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Optimising oak woodland establishment into UK upland pastures in the context of climate change; and the role of oak woodland in soil hydrological recovery for natural flood management

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Optimising oak woodland establishment into UK upland pastures in the context of climate change; and the role of oak woodland in soil hydrological recovery for natural flood management

by

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At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee.

Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment.

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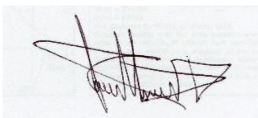

Signed: ________________________

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Abstract

Thomas Richard Apollos Murphy -

Optimising oak woodland establishment into UK upland pastures in the context of climate change; and the role of oak woodland in soil hydrological recovery for natural flood management

Increases in the magnitude and extremity of upland (>250-300m a.s.l.) precipitation associated with anthropogenic climate change (ACC) and coinciding with soil compaction leave downstream communities at elevated flood risk. The study examines changes in upland precipitation and the impact of upland 'Atlantic' oak (*Quercus robur, Quercus petraea*) woodland establishment on the recovery of soils for natural flood management (NFM). The soil moisture, livestock grazing and dispersal constraints for potential oak woodland expansion in upland pastures are assessed. The study is located within Dartmoor National Park (DNP) and finds greater increases in precipitation in upland areas than the lowland site, with long term (1879 - 2012) significant increases in spring, autumn, winter and annual total precipitation. Deviation between observed and latest projected changes (UKCP18) (%) in precipitation are greatest (higher observed precipitation trends) in upland areas. Upland oak woodland establishment offers a rapid (< 12 years) mechanism to improve the hydrological functioning of soils for the mitigation of flood risk associated with ACC and soil compaction. The development of oak seedlings and response of saplings in organic upland soils suggest there is a high degree of diversity within UK native oak to varying soil saturation expected with changes in upland precipitation. Natural colonisation of oak saplings is most frequent on west-facing, freely-draining acid grassland pastures, establishment is constrained by dispersal outside the woodland edge (13m average), and the character of livestock grazing. There is growing interest in woodland establishment for the provision of multiple climate mitigation and ecosystem services (ESS), the thesis discusses the role of upland afforestation and its application in land–use management based natural climate mitigation. Research findings suggest effective and rapid establishment of upland oak woodland for NFM will require the planting of native oak trees within livestock exclosures, strategically placed in valley pasture slopes within catchment headwaters.

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Chapter 1.

Introduction

Of the many extreme climate challenges associated with anthropogenic climate change (ACC), major shifts in precipitation and concomitant increases in regional flooding along river catchments are perhaps the most pressing (Arnell & Lloyd-Hughes 2013; IPCC 2014b; Prein et al. 2017; Bevacqua et al. 2019). Flooding is associated with multiple, often severe, economic and social costs (WHO 2013; Dotorri et al. 2018). Social impacts include: the loss of life, loss of possessions, damage to livelihood and damage to physical and mental health (WHO 2013, Carroll et al. 2010). Global flood damage on average is expected to increase 160–240%, with human loses rising by 70–83% under 1.5^{o}C temperature increases (Dotorri et al. 2018).

The economic impacts are also considerable, global direct river flood damages are estimated at €110 billion (£94 billion) per year on average, and are projected to increase most steeply in Europe (Dotorri et al. 2018). In the UK, economic losses associated with the winter flooding of 2013/14 amounted to £1.5 billion (Chatterton et al. 2016) and the UK summer floods in 2007 cost the economy £3 billion, roughly equivalent to the annual cost of agricultural-subsidy (Pitt 2007).

Increasing autumn and winter rainfall has resulted in increasing floods in northwestern Europe linked with advancement in soil moisture maxima (Blöschl et al. 2017, 2019). This trend is projected to continue within the UK, associated with increases in winter precipitation (Lavers et al. 2013; Murphy et al. 2018). The shift to higher UK winter river flows in recent decades poses significant implications for future flood-risk-management (Black & Burns 2002; Orr & Carling 2006).

1.1.1. Natural flood management -

In Europe, the ‘Floods Directive’ (Directive 2007/60/EC) encourages the use of natural based catchment solutions or natural flood management (NFM) in alleviating flood risk (European Commission 2007). NFM seeks to restore a more naturally functioning hydrological system with attenuation of peak river flows (Figure 1.1) by introducing more natural processes to reduce flood risk, particularly where human activity and/or other impacts (such as climate change) have increased peak river flows. NFM may also involve the use of natural kinds of infrastructure (such as woody dams), which offer flood-water attenuation as an supplementary approach to hard engineering solutions (Lane 2017; Burgess-Gamble et al. 2017). Integral to this strategy is a whole catchment based method to flood management. NFM aims to reduce flood risk whilst protecting and enhancing natural ecosystem services (ESS) including carbon sequestration, habitat creation, water purification and public health benefits, whilst minimising the social, environmental, and economic costs (Iacob et al. 2014; Burgess-Gamble et al. 2017; Lane 2017). NFM schemes are also considered potentially more resilient to climate changes with focus on attenuating water at the source (upper catchment), in addition to maintaining physical barriers (traditional hard engineering) downstream around infrastructure receptors (villages, towns, cities) (Iacob et al. 2014).

