance of *Juncus subnodulosus*, a species with low leaf  $\delta^{15}\text{N}$  (Appendix 3, 2.10g), in the contemporary herbaceous communities, notably in Upton and in the sedge fen in Woodwalton (Appendix 1), may have reduced the signal of leaf  $\delta^{15}\text{N}$  in the modern vegetation, resulting in the significant differences between the fossil and modern herb-dominated assemblages. As stated previously, rushes are not normally preserved in pollen records due to the fragility of the pollen they produce. Additionally, the significant differences in leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$  between the herb-dominated pollen assemblages and the modern woody fen average in Brookland (Fig. 6.6) were likely caused by the relatively high pollen values of *Myrica gale* in these fossil assemblages, a species with comparatively high leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$  (Appendix 3, 2.9c and 2.10c) that was absent from the contemporary wooded sites (Appendix 1).

Several factors make these pollen-vegetation relationships complex, most notably the presence of a 'regional component' in pollen records (pollen from outside the sedimentary basin) and, as discussed above, the inter-taxonomic differences in pollen productivity (Marquer *et al.*, 2014). Consequently, estimation of plant abundances from pollen count data is difficult (Sugita, 1994). Several approaches have been proposed to circumvent these limitations when using pollen to reconstruct past vegetation, including the use of R-values to compensate for differences in pollen productivity between taxa (Andersen, 1970; Bradshaw, 1981), the modelling of pollen-accumulation rates (Seppä *et al.*, 2009) and the comparison of contemporary observations of vegetation cover from high-resolution radiometer sensors with modern pollen data (Tarasov *et al.*, 2007). In particular, the Landscape Reconstruction Algorithm (LRA) modelling has been advanced as an alternative for quantitative reconstructions of vegetation abundance at regional and local spatial scales (Sugita, 2007a, b), possibly providing the most appropriate data correction method for the type of analysis presented here. The LRA uses pollen counts and proportions to reduce pollen productivity and dispersal biases and, crucially, quantifies and then subtracts background pollen (pollen coming from beyond the relevant source area) in order to quantitatively reconstruct local vegetation, while accounting for differences in basin size and the spatial heterogeneity of vegetation (Sugita, 2007b). Additionally, the LRA corrects for the non-linear nature of the pollen-vegetation relationship and allows for the reconstruction of past abundances of individual plant taxa around pollen sites (Marquer *et al.*, 2014). Therefore, prior to the calculation and interpretation of abundance-weighted trait means of past vegetation, it would be desirable to incorporate such models to better characterise differing regional vegetation taxa compositions over time and space. However, the application of the LRA requires estimates of regional vegetation abundance obtained from pollen records originating from large sites (Hultberg *et al.*, 2015). Hence, due to logistical constraints it was not possible to apply the LRA approach to the current analysis.

Traits of the predominant plant taxa are normally closely related to the environmental conditions in which they are found (Garnier *et al.*, 2016). Therefore, despite the limitations discussed above, the use of fossil pollen assemblages, particularly assemblages dominated by woody taxa, should provide a useful way to tentatively assess the links between community functional composition and changing environmental conditions over long ecological timescales (Lacourse, 2009). To that end, nutrient traits proved particularly useful in determining changes in mean trait values of the dominant

plant taxa and, although none of the pollen-vegetation modelling approaches described above could be adopted here, their inclusion was validated by the fact that they showed the best fit amongst leaf traits between modern pollen and vegetation assemblages (Fig. 6.5). The dominant herbaceous plants of the mid- to late-Holocene assemblages in Romney Marsh and Fenland were generally characterised by taxa with fairly high LDMC and relatively low leaf N content (Fig. 6.6 and 6.7), suggesting the predominance of conservative economic strategies along the leaf economics spectrum (see Chapter 3), typically associated with the conservation of resources within thick leaves of high dry mass-to-surface area ratios (Wright *et al.*, 2004). Crucially, the implications of predominantly low leaf N concentration and high leaf dry mass tissue in vegetation go beyond a plant's ability to grow and assimilate carbon, but are rather closely linked to ecosystem processes such as the breakdown of leaf litter and soil carbon retention (Bardgett *et al.*, 2008). Poor quality litter that are low in nutrients and high in recalcitrant compounds, such as lignin and phenolic acids, tend to decompose slowly due to retardation of microbial activities, creating a negative feedback on carbon exchange owing to reduced heterotrophic respiration (Cornelissen *et al.*, 2007). Therefore, the characteristic herb-dominated assemblages present between c. 5000 and 700 cal. yr BP in Romney Marsh and Fenland are suggestive of an environment with high carbon retention and low mineralisation rates in the top litter layer of soil. That would somehow contrast with present conditions in Woodwalton and Upton, where the prominence of forbs with nitrogen-rich leaves and high leaf surface area-to-dry mass ratio, such as *Urtica dioica*, *Solanum dulcamara*, *Glechoma hederacea* and *Galium aparine*, would induce a positive feedback on microbial activity (and hence on carbon mineralisation rates) due to enhanced soil nutrient availability and decomposition of nutrient-rich litter (Bardgett *et al.*, 2008), promoting higher rates of carbon loss from the top soil layer.

Carbon isotope discrimination can be used as a proxy reflecting both changing climatic and hydrologic conditions (Ferrio *et al.*, 2005), while nitrogen isotope results may reflect soil fertility conditions and terrestrial N availability, i.e. the supply of N relative to demand by plants and microbes (Craine *et al.*, 2009b). Therefore, it would be tempting to conclude that the higher stable isotope values revealed by the fossil assemblages compared to the contemporary vegetation, particularly in Fenland (Fig. 6.7), were suggestive of higher water and N availability to plants during the mid- to late-Holocene than at present. However, stable isotopes measured from organic material integrate fractionation processes and complex physiological responses of plants to local conditions

(Robinson *et al.*, 2000), such that isotope values provide an index of the processes in the nutrient cycles of carbon and nitrogen that discriminate against a particular isotope ( $^{13}\text{C}$  or  $^{15}\text{N}$ ; Houlton and Bai, 2009). For instance, when N supply is high relative to biotic demand, N is lost through fractionating pathways and the remaining N in the ecosystem is enriched in  $^{15}\text{N}$  (McLauchlan *et al.*, 2013). Similarly, carbon isotope discrimination occurs in the incorporation of  $\text{CO}_2$  into plant biomass (Farquhar *et al.*, 1989), and may thus be dependent on atmospheric  $\text{CO}_2$  concentrations (McLauchlan *et al.*, 2010). Therefore, the use of leaf isotopic signatures collected from contemporary organic tissue to characterise fossil assemblages may not have been the best approach to infer past ecosystem processes from community functional composition, since they are highly context-dependent. In hindsight, the use of traits that are better conserved within phylogenetic groups and are not highly sensitive to local conditions may be a better approach in the type of study conducted here.

The current set of analyses provided a potentially promising approach to infer changes in ecosystem processes using pollen assemblages and plant functional traits, and consequently a better understanding of past environmental conditions. The patterns revealed by such analyses may demonstrate that community functional composition reflects significant interactions between environmental change and plant ecological strategies over thousands of years (Lacourse, 2009). However, as discussed above, issues that remain to be resolved include the use of appropriate pollen-vegetation models to better reflect past vegetation abundances, as well as a careful consideration of which species-specific functional traits to incorporate that would enhance the interpretation of past ecosystem processes.