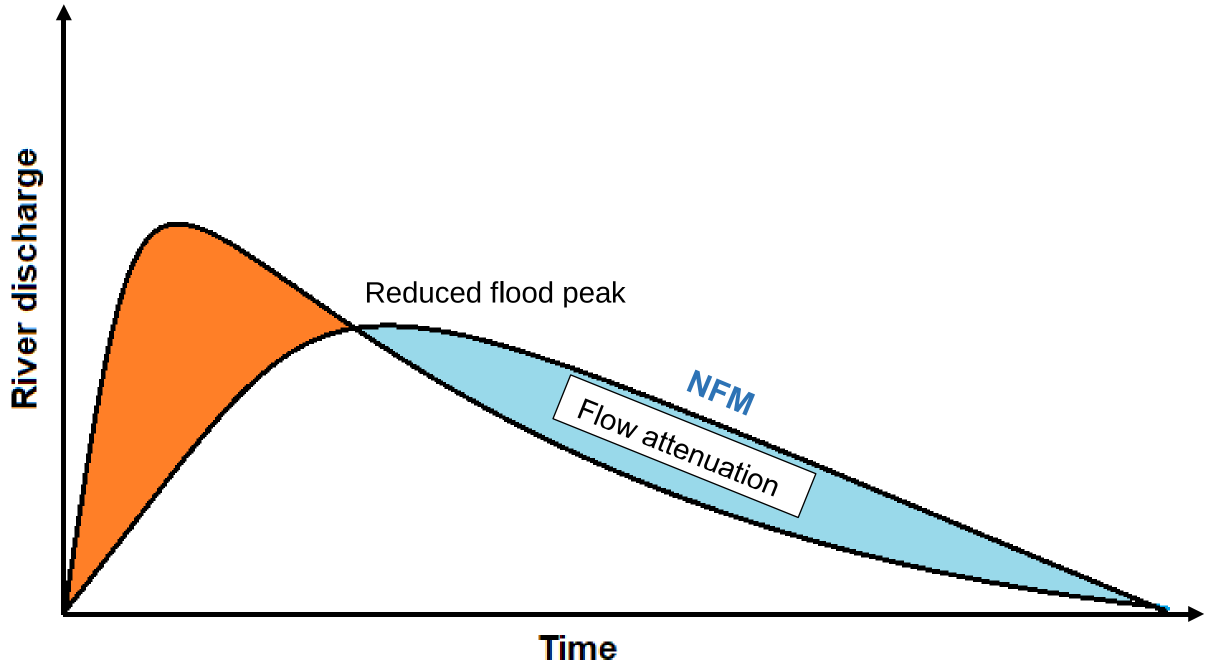

Figure 1. 1 – Schematic diagram outlining principles of NFM, which aims to manipulate (typically increase) water attenuation upstream to complement and reduce risk on traditional approaches downstream whilst providing multiple ESS.

1.1.2. UK uplands

UK 'Upland' areas are generally defined as areas >250 - 300m above sea level (a.s.l)(Ratcliffe & Thompson 1988). The uplands cover around one third of the UK's land area and are considered of national and international importance due to their biodiversity, cultural heritage, and carbon stocks in the form of peatland (Holden et al. 2007; Reed et al. 2009; Billett et al. 2010). As the source of the majority of UK's freshwater, and as areas of greatest precipitation; the uplands and headwaters of catchments are of significant hydrological importance as key areas for flood-water attenuation (Burt & Holden 2010; Van der Wal et al. 2011; Curtis et al. 2014; Burgess-Gamble et al. 2017). The sheer multiplicity of ecosystem services that are, or could be, provided by the uplands means that there is much competition for land among different stakeholders (Bonn et al. 2009; Reed et al. 2009; Curtis et al. 2014). Added to this many of these areas have complicated land tenure arrangements (McCrone et al. 2008).

1.1.2.1. Historic degradation

In the UK especially, upland areas are typified by very low woodland cover (Bunce et al 2018a; Baarda 2005). Extensive agricultural 'improvement', via burning, drainage and heavy grazing to maximise livestock productivity, has converted areas previously dominated by woodland to grassland and heathland vegetation (Fyfe & Woodbridge 2012; Fyfe et al. 2014). More recent degradation in upland areas, has resulted in significantly diminished nature conservation and carbon storage potential (Bardgett et al. 1995; Tallis 1998; Sansom et al. 1999).

The number of grazing animals (particularly sheep - *Ovis aries*) in the uplands increased dramatically between the 1950s and 2000 in response to market trends and European Union (EU) Common Agricultural Policy (CAP) support payments (Baldock et al. 2002; Sansom et al. 1999). Sheep numbers increased from 19.7 million in 1950 to 40.2 million in 1990, representing a 142% and 181% increase in England and Wales respectively (Fuller & Gough 1999). Over-grazing was identified as a major threat to biodiversity in upland areas, seriously limiting woodland regeneration and resulting in widespread soil compaction (English Nature 1996; Sansom et al. 1999). In the Scottish uplands, steady increases in sheep but particularly deer (mainly red deer - *Cervus elaphus*) numbers have been problematic for nature conservation efforts and an impediment to native tree regeneration (Palmer & Truscott 2003; Palmer et al. 2004; Bunce et al. 2014).

During the 20th century, the UK uplands (particularly Scotland) also experienced large-scale exotic conifer afforestation (largely sitka spruce - *Picea sitchensis*), which was associated with considerable environmental damage (Bunce et al. 2014; Sloan et al. 2018). Negative impacts included river acidification (associated loss of *Salmonid* populations), and loss of active mire/bog habitats due to widespread drainage and burning management (Harriman & Morrison 1982; Johnson 1995; Hornung & Newson 2007). In many areas, poor tree rooting and wind-throw of conifers, have reduced the quantity and quality of timber and there is debate on whether to restock with commercial or native broadleaf species (Bunce et al. 2014; Sloan et al. 2018)

1.1.2.2. A challenging legacy

There has been improvements in management practices since the turn of the century with a stabilisation and reduction in sheep numbers across the UK uplands (Silcock et al. 2012). However, unsustainably high (and growing) deer numbers and locally significant sheep numbers in UK upland sites represent a challenge for meeting nature conservation and ESS priorities (Goldberg & Watson 2012; Bunce et al. 2014). Perhaps more significantly, historic soil compaction, the legacy of heavy grazing and miss-management in the UK uplands, represent a challenge for mitigating the impacts of future flood risk associated with ACC (Sansom et al. 1997; Shuttleworth et al. 2019). Sites with compacted soils can become 'active source areas' for runoff generation by lowering the threshold between dry and wet soil states ('wetness threshold') (Meyles et al. 2006; Holden et al. 2007c). Increased runoff leads to unnaturally high flows in wet periods and decreased river base-flow in dry periods (Sansom et al. 1997; Shuttleworth et al. 2019). As such, these degraded upland soils pose a considerable risk of increasing flooding for downstream communities.

1.1.2.3. Future prospects?

Whilst perverse incentives and bad management are responsible for historic deterioration in upland ESS provision, the UKs imminent exit from the EU provides a window of opportunity (Bateman & Balmford 2018; Burton et al. 2019). Cessation in EU agricultural payments (CAP), alongside relatively ambitious climate change commitments and UK environmental policy, suggest there is considerable and imminent prospect of change in upland management (Bunce et al. 2018b; Defra 2018a; Climate Change Committee 2019). Changes have the potential to accelerate the 'public money for public goods' approach to agriculture which focuses on the provision of key ESSs including flood mitigation, carbon sequestration and nature conservation (Bateman & Balmford 2018; Baldock et al. 2019). Impacts are likely to be greatest in marginal, often disadvantaged upland sites, where farms are disproportionately dependent on public subsidy (Hanley et al. 2007; DEFRA 2018b; Pakeman et al. 2018).

Of particular relevance considering the growing attention on ESS are negative climate change impacts and loss of biodiversity as a result of historic intensification across Europe; where 30% of habitats are deteriorating and 10% of species near threatened (European Environment Agency 2015). Indeed, despite efforts such as the UKs environmental and countryside stewardship schemes, there has been a 41% decrease in UK species abundance since the 1970s, with 15% of species near threatened (Hayhow et al. 2019). This failure has cemented the view that traditional conservation approaches are not working, and that a fresh approach is needed (Jepson 2015; Monbiot 2013; Tree 2018), necessitating bigger, better and more joined up nature conservation policy and land management (Lawton et al. 2010). In this context, there is growing interest in what is loosely termed 'rewilding', 'wilding' and other forms of ecological restoration (Soule & Noss 1998; Monbiot 2013; Jepson 2015; Sandom et al. 2018; Pettorelli et al. 2018; Tree 2018).

1.1.3. Woodland (re-)establishment?

The growing evidence for the global environmental and public benefits of trees, in addition to historic and ongoing global forest loss, has led to increasing calls for woodland (re-)establishment (Ciccarese et al. 2012; Griscom et al. 2017; IPCC 2018; Bastin et al. 2019). Woodland (re-)establishment is now recognised as potentially the most effective climate change solution to date, with the potential to store 205 giga-tonnes of carbon globally (Griscom et al. 2017; Bastin et al. 2019), attenuate river flows (Nisbet et al. 2011; Evaristo & McDonnell 2019) and facilitate the movement of species threatened by ACC (Heller & Zavaleta 2009; Lawler 2009). Afforestation is an important strategy for climate mitigation under the Paris agreement, and for global ecological restoration targets such as the New York declaration on forests (UNDP 2014; UNFCCC 2015). As one of the least wooded countries in Europe, the UK requires significant woodland expansion to meet its climate change commitments and deliver ESSs such as NFM (Defra 2018a; Committee on Climate Change 2019). Woodland cover in the UK (2019) is estimated at 13% (10% England, 15% Wales, 19% Scotland, 8% Northern Ireland) of total land area (EU average 42%)(EUROSTAT 2018; Forestry Commission 2019).

The growing public support for woodland expansion is now being backed by all UK political parties and government policy support in the form of a woodland carbon guarantee scheme and other measures announced in the UK 25 year environment plan (DEFRA 2018a, 2019a). It is recommended that 30,000 hectares of woodland (1.5 billion extra trees) are planted annually in order for the UK government to reach its net zero greenhouse gas emissions targets by 2050 (DEFRA 2018a; Committee on Climate Change 2019). As areas of marginal agricultural value and most reliant on public subsidy, with low woodland cover, and at the headwaters of the majority of UK river catchments (Van der Wal et al. 2011; Curtis et al. 2014; Bunce et al. 2018a), UK upland areas represent ideal areas for woodland expansion.

1.1.4. Woodland NFM

The establishment of woodland is increasingly recognised as a potential means of attenuating peak river flows by reducing the rapid generation of surface run-off (Evaristo & McDonnell 2019; Lane 2017). Woodland for NFM is placed into four categories, catchment woodland, riparian woodland, cross slope woodland and flood plain woodland (Burgess-Gamble et al. 2017). Trees may offer NFM via three potential mechanisms; 1) greater water use 2) increase in hydraulic ‘roughness’ and 3) amelioration of soil structure (Robinson et al. 2003; Nisbet & Thomas 2006; Nisbet et al. 2011, Birkinshaw et al. 2014). Despite this, there are just a handful of studies which explore the role of native woodlands on soil infiltration in upland catchments and the transferability of results is unknown (Ford et al. 2016; Burgess-Gamble et al. 2017). Indeed, our understanding of how trees affect soil hydraulic properties more generally is extremely limited (Chandler et al. 2018). Studies relating to the regulation of water by woodland are dominated by studies of conifer plantations (Burton et al. 2018).

1.1.5. Upland oak woodland

Currently there is estimated to be between 70,000 and 100,000ha of upland oak woodland in the UK (Baarda 2005). Historically, large areas of oak (*Quercus spp*) woodland were cleared as part of agricultural expansion across Europe (Woodbridge et al. 2014; Roberts et al. 2018). Pollen evidence suggests oak woodland would have dominated many UK upland sites in prehistory before clearance; this happened in stages, but largely began in the late Neolithic (6400–6000 cal. BP) (Woodbridge et al 2014; Fyfe et al. 2014). Upland oak woods are recognised as globally important and highlighted under the European habitats directive due to their now fragmented distribution and support of specialist lower plant (ferns and bryophytes), lichen, and animal assemblages (Baarda 2005; JNCC 2014; Lamacraft et al. 2018). Upland oak woodlands are characterised by woodland NVC - W11 and W17, which along oceanic west coast uplands are described as 'Atlantic' rainforests (Rodwell 1991; Baarda 2005). These woodlands, associated with the north and west of the UK and areas of highest rainfall and lowest temperature extremes, have the richest bryophyte cover in Europe, possibly the world due to their high humidity and number of available niches (Baarda 2005; Rothero 2005).

UK Native oak trees (*Quercus robur, Quercus petraea*) are of considerable importance in nature conservation, support a listed 2,300 species (326 obligate species), including birds (38), bryophytes (229), fungi (108), invertebrates (1,178), lichens (716), and mammals (31)(Mitchell et al. 2019). The observed very slow growth of oak trees in exposed upland oak woods, their occurance particularly on west facing slopes, and their typically ‘Atlantic’ maritime or oceanic climatic distribution within the UK, suggests oak woodland expansion may be significantly limited by low temperature and exposure to easterly winds in upland locations (Proctor et al. 1980; Mountford 2001; Baarda 2005). Yet the principle constraint to the health and establishment of these woodlands has been livestock and deer grazing (Barkham 1978; Palmer et al. 2004). Many oak woods have been neglected and heavily grazed by sheep and deer, overgrazing has preventing natural recruitment of saplings to the canopy, and the growth of sub canopy species (Humphrey et al. 2004; Palmer et al. 2004). The regeneration of native oak trees in upland woodlands are of heightened significance given its evidenced decline across Europe (Denman et al. 2014), linked to climate changes (and interaction with biotic stressors), including elevations in precipitation in exposed coastal Atlantic sites (Rozas & García-González 2012a; Rozas & Sampedro 2013). Additionally, oaks high biodiversity provision combined with the potential loss of canopy tree species - ash (*Fraxinus excelsior*) due to ‘ash dieback’ (*Hymenoscyphus fraxineus*) make the fate of this species particularly important (Broome et al. 2019; Mitchell et al. 2019).