## Chapter 7

### Conclusions

Although biodiversity can be defined using different components (e.g., taxonomic, phylogenetic), the diversity of traits, or functional diversity, is receiving considerable attention as the main biotic component by which individual organisms and biological communities influence ecosystem processes, which in turn modulate ecosystem services (de Bello *et al.*, 2010). The set of analyses presented here confirmed the wide applicability of the trait approach in studies investigating the effects of biodiversity on ecosystem processes and community dynamics, as well as its response to human intervention. As demonstrated in Chapter 3, the functional characteristic of lowland fen communities responds strongly to changing disturbance intensity, and is not necessarily coupled with the response of taxonomic diversity. While species richness responded positively to disturbance, mostly as a result of management preventing the development of fen carr over herb fens, the functional diversity of plant communities decreased from unmanaged woods to managed herbaceous sites. That is most likely due to herb fens being dominated by perennial monocotyledons, while fen carr typically comprises diverse life forms (tall deciduous trees with forbs, slender grasses and thick-leaved monocots; Appendix 1). However, the traits and ecological strategies of neighbouring plants tended to diverge with increasing disturbance intensity among managed communities. The increasing levels of functional diversity, richness and divergence seen along a management gradient (Chapter 3) were probably a result of increased forb diversity in the mostly managed sites (Appendix 1). Therefore, conservation-focused management practices intended to increase the taxonomic diversity of fen communities seems to be additionally enhancing diversity at the functional level in herb fens. Moreover, as discussed in Chapter 3, the higher number of species per functional group (grasses, sedges, rushes and forbs) in the mostly managed sites (Appendix 1) supposedly increased their functional redundancy, which may enhance their resilience to future disturbances (Folke *et al.*, 2004; Brown *et al.*, 2011). Communities with higher numbers of functionally similar species have greater chances of preserving at least some of these species under stochastic or directional changes in the environment and maintain the current properties of the ecosystem (Chapin III *et al.*, 2000). However, the resulting functional composition of communities tends to be highly dependent on the

choice of metric used, particularly between those that only consider species' presence/absence and those that are abundance-weighted. Therefore, it is useful to consider different aspects of functional diversity when assessing the impact of human intervention on plant communities, since other metrics could yield different results.

Single-trait measures of mean functional composition have also been shown to be valuable tools in determining relationships between plant traits and ecosystem processes. The results presented in Chapter 3, for instance, would suggest functional traits play an important role in the biogeochemical cycles of C and N, supporting the relevance of a leaf economics spectrum in which the traits of green leaves can have important effects on soil processes. Results showed that communities under intensive management are recruiting species characterised by photosynthetic tissue of extended durability, favouring C and N retention in the substratum due to low decomposition rates. These findings lend some support to current management practices, particularly at Woodwalton, which are contributing not only to enhanced floristic diversity but to the provision of important ecosystem services commonly associated with peatland environments, notably soil C stock and N retention. In fact, the provision of such services are some of the stated objectives of current long-term conservation projects in the region (Gauci, 2008).

When considering the concurrent effects of biotic and abiotic components on ecosystem processes (Chapter 4), management intervention and environmental variables seem to be the major controlling factors, since path models suggested plant leaf traits play a secondary role in the regulation of ecosystem processes in this type of habitat. However, as discussed in Chapter 4, capturing the effect of trait functions on ecosystem processes may be impaired when considering communities with low variation in leaf life span between co-occurring species (not measured for the present analyses), which seems to occur often in many herbaceous and woody deciduous communities (Funk and Cornwell, 2013). Therefore, these findings suggest the significant effects plant leaf traits might have on ecosystem functioning in some habitats may not be repeated across ecosystems, and will depend on the range of trait variation and leaf life span present within and across communities. It is also possible that belowground organs in this type of environment play a larger role in soil processes, given the number of unique characteristics wetland taxa have developed to adapt to waterlogged conditions (Keddy, 2010). Measuring and quantifying the role belowground traits (e.g., root architecture and biochemistry) play on soil processes could provide more detailed information on the role of plant species in wet environments. Further studies should hence attempt to investigate not only the influence of belowground



organs, but the interactions between above- and belowground traits, abiotic factors and soil microbial communities (de Vries *et al.*, 2012). Moreover, these results may reflect the significant regulating effects of constantly changing conditions peatlands are typically subjected to, receiving water input from external sources and being under varying degrees of flooding throughout the year, which has consequences for the amount of organic content in the substratum (Keddy, 2010; Mitsch and Gosselink, 2015). Local environmental conditions and land use change should thus be accounted for when quantifying the contribution of different ecosystem components to the provision of ecosystem processes (and ultimately services).

Management of lowland fens also seems to have pronounced effects on plant community dynamics (Chapter 5). The use of an index of variance to quantify the relationships between observed data and simulated communities generated along orthogonal trait axes with random distributions has allowed for different assembly processes (stochastic and deterministic) to be determined, revealing the simultaneous influence of contrasting processes within and across plant communities in fens. These results confirm previous suggestions that communities can be both stochastic and deterministic (Fukami *et al.*, 2005) and validates the search for the concurrent presence of both processes. Overall though, they have mostly shown a niche-based scenario of plant assemblages in lowland fens, where habitat specialisation, adaptation to disturbance and strategy differentiation allow different life forms to coexist. These findings would be in accordance with expectations for this type of habitat, where taxa that pass through the biotic and abiotic filters are typically characterised by ecological and adaptive strategies developed to cope with environmental and disturbance constraints (Keddy, 2010).

Additionally, the use of a functional approach to determine vegetational and environmental history on long ecological timescales through the use of palaeoecological datasets still seems to be in its early stages (Lacourse, 2009). However, the methods applied in Chapter 6 to reconstruct the mean trait composition of past fen communities provides a promising approach in understanding how temporal changes in the functional composition of vegetation can potentially affect ecosystem functioning, since plants are known to exert significant control over the availability and cycling of nutrients through changes in photosynthetic, growth and decomposition rates (Díaz and Cabido, 2001). Limitations commonly associated with conventional pollen analysis need to be addressed though, particularly issues regarding the estimation of plant abundances from pollen count data (Sugita, 1994). Future studies should therefore consider the use of modelling

algorithms to more accurately reconstruct vegetation abundances at regional and local spatial scales, particularly when using abundance-weighted measures of trait diversity and composition. This seems to be a promising field of future research and one that needs to be explored further.

To conclude, the findings presented here can be useful to long-term restoration programmes (e.g., The Great Fen Project) to develop appropriate management strategies. Regular cutting of herbaceous fens was shown to not only promote higher biodiversity (both taxonomic and functional) and to preserve some key fenland species (e.g., *Molinia caerulea*), but to increase the potential of fen soils to sequester and store carbon. The maintenance of a disturbance regime in such habitats seems thus to be a better option than allowing for natural succession to take place (i.e., the gradual development of fen carr communities over herb fens), since monocot-dominated herb fens seem to support anaerobic soil processes and associated soil fauna characteristic of wet habitats. However, the presence of both longer and shorter vegetation, as well as of carr communities that include a lush herbaceous flora beneath tall canopy with a different character from that of open fen (Appendix 1), promotes biodiversity and the aesthetic value of protected fens, and help to preserve some key fenland habitats (e.g., drainage channels and their banks along transition zones). The maintenance of such a mosaicked fen landscape is currently kept by the rotational management regime already practiced at both Upton and Woodwalton fens, and should be continued for the long-term conservation of these wet habitats.

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## Appendix 2

### Pollen investigations from the surface sediments at Upton and Woodwalton

The near surface sediment at both Upton and Woodwalton is highly decomposed and large plant remains are difficult to identify. Therefore, pollen analysis was used to determine whether the upper 10 cm of sediment was likely to be derived from the contemporary vegetation. Samples were extracted from one plot within each of the communities investigated; at Upton: mixed woodland (prefixed MU), alder carr (prefixed AU), *Juncus subnodulosus* fen (prefixed JU), reedswamp (prefixed RU) and *Cladium* fen (prefixed CU); at Woodwalton: alder carr (AW), glades (GW), *Phragmites* fen (TW) and sedge fen (SW). Pollen data are presented as percentages of the sums indicated on figures 1 (Upton) and 2 (Woodwalton).