1.2. Outline of thesis:

Considering the severe risks associated with flooding, the compacted nature of many upland soils, the potential application of woodland for NFM, and the importance of upland oak woodland for nature conservation this thesis aims to: 1) Evaluate the impact of oak woodland establishment on the recovery of soils in upland catchments for the potential mitigation of downstream flood risk associated with ACC. 2) Assess the constraints on oak woodland establishment associated with increased soil moisture, livestock grazing, and the potential for oak woodland expansion in UK upland pastures. Presented below is an outline of the thesis structure, which includes four ‘stand-alone’ data chapters of original research (chapters 2 – 5) and is concluded by a synthesis chapter (chapter 6), to summarise the key findings and to discuss the implications of the results:

Chapter 2 - *Taste of what's to come? - Examination of UK upland precipitation trends in relation to latest UK climate change projections.*

Considering the application of climate projections in framing land use policy this chapter contextualises the latest UK climate change projections (UKCP18) by comparing projected changes in future precipitation with observed seasonal precipitation trends from long running 'upland' (>250-300m) and 'lowland' stations in South West (SW) England. The records from upland Cowsic Valley (445m) (Dartmoor National Park [DNP]) and lowland Plymouth (50m) represent one of the longest pair (1879 – 2012) of upland and lowland observation sites in Europe. The study also compares precipitation trends from multiple upland Dartmoor sites since the 1960s. This chapter is published as: *Murphy TR, Hanley ME, Ellis JE, Lunt PH (2019) Deviation between projected and observed precipitation trends greater with altitude. Climate Research 79: 77 – 89*.

Chapter 3 - *Native woodland establishment aids soil recovery to mitigate flood risk in upland pastoral catchments?*

Considering the extremity of projected changes in climate and recent damaging flood events, and the potential role for upland catchments to mitigate this risk; chapter three presents evidence of the effectiveness of mixed oak woodland establishment as a natural flood management (NFM) solution for UK upland catchments. The study compares soil physical and hydrological characteristics in areas of formerly grazed pasture following native woodland establishment, with adjacent pasture plots in DNP, SW England. The viability of catchment and cross-slope woodland as NFM solutions and management implications are discussed. This chapter is currently submitted for review in: *Land Degredartion and Development.*

Chapter 4 - *Too much of a good thing? – Hydrological limits to UK native oak expansion in organic soils typical of UK upland pastures.*

The response of oak trees to soil moisture will be crucial in determining the character and extent of upland oak woodland, as well as its resilience to ACC. In the context of the observed and projected changes in upland precipitation (outlined in chapter two), and the potential use of native woodland as a NFM measure (chapter three); chapter four assesses the impacts of changes in soil saturation on the survival, early development and performance of seedling and juvenile (<4 years-old) native oak (*Quercus robur* and *Quercus petraea*) in organic soils characteristic of UK upland pastures. The study uses a Plymouth based pot experiment, alongside a field trial, and surveys of naturally colonising oak trees in the upland pastures of DNP, SW England. The results are discussed in relation to expected changes in future climate and ESS management implications for upland areas. Results are likely to have significant importance for the implementation of NFM in UK upland catchments and the resilience of upland oak woodland in the face of projected climate changes.

Chapter 5 - *To plant or not to plant? Native oak establishment in upland pastoral systems*

The regeneration of internationally recognised UK upland oak woodland is of key importance considering concomitant threats on this woodland type brought about by ACC and potential applications in NFM. The establishment of native woodland in upland areas is particularly prescient considering current grazing pressures, potential for changes in agricultural policy and the movement towards 'public money for public goods' identified in government 25 year environment plan. Considering this, chapter five assesses the dispersal distance of UK native *Quercus spp* and the performance and survivorship of oak saplings (<12 years) in the open upland pastoral catchments of Dartmoor, SW England. Results are discussed in relation to upland vegetation and livestock/grazing management and are likely to prove important for determining the practical management requirements for the establishment of native oak woodland for NFM application in UK upland catchments. This chapter is submitted for review in: *Journal of Applied Ecology*

Chapter 6 – *Final discussion on findings, implications and a new research framework*

General discussion on the implications of results and synthesis of findings. This chapter also identifies key areas of future research priority and outlines a potential framework for further study.

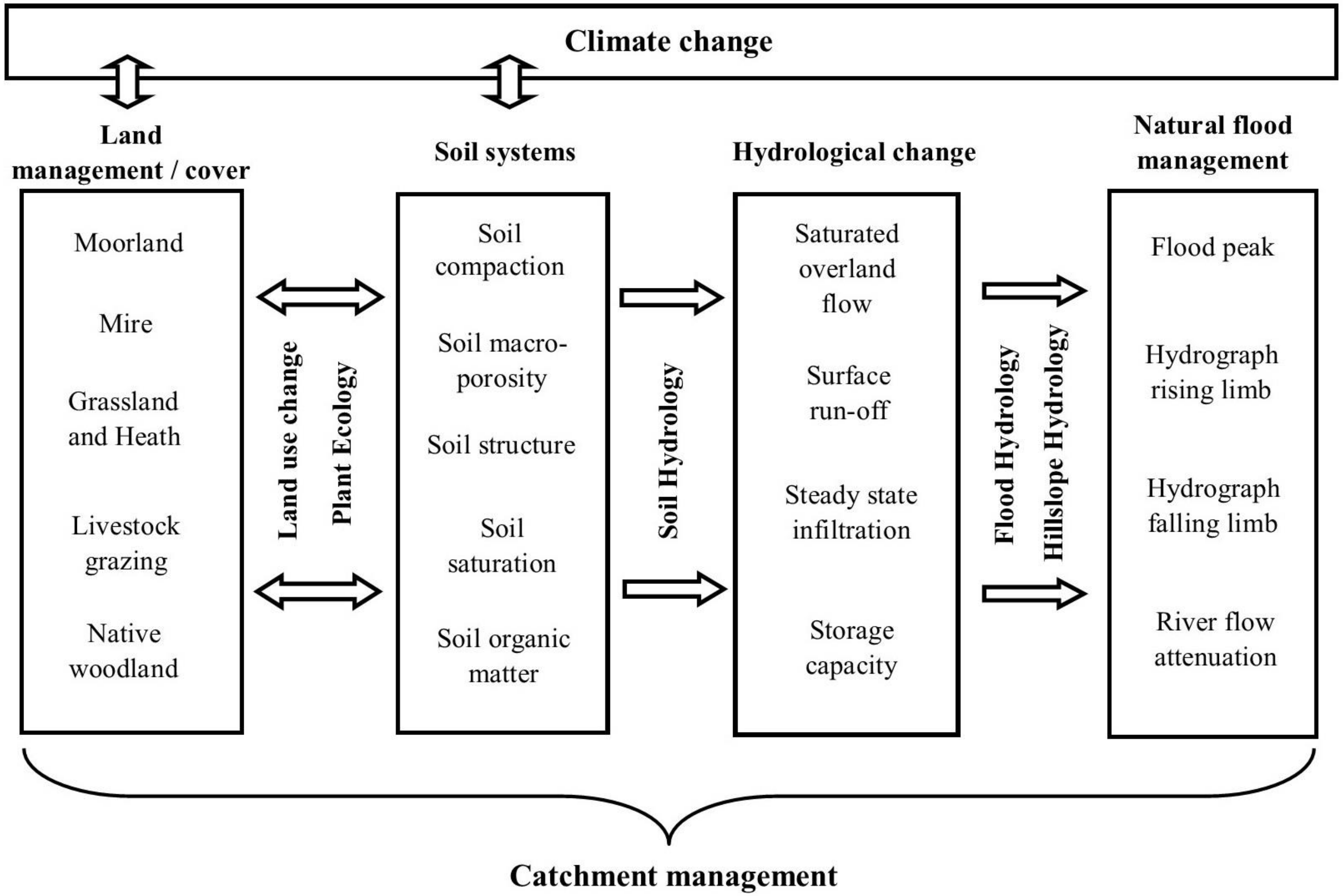

Figure 1. 2 – Importance of climate change – land management – soil systems – hydrological change – natural flood management (NFM) interactions in catchment management, providing the reasoning behind, and linkages between components of the thesis. Arrows indicate the direction of the hypothetical causal relationship. Double-headed arrows indicate potential two-way association.

Chapter 2.

Deviation between projected and observed precipitation trends greater with altitude

Abstract:

Variation in the amount and intensity of precipitation is one of the most important factors determining how biological systems respond to anthropogenic climate change. Moreover, given the importance of climate projections for influencing (inter)national policy, there is a pressing need to contextualise contemporary projections with observed trends to better inform environmental strategy and planning. This study examines trends from one of the longest paired time series of upland (>250 - 300m) and lowland precipitation records (1879 – 2012), and shorter-term observations (1961 – 2015) from multiple upland locations in South West (SW) England (Dartmoor National Park). In the period 1879 – 2012, total precipitation in the upland site increased by more than 10% for spring, autumn, winter, and annually; for the lowland site, only spring experienced a significant increase (8%) in precipitation. Increases in autumn, winter and annual precipitation were recorded at upland sites since the 1960s. Observed precipitation trends with the latest UK climate projections (UKCP18) for the region were compared across two timeframes (60 and 90 years). Changes in the 30 year average between reference (1981 – 2010) and observed and projected precipitation totals were compared and deviations calculated. Comparisons between model projections and observed trends show large deviation for spring, summer and autumn precipitation in the mid to late 21st century, with the deviation greatest in upland localities. Winter projections however, were broadly consistent with observed trends. Results suggest uncertainties in future precipitation change are greatest in the uplands where the impacts on ecosystem services are the largest.

2.1. Introduction

Upland areas (>250 - 300m) cover around one third of the UKs land area and are considered of national and international importance due to their biodiversity and cultural heritage (Reed et al. 2009). In South West (SW) England, regionally (i.e. NW Europe) important habitats such as upland heathland, Atlantic oak woodland and blanket bog, are associated with the upland granite plateaus of Dartmoor and Exmoor National Parks (JNCC 2019). These areas are vital for important ground nesting birds such as the Ring Ouzel *(Turdus torquatus),* Dunlin (*Calidris alpina*) and Golden Plover (*Pluvialis apricaria*) (Mercer 2009; DNPA 2019), and the conservation of globally significant lichen and bryophyte communities (Lamacraft et al. 2018).

Understanding precipitation change in the UK uplands is particularly important. These areas are integral for the delivery of multiple provisioning, regulating and cultural services (Holden et al. 2007a; Curtis et al. 2014), being the source of 68% of the UK's freshwater (Van der Wal et al. 2011) and an estimated 40% of UK soil carbon stocks (Bradley et al. 2005). UK upland landscapes may provide significant future carbon farming opportunities (Brocket et al. 2019; Lunt et al. 2019).

Levels of precipitation in the SW uplands are over twice the average for UK lowland sites (Burt & Holden 2010; Perry 2014). Changes in precipitation patterns and distribution are significant because rainfall more than any other climatic variable has the greatest effects on below ground carbon storage and plant species growth and composition (Collins et al. 2018; Lunt et al. 2019). This is particularly critical for SW England, where blanket bogs are considered climatically marginal (Clark et al. 2010).

Changes in precipitation can change the distribution of semi-natural plant communities via soil moisture (Morecroft et al. 2009; Walck et al. 2011; Le Roux et al. 2013; Cowles et al. 2018), particularly vital during the 'growing season', between spring and autumn for northern European blanket mire (March – October) and Atlantic oak woodland habitats (April – September). Reduced precipitation is associated with lower viability of sphagnum and bryophyte communities (Ellis 2015), and a contributing factor for oak (*Quercus spp*) decline (Thomas 2008; Sohar et al. 2013).

Increases in precipitation are associated with surface run off and considerable downstream infrastructure damage and crop losses via flooding (Collaku & Harrison 2002; Meyles et al. 2003; Shaller et al. 2016). The economic and social costs are significant; the UK summer floods of 2007 for example, incurred an estimated £3.2 billion in economic losses (Chatterton et al. 2010), and the wet winter of 2013/2014 between £1 – 1.5 billion (Chatterton et al. 2016). Impacts are likely to be greatest in higher elevation areas, where total precipitation is higher, soils poorer, and agricultural productivity marginal (Reed et al. 2009; Burt & Holden 2010; Short & Dwyer 2012). The exceptionally wet summer of 2012 was associated with high economic costs to UK upland agriculture; severe rumen fluke outbreak was reported in livestock for the first time (Gordon et al. 2012). As a result, total productivity fell by 3.2%, the largest single year fall since records began in 1973 (Morison & Mathews 2016).

In the UK, the frequency of precipitation is largely determined by the position of the jet stream, pressure patterns in the NE Atlantic and the movement of extra-tropical cyclones over the North Atlantic (Lavers et al. 2013). The jet stream helps determine the position of Atmospheric Rivers (ARs), which are narrow ribbons (300km) of atmospheric vapour, transporting moisture from the tropics to mid latitudes. ARs are responsible for the majority of rainfall events in Western Europe and are connected with extreme winter precipitation and flood events in the UK (Lavers et al. 2011).