At Upton (Fig. 1), pollen was sparse and the pollen sum was not attained in two samples (MU52 0-1 cm and JU27 9-10cm). Here, the pollen assemblages from the herbaceous communities are dominated by Poaceae pollen, with high Cyperaceae representation limited to the reedswamp. The woodland communities have high values for fern spores. Tree pollen values, notably for *Alnus glutinosa*, are surprisingly low. Similar results have been reported from surface pollen investigations of alder dominated vegetation in Germany (Prager *et al.*, 2006; 2012) and attributed to poor pollen preservation. Variation in pollen abundance with depth is limited at all of the sites investigated. In addition, the different vegetation types appear to have distinct pollen signatures. These two features suggest that the near surface sediment at Upton was derived from, and therefore is contemporary with, the modern vegetation.

In contrast, high *Alnus glutinosa* pollen values are recorded from the sites within the fen carr at Woodwalton (Fig. 2). Elsewhere, herbaceous pollen dominates though, as might be expected. Tree percentages (*Betula* and *Alnus*) are relatively high for the sites within the glades. Again, there is little variation in pollen abundance with depth and the pollen assemblages from the different communities appear distinct. Therefore, the near-surface sediment at Woodwalton also appears to be derived from the contemporary vegetation.

Appendix 2 continued

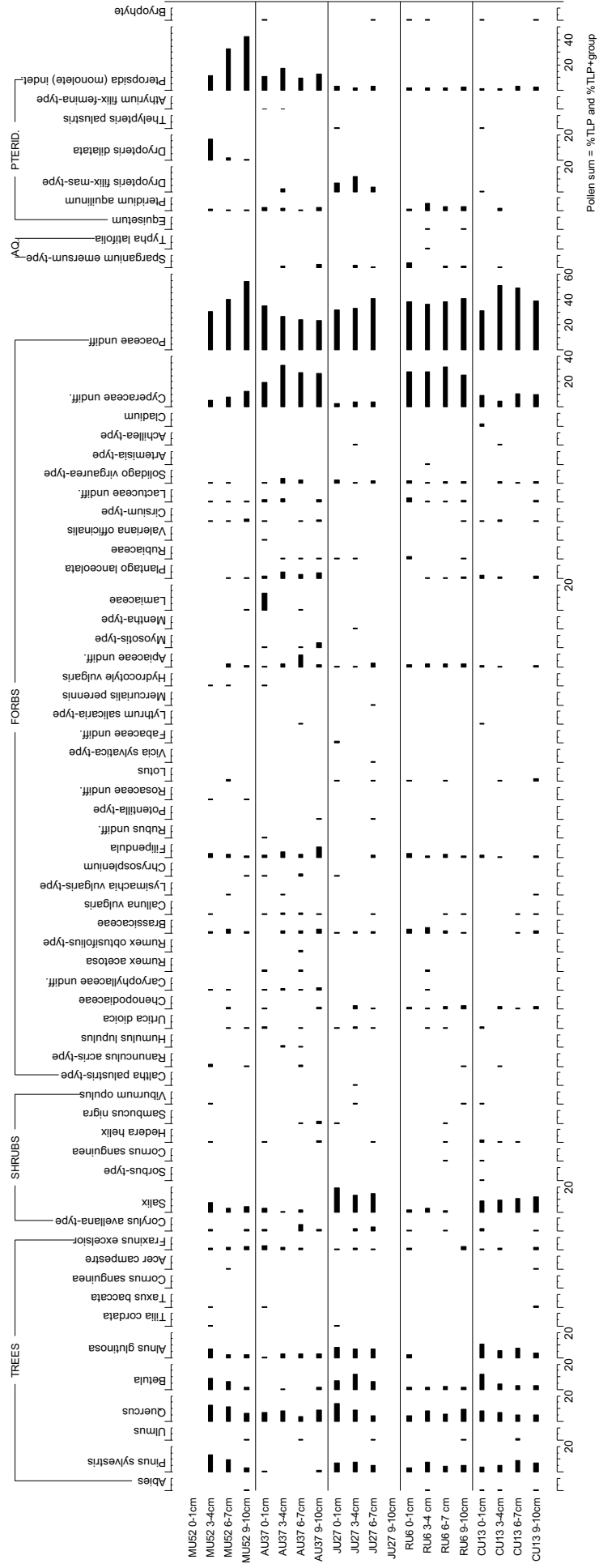


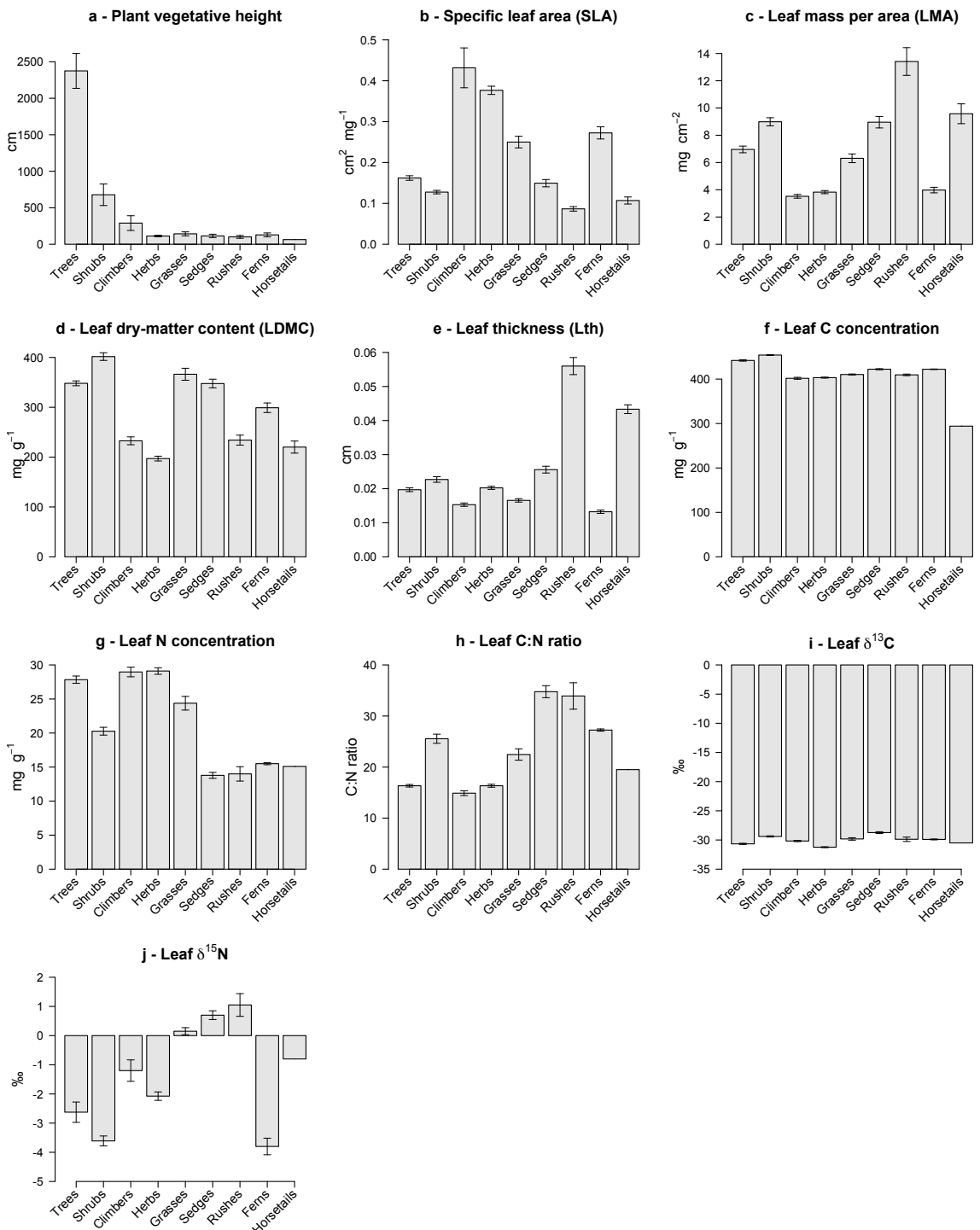
Fig. 1: Pollen diagram of the near surface sediment at Upton Fen. Site abbreviations are shown on the left-hand side. Pollen diagram produced by Martyn Waller.