In the summer months the position of the jet stream over the UK can be predicted by spring North Atlantic sea surface temperatures (SSTs), with warm spring SSTs associated with a higher probability of wet summer weather (Osso et al. 2018). De-trended averaged North Atlantic SSTs known as the Atlantic Multi-decadal Oscillation index (AMO) naturally oscillates from positive to negative states at a periodicity of 60 years (Knudsen et al. 2011). A positive AMO is associated with more storms tracking across the Atlantic to the UK and into north western Europe, leading to wet summers in these regions (Dong et al. 2013).

Rising temperatures are projected to result in increased precipitation during existing rainfall events due to increased water holding capacity of the atmosphere, as predicted by the Clausius-Clapeyron equation (Held & Soden 2006; Rajczak & Schär 2017). On current projections, parts of SW England are expected to experience some of the greatest climate changes within the UK. South West England is set to be the first UK region to experience extreme winter rainfall associated with anthropogenic climate change (Fowler & Wilby 2010). Winter projections suggest median increases in winter precipitation of 10 to 20% in areas of the region under all climate change scenarios (RCP2.6, 4.5, 6.0, 8.5) by 2040 – 2059, according to the latest UK Met Office (UKCP18) probabilistic projections (Murphy et al. 2018). Projections are linked to expected changes in the North Atlantic winter storm track (Zappa et al. 2013) and to a greater magnitude and frequency of winter storms along Atlantic European coasts; leading to higher rainfall totals and greater winter flooding (Lavers et al. 2011, 2012, 2013; Kendon et al. 2014; Ramos et al. 2016).

Summer projections suggest median reductions of 20% to 30% in parts of the region under all climate change scenarios by 2040 – 2059 (Murphy et al. 2018), linked to positive Summer North Atlantic Oscillation (SNAO) (Belleflamme et al. 2015) and associated with increased prevalence of anti-cyclonic pressure systems and below average precipitation. High resolution (convection permitting) modelling also suggests that heavier rainfall events are likely in the summer (Kendon et al. 2014). The lowest confidence projections are for summer precipitation (Rowell 2006; Murphy et al. 2018), particularly in 'upland' regions (> 250 - 300m) where seasonal variation in rainfall gradients and lapse rates challenge upland climate projections. Moreover, although upland areas cover around one third of the UK land area, they contain less than 10% of UK climate recording stations (Burt & Holden 2010).

Considering the recent release of UKCP18 land projections (Murphy et al. 2018), the importance of changes in upland precipitation and the likely use of projections in conservation and land management decisions; there is a pressing need to contextualise projected changes in seasonal precipitation with observed trends. The aim of this study was to scrutinise one of the longest running (1879 to 2012) 'upland' (>250 - 300m) (Cowsic river - Dartmoor National Park) and 'lowland' (Plymouth) precipitation records in Western Europe, alongside shorter-term records from multiple upland sites. The study evaluates long term records for SW England in the context of recent model projections (Murphy et al. 2018) across two timeframes (2040 - 2069, 2070 - 2099), whilst assessing the nature and drivers of precipitation trends in this region. Results are likely to be important at a local scale within SW England, but also for maritime influenced upland sites throughout the NE Atlantic.

2.2. Methods

2.2.1. Climate data and quality control

Monthly precipitation totals were obtained from the UK Meteorological Office's (UKMO) Integrated Data Archive System (MIDAS) database via the British Atmospheric Data Centre (BADC) using the Centre for Environmental Data Analysis's (CEDA) web processing service (Met Office 2012). Climate data were also obtained directly from the UK Environment Agencies Hydrometric Archive (Environment Agency 2018) (quality controlled by the UKMO) and the UKMO National Meteorological Archive (NMA) (Met Office 2018a).

Due to the long-term nature of precipitation records, stations have experienced instrumentation and locational changes over the observation periods (Table A2.1), with Plymouth and Princetown records subject to homogenization (Table 2.1), a potential source of inaccuracy (Zhang et al. 2014). To mitigate potential errors, all data were subject to rigorous UK Met Office on site and off site quality control procedures, these include: 1) Basic point of observation checks. 2) Input checks, ensuring values do not lie outside long-term climate extremes for the locality and time period. 3) Checks against neighbouring stations for consistency. 4) Flagged manual quality control correction. 5) Final quality control sweep to eliminate remaining gross errors (Met Office 2018a). Small gaps (< 2%) in Plymouth and Princetown records were infilled using the UKMO gridded (5km) observation datasets (Hollis & McCarthy 2017).

Table 2.1 – Location of weather stations used in precipitation trend analysis with time period covered. Data source: climate records as monthly precipitation totals from the UK Meteorological Office (2012, 2018a), Environment Agency (2018).

Location (abbreviation)	Latitude: Longitude	Elevation	Period of record covered in analysis
Plymouth Mountbatten(PLY)*	50.3548: -4.1211	50m	1879 – 2015
Cowsic Valley (COW)	50.5735: -3.9861	445m	1879 – 2012
Deancombe Farm (DCF)	50.5015: -4.0058	309m	1920 – 2012
Princetown (PRT)*	50.5485: -4.0014	433m	1961 – 2015
Hurston Ridge (HRR)	50.6296: -3.8832	418m	1961 – 2015
White Ridge (WHR)	50.6256: -3.9099	488m	1961 – 2015
Double Waters (DBW)	50.5330: -4.0106	355m	1961 – 2015

**denotes use of multiple stations within same locality, use of correction factor (averaged divergence between stations) for overlapping periods to minimise specific locational differences by creating an homogenised record following standardised methodology (Burt & Holden, 2010).*

Seasons were divided as follows: spring (March, April, May), summer (June, July, August), autumn (September, October, November), winter (December, January*, February*), *note the winter season for the year includes December and the immediately following January and February of the following year. Annual change represents the 12 month period from March (start of spring) to February (end of winter).

2.2.2. Study location

Climate records come from stations located in the SW peninsula of England (SW England – approximately 50^{o} latitude north), United Kingdom in Western Europe, an area characterised by its proximity to the North Atlantic Ocean and its temperate, largely mild, maritime oceanic climate (Perry 2014) (Figure 2.1). Mean temperatures typically fall between 20°C - 13°C in summer (June, July, August) and 8°C – 4°C in winter (December, January, February). Annual precipitation totals are typically close to 1000mm in lowland coastal areas of the region, but doubling in 'upland' moorland areas such as Dartmoor National Park (DNP). Six 'upland' precipitation records come from within DNP , an area dominated by a granite plateau, which forms the highest point (621m) and largest open access area (953 km^2) in southern England (Mercer 2019). One 'lowland' record (Plymouth) is located just outside DNP on the windward south west coast. UKCP18 twenty-five km grid cells covering stations used in the observed vs projected trend analysis were centred over latitude^{o}: longitude^{o} positions (climate stations): 50.439794:-4.2897746 (Plymouth), 50.670882:-3.9471840 (Cowsic Valley), 50.446188:-3.9379437 (Deancombe Farm).