## Appendix 3

Mean trait values (plant height and nine leaf traits – SLA, LMA, LDMC, Lth, leaf C, leaf N, leaf C:N ratio, leaf  $\delta^{13}\text{C}$  and leaf  $\delta^{15}\text{N}$ ) of life forms (1) and individual species sampled (2). Trait means of life forms are computed from the trait values of each individual species within that group, while means of species are those from each individual leaf measurement. Standard error bars ( $\pm 1$  S.E. of the mean) are shown where more than one measurement was made (available for all 69 species with leaf area/mass traits and for 21 out of 66 species with leaf nutrient traits). Species plant heights are a single value from Plantatt (no error estimate). Individual species codes are given in Appendix 4.

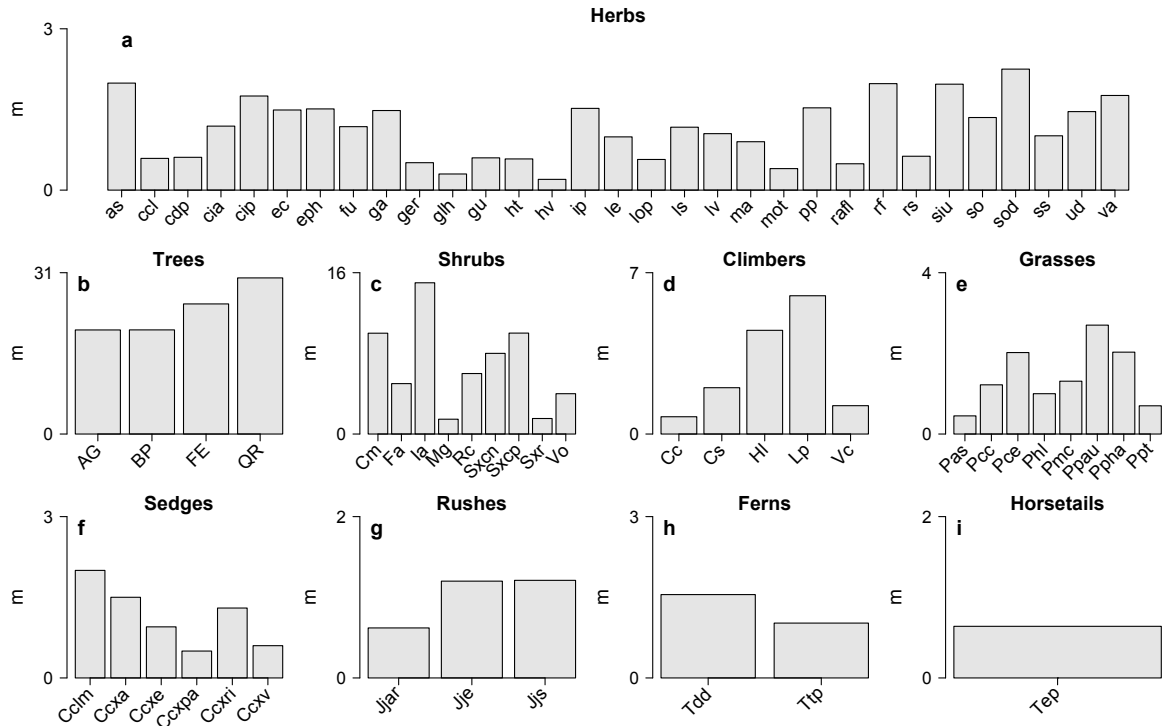
### 1 – Mean trait values of the different life forms sampled