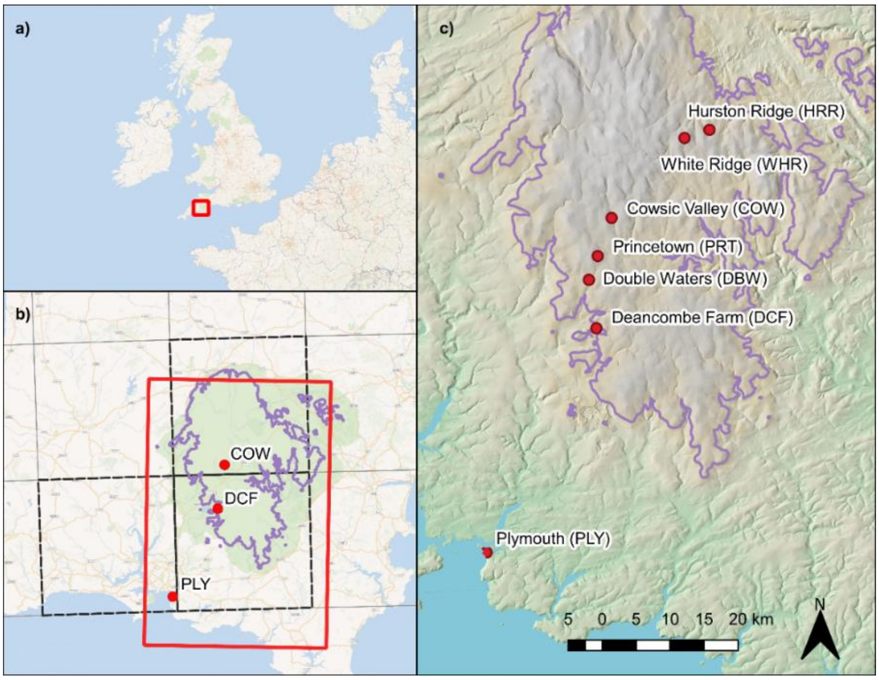

Figure 2. 1 – a) Location of study area (southwest England) within north-western Europe. b) Locations of climate observation sites and UKCP18 twenty-five km grid cells used in observed vs projected trend analysis, with 300m 'upland' isoline and DNP denoted in green c) Location of climate observation sites in reference to 'upland' isoline.

2.2.3. Model projections

UKMO 25 km, horizontal resolution probabilistic climate projections (UKCP18) (Murphy et al. 2018) were accessed via the 'user interface' (Lowe et al. 2018). These projections are intended to represent a useful starting point for risk assessments, aimed to represent the uncertainty consistent in existing climate models combined with internal climate variability effects (Murphy et al. 2018). Probabilistic 'strand one' projections combine 3 Pertubed Parameter Ensembles (PPEs) (HadCM3) and 12 earth system multi-models (CMIP5) to produce broad ranges using a Bayesian statistical framework, and range wider than those derived from multi-model information in isolation (Sexton & Murphy 2012, Sexton et al. 2012, Harris et al. 2013). The 3-stage process (1) integrates HadCM3 PPEs and earth system models, (2) timescales model outputs (Sexton & Harris 2015) and (3) downscales projections (Murphy et al. 2018). Our analysis makes use of a 3000 member sub-sample taken from the 106 members produced in Stage 1. This subsample was accessed for each 25 km grid cell covering climate stations used in the ana lysis, and median change (%) for these grid cells was then calculated. These projections represent 'emissions− driven' projections and account for uncertainties under a range of climate change scenarios (Murphy et al. 2018).

Projections show expected change (%) in monthly precipitation totals (mm) between the reference 30 yr mean (1981−2010), and future 30 yr means for a range of future climate change scenarios represented by representative concentration pathways (RCPs). Probabilistic projections are available for a range of RCPs: 2.6, 4.5, 6.0 and 8.5, which represent median levels of radiative forcing (Wm^{-2}) under a range of climate change scenarios resulting from different CO2 emission pathways and associated temperature changes by 2100 (Moss et al. 2010, Van Vuuren et al. 2011). RCP 2.6, 4.5, 6.0 and 8.5 scenarios are equivalent to mean increases of respectively 1, 1.8, 2.2 and 3.7°C in global mean surface temperature by 2081− 2100, compared to the 1986−2005 reference period (Stocker et al. 2013). RCP 2.6 is an emission pathway that assumes very low greenhouse gas concentration levels and represents a peak in CO2 concentration of 490 ppm before declining by 2100 (Van Vuuren et al. 2007). RCP 4.5 represents a stabilization scenario in which total radiative forcing is stabilized shortly after 2100, without overshooting the long-run radiative forcing target level; this pathway represents a peak of 650 ppm CO2 before stabilizing after 2100 (Smith & Wigley 2006, Wise et al. 2009). RCP 6.0 representsan emissions stabilization scenario with a peak of 850 ppm CO2 before stabilizing after 2100 by using a combination of technology fixes (Fujino et al. 2006, Hijioka et al. 2008). RCP 8.5 represents a scenario of high greenhouse gas concentrations with a rising radiative forcing pathway and 1370 ppm CO2 by 2100 (Riahi et al. 2007).

2.2.4. Trend tables and statistical analysis

The trend of local, observed climate records was determined using linear least squares fit, a standard method for analysing climate trends (Burt & Holden 2010). Whilst the linear least squares fit method is more vulnerable to outliers than other methods in climate analysis, it is often difficult to distinguish variability from trend (Santer et al. 2000). The magnitude of any changes over the period were calculated by subtracting the period mean from the trend value for the last recorded year. Significance was determined using a Mann Kendall trend test, commonly em ployed to detect monotonic trends in environmental and climate series data (Yue et al. 2002, Dixon et al. 2006, Pohlert 2018), due to its robustness with outliers (Kundzewicz & Robson 2004). The strength of time series trends was determined by Kendall- or T-statistic (tau value). Least squares fit linear regressions were used to represent trends, and LOESS smoothing curves were fitted. This is a non-parametric method of local re gression, suitable for data sets with outliers (Cleveland 1979) and used to measure environmental variability at multi-decadal scales (Hannaford 2013). Statistics were performed using R studio (R Core Team 2017), trend analysis and the graph-production packages 'kendall' (McLeod 2011) and 'ggplot2' (Wickham 2009).