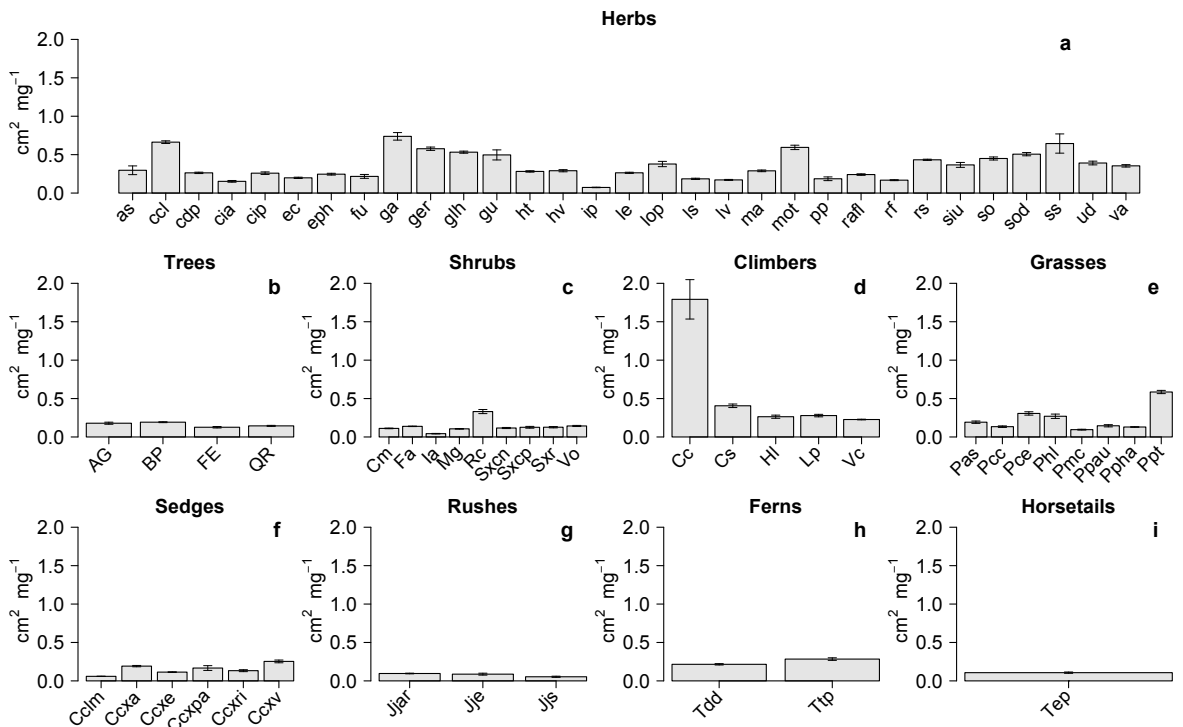
Appendix 3 continued

2 – Mean trait values of individual species

2.1 – Plant vegetative height

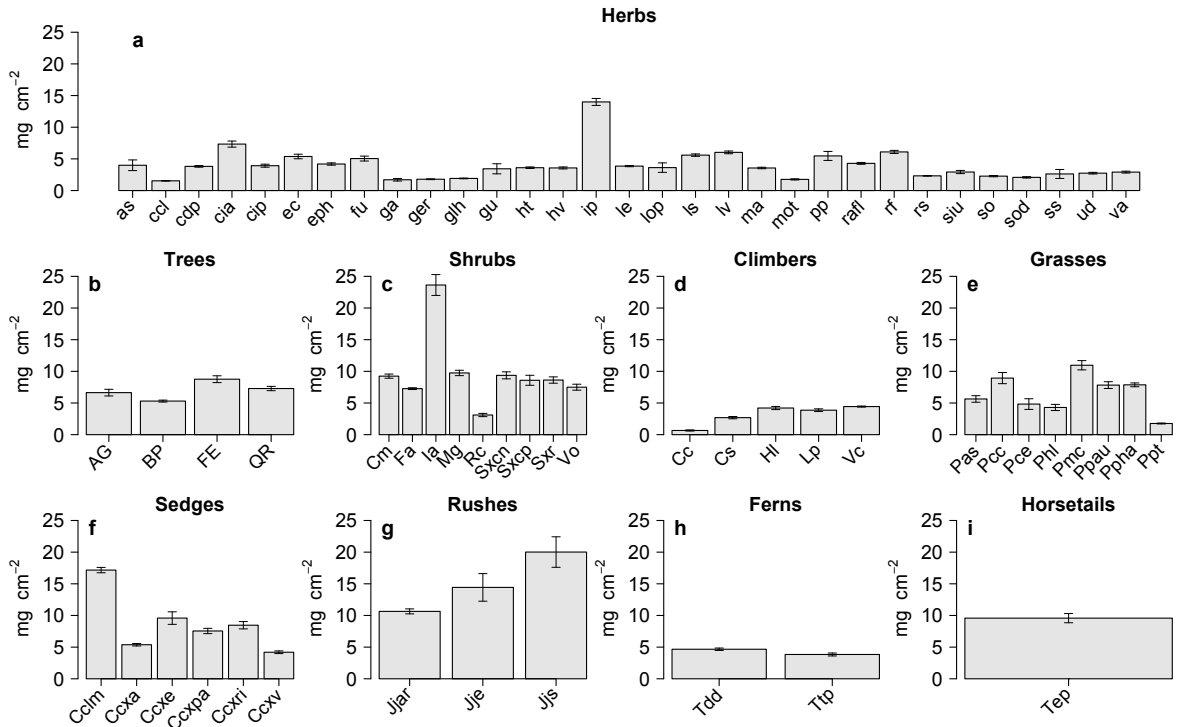


2.2 – Specific leaf area (SLA)

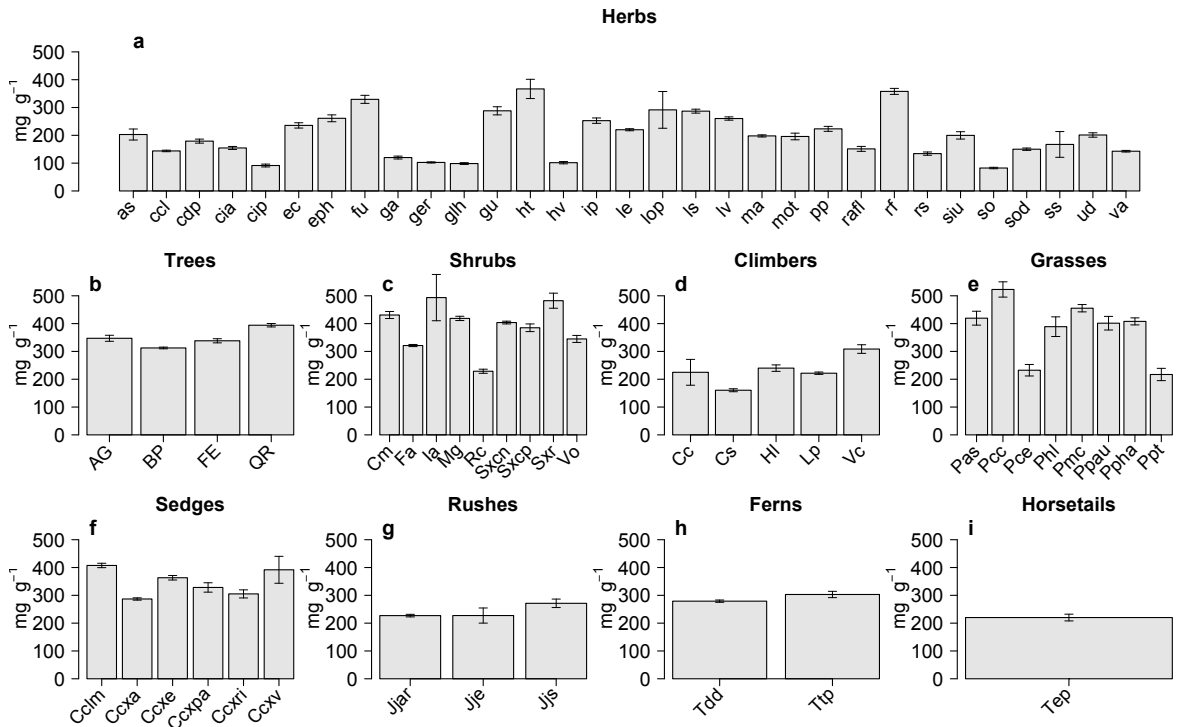


Appendix 3 continued

2.3 – Leaf mass per area (LMA)



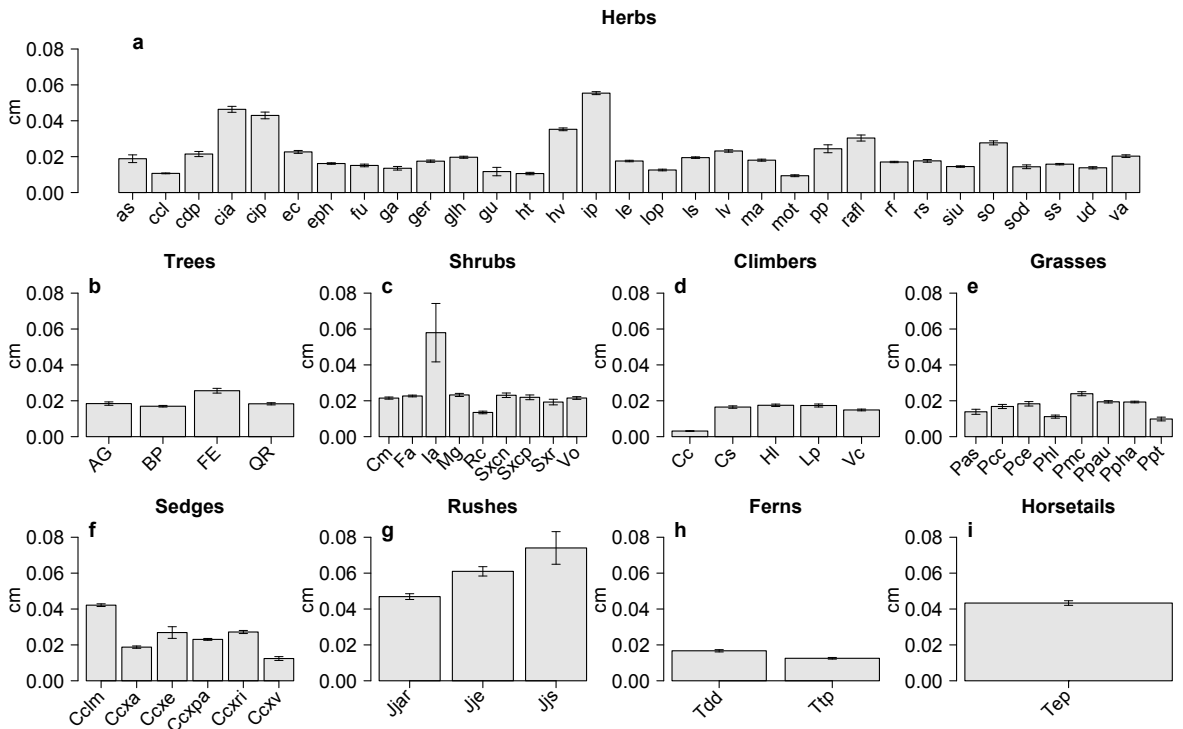
2.4 – Leaf dry-matter content (LDMC)



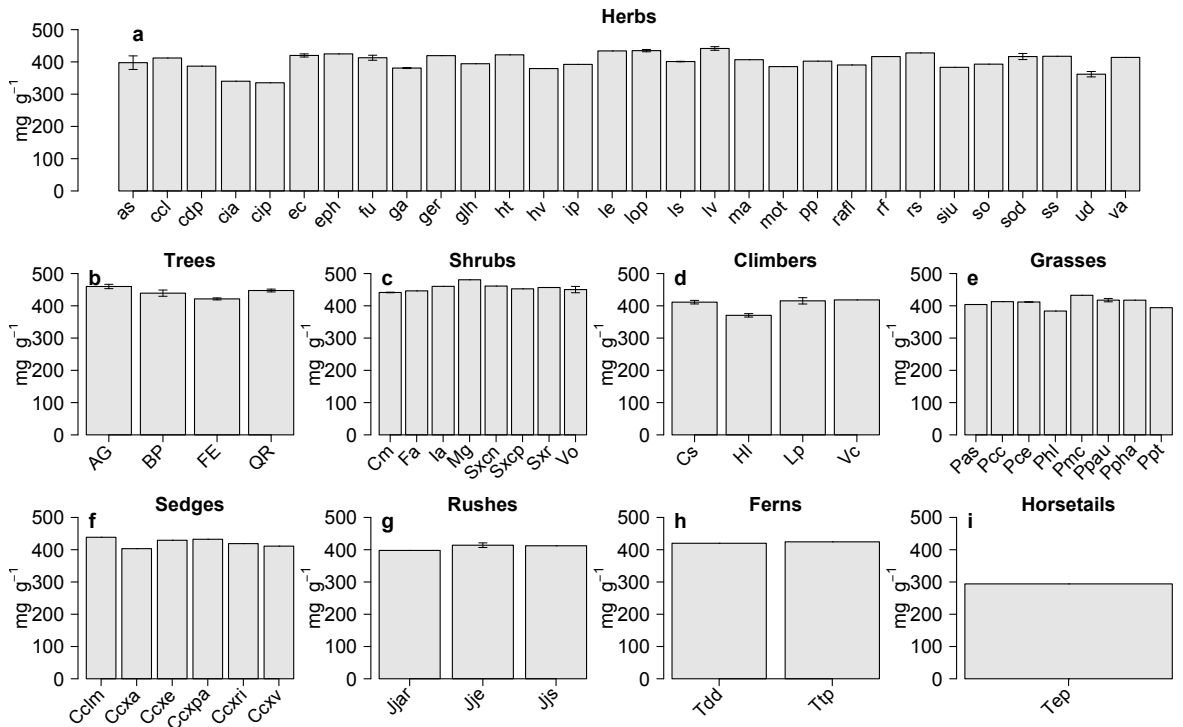


Appendix 3 continued

2.5 – Leaf thickness (Lth)

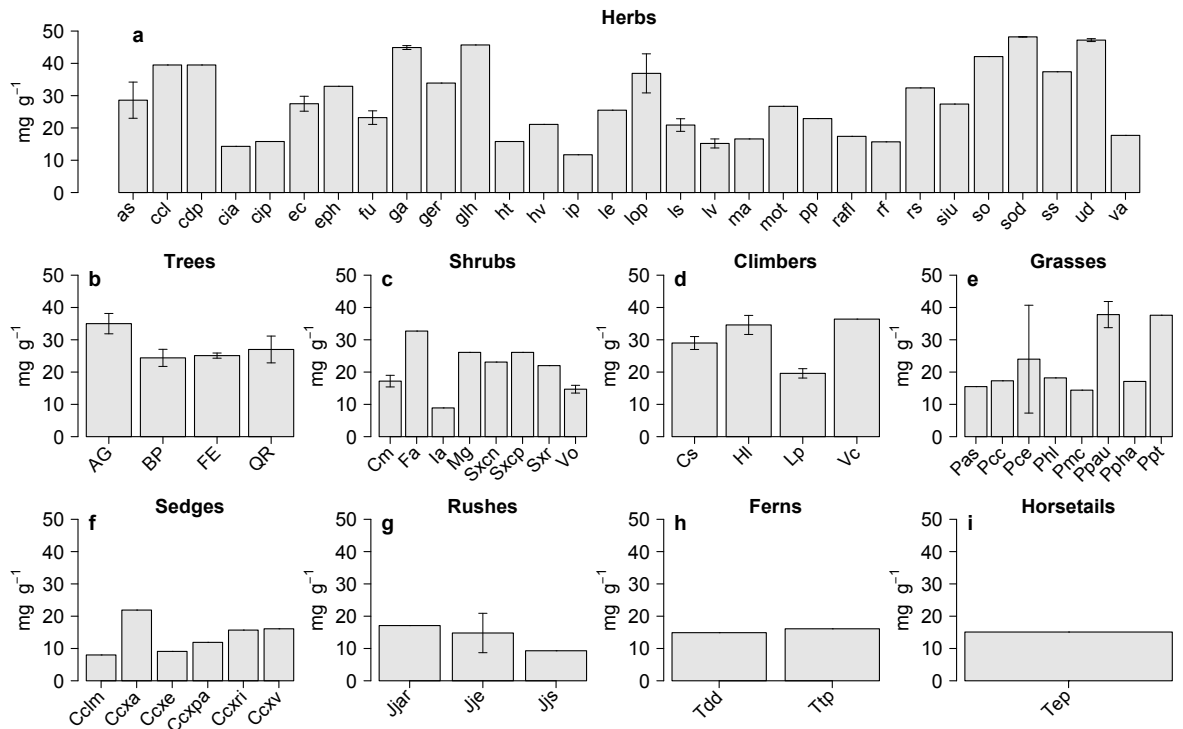


2.6 – Leaf carbon concentration

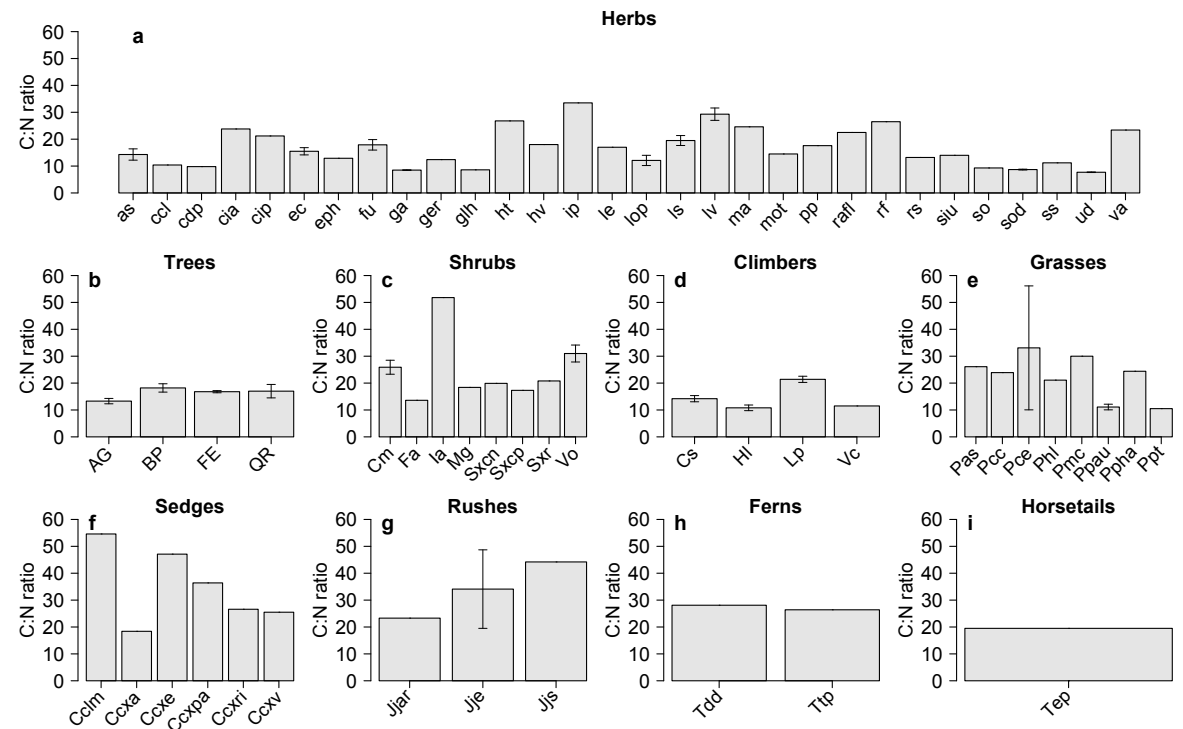


Appendix 3 continued

2.7 – Leaf nitrogen concentration

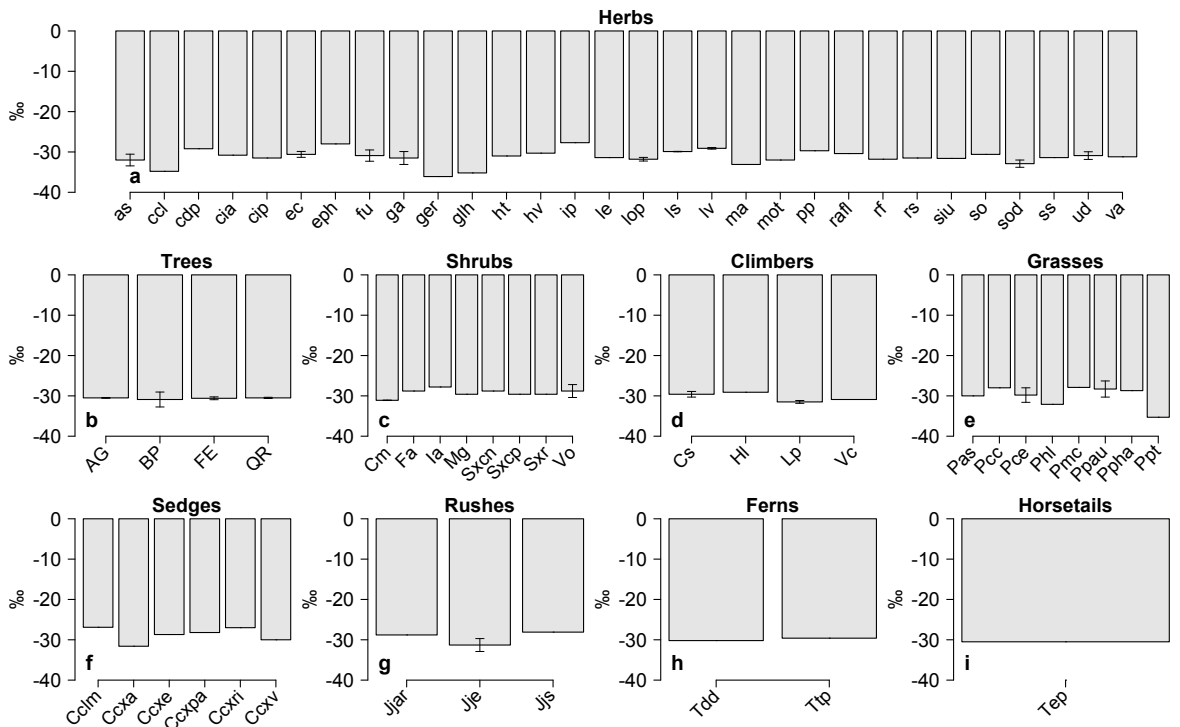


2.8 – Leaf C:N ratio

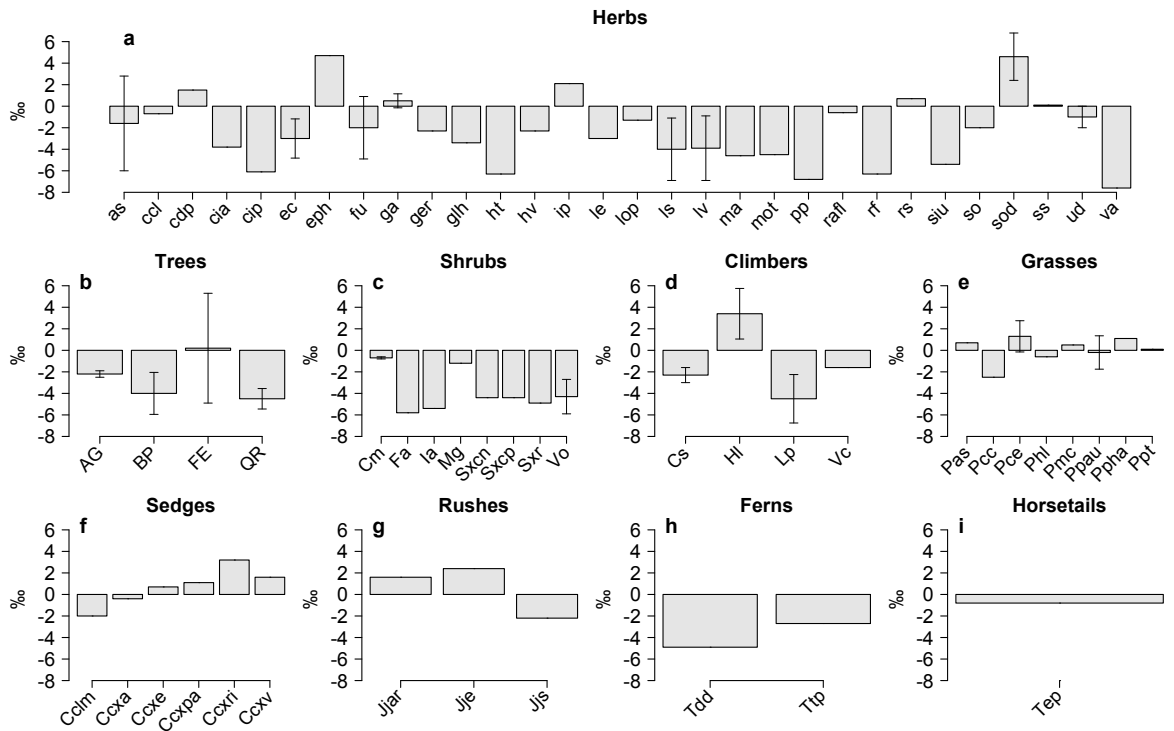


Appendix 3 continued

2.9 – Leaf  $\delta^{13}\text{C}$



2.10 – Leaf  $\delta^{15}\text{N}$



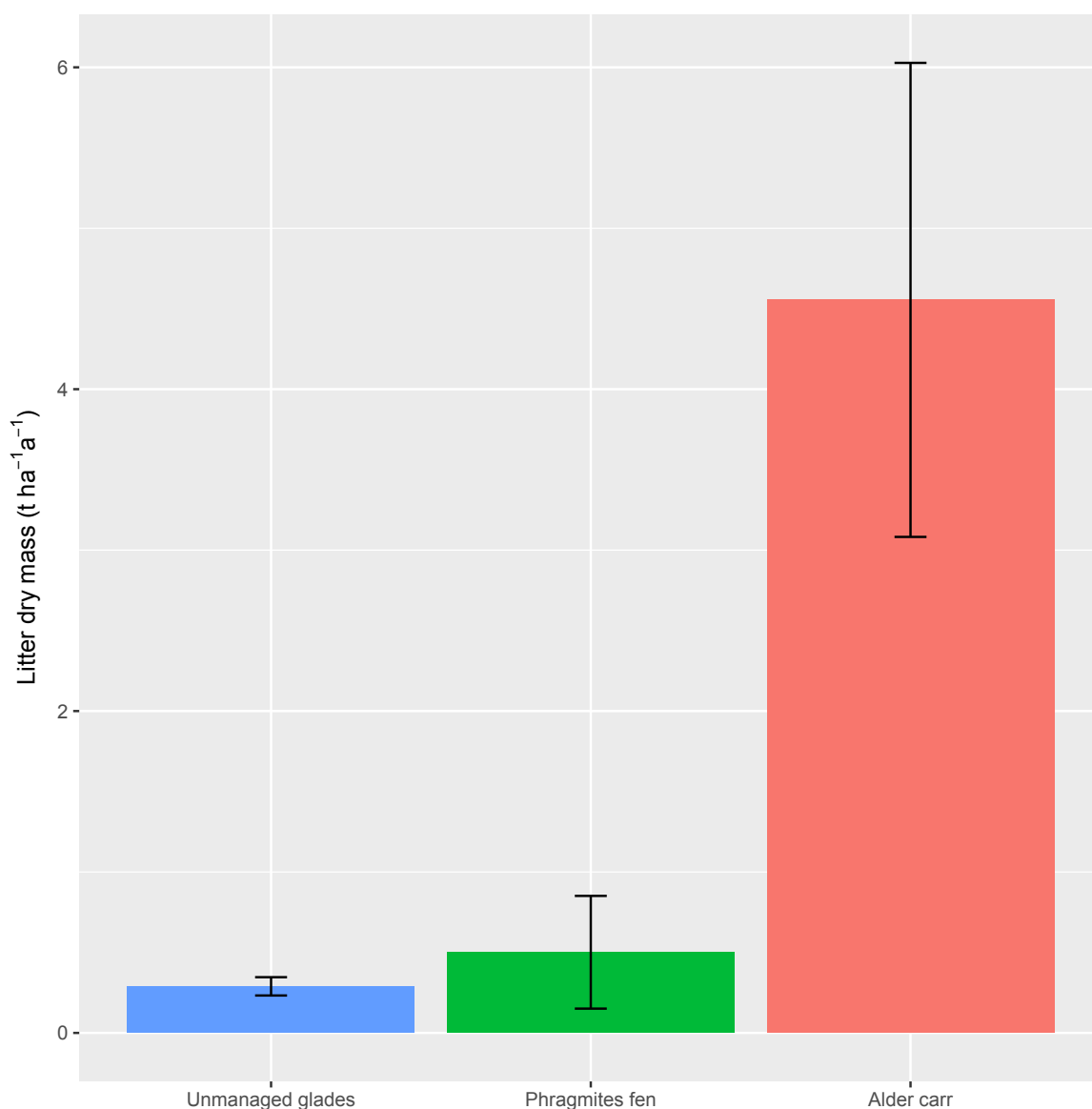
## Appendix 4

Species codes used in Appendices 1 and 3. Only the 69 species for which trait measurements were performed are shown (alphabetically), as well as their life form.

Species name	Code	Life form	Species name	Code	Life form
<i>Agrostis stolonifera</i>	Pas	Grass	<i>Iris pseudacorus</i>	ip	Herb
<i>Alnus glutinosa</i>	AG	Tree	<i>Juncus articulatus</i>	Jjar	Rush
<i>Angelica sylvestris</i>	as	Herb	<i>Juncus effusus</i>	Jje	Rush
<i>Betula pubescens</i>	BP	Tree	<i>Juncus subnodulosus</i>	Jjs	Rush
<i>Calamagrostis canescens</i>	Pcc	Grass	<i>Lonicera periclymenum</i>	Lp	Climber
<i>Calamagrostis epigejos</i>	Pce	Grass	<i>Lotus pedunculatus</i>	lop	Herb
<i>Calystegia sepium</i>	Cs	Climber	<i>Lycopus europaeus</i>	le	Herb
<i>Cardamine pratensis</i>	cdp	Herb	<i>Lysimachia vulgaris</i>	lv	Herb
<i>Carex acutiformis</i>	Ccxa	Sedge	<i>Lythrum salicaria</i>	ls	Herb
<i>Carex elata</i>	Ccxe	Sedge	<i>Mentha aquatica</i>	ma	Herb
<i>Carex panicea</i>	Ccxpa	Sedge	<i>Moehringia trinervia</i>	mot	Herb
<i>Carex riparia</i>	Ccxri	Sedge	<i>Molinia caerulea</i>	Pmc	Grass
<i>Carex viridula</i>	Ccxv	Sedge	<i>Myrica gale</i>	Mg	Shrub
<i>Ceratocarpus claviculata</i>	Cc	Climber	<i>Peucedanum palustre</i>	pp	Herb
<i>Circaea lutetiana</i>	ccl	Herb	<i>Phalaris arundinacea</i>	Ppha	Grass
<i>Cirsium arvense</i>	cia	Herb	<i>Phragmites australis</i>	Ppau	Grass
<i>Cirsium palustre</i>	cip	Herb	<i>Poa trivialis</i>	Ppt	Grass
<i>Cladium mariscus</i>	Cclm	Sedge	<i>Quercus robur</i>	QR	Tree
<i>Crataegus monogyna</i>	Cm	Shrub	<i>Ranunculus flammula</i>	rafl	Herb
<i>Dryopteris dilatata</i>	Tdd	Fern	<i>Rhamnus cathartica</i>	Rc	Shrub
<i>Epilobium hirsutum</i>	eph	Herb	<i>Rubus fruticosus</i>	rf	Herb
<i>Equisetum palustre</i>	Tep	Horsetail	<i>Rumex sanguineus</i>	rs	Herb
<i>Eupatorium cannabinum</i>	ec	Herb	<i>Salix caprea</i>	Sxcp	Shrub
<i>Filipendula ulmaria</i>	fu	Herb	<i>Salix cinerea</i>	Sxcn	Shrub
<i>Frangula alnus</i>	Fa	Shrub	<i>Salix repens</i>	Sxr	Shrub
<i>Fraxinus excelsior</i>	FE	Tree	<i>Sium latifolium</i>	siu	Herb
<i>Galium aparine</i>	ga	Herb	<i>Solanum dulcamara</i>	sod	Herb
<i>Galium uliginosum</i>	gu	Herb	<i>Stachys sylvatica</i>	ss	Herb
<i>Geranium robertianum</i>	ger	Herb	<i>Symphytum officinale</i>	so	Herb
<i>Glechoma hederacea</i>	glh	Herb	<i>Thelypteris palustris</i>	Ttp	Fern
<i>Holcus lanatus</i>	Phl	Grass	<i>Urtica dioica</i>	ud	Herb
<i>Humulus lupulus</i>	HI	Climber	<i>Valeriana officinalis</i>	va	Herb
<i>Hydrocotyle vulgaris</i>	hv	Herb	<i>Viburnum opulus</i>	Vo	Shrub
<i>Hypericum tetrapterum</i>	ht	Herb	<i>Vicia cracca</i>	Vc	Climber
<i>Ilex aquifolium</i>	la	Shrub			

## Appendix 5

Mean annual litter production rate (dry mass, in tonnes per ha per year) at three plant communities in Woodwalton Fen. Error bars are one standard error of the mean ( $\pm 1$  S.E.) of the two litter traps in each community. The alder carr, dominated by deciduous tree species (e.g., *Alnus glutinosa*, *Fraxinus excelsior*), produced considerably more plant litter than the two herb-dominated communities, where tall monocotyledons prevailed (e.g., *Phragmites australis*, *Calamagrostis canescens*; see Appendix 1).



## Appendix 6

Mean aboveground biomass (AGB; in tonnes per ha) of the herbaceous communities in Woodwalton Fen. Error bars are one standard error of the mean ( $\pm 1$  S.E.) of the 10 samples in each community [glades (five samples in each of the managed and unmanaged glades), *Phragmites* fen and sedge fen; see section 2.2.5 in Chapter 2]. The *Phragmites* fen (low management intensity) and the unmanaged glades showed the highest proportion of dead AGB, while most of the AGB in the intensively managed glades and sedge fen were live AGB.