2.2.5. Deviation tables (observed vs projected trends)

Observed trends represent the difference between reference (1981 – 2010) and past 30 year averages as a proportion of the current total (% change) and use climate station data (Table 1). Model projections use UKCP18 probabilistic projections which define changes in precipitation (%) between reference and future 30 years averages. Observed and projected trends are compared over equivalent time-periods e.g. 60 years before and beyond the 'reference' (1981 – 2010) 30 year period. Examining the difference between the 'Trend' and 'Model Projections' forms the basis of the analysis (Figure 2.2), and is termed the 'deviation'.

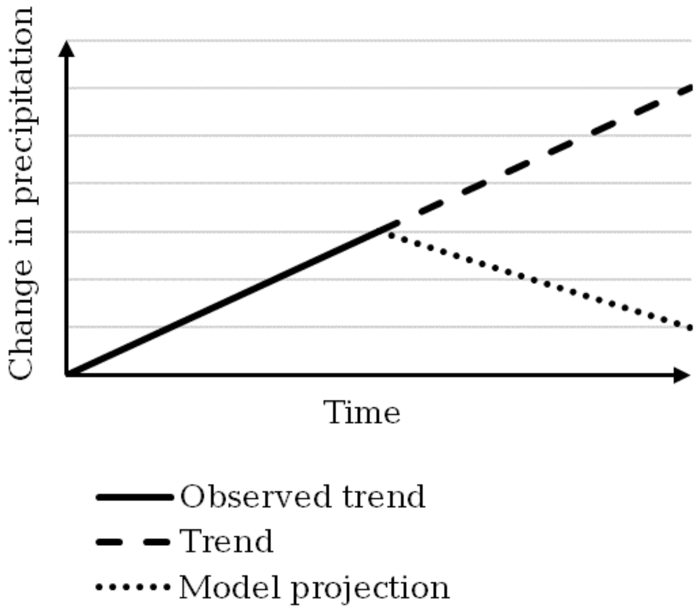

Figure 2. 2 – Example schematic representation of the approach for comparing trends in observed data with median model projections. This example shows a positive deviation between 'Trend' from 'Model projection' as depicted by the green upwards arrow symbol ▲ in deviation tables. Trends could be higher (positive deviation) or lower (negative deviation) than model projections.

2.3. Results

2.3.1. Observed trends

While there was a significant ($P \leq 0.05$) positive trend (1879 – 2012) in total annual precipitation at the Cowsic Valley station (upland) (+226mm, +11%), there was no concomitant significant change at the lowland, Plymouth station (Figure 2.3, Table 2.2). Spring precipitation increased in both lowland (16mm, +8%) and upland (49mm, +13%) stations over the period, with greater increases at the upland station (Table 2). Although there was no significant change in summer precipitation (1879 – 2012), the lowland station showed a 3% decrease and the upland station a 4% increase (Table 2.2). Autumn and winter records match annual precipitation; i.e. significant precipitation increases at the upland station (autumn +12%, winter + 14%), but no significant change (1879 – 2012) at the lowland station (Table 2.2).

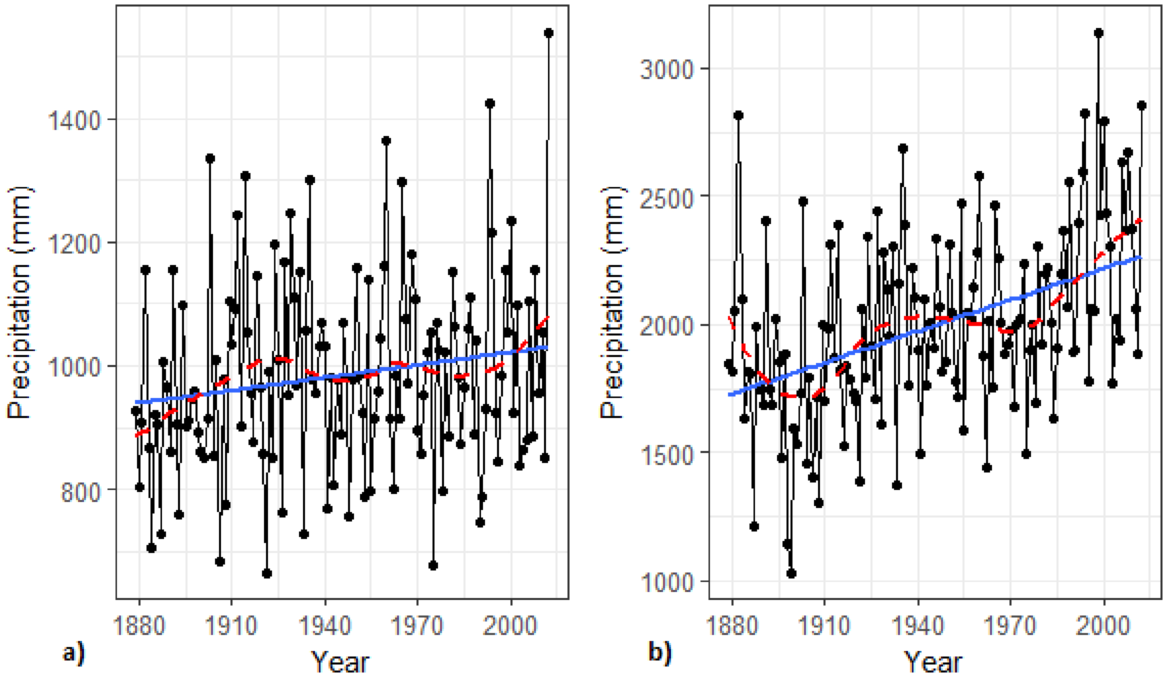

Figure 2. 3 – Total annual precipitation recorded in a) Plymouth and b) Cowsic Valley between 1879 – 2012. *Black dots represent total annual precipitation recorded.* The blue line is the least squares fit linear trend. The red line is a LOESS (local regression) smoothing curve (span = 0.5).

Table 2.2 – Annual and seasonal trends in monthly precipitation totals in lowland Plymouth (PLY) and upland Cowsic Valley (COW) (Dartmoor) 1879 – 2012. Values show observed change (mm and %) from the mean, calculated by subtracting the mean for 1879 – 2012 from the 2012 trend line (linear least squares fit). Statistically significant $P \leq 0.05$ linear trends using the seasonal Mann Kendall test are denoted in bold (* $P \leq 0.001$).

	Lowland		Upland	
	PLY		COW	
Season	mm	%	mm	%
Spring	**16**	**8**	**49***	**13***
Summer	-6	-3	16	4
Autumn	14	5	**68**	**12**
Winter	18	6	**89**	**14**
Annual	46	5	**226***	**11***

Examination of multiple upland Dartmoor stations (1961 – 2015) shows significant increases in annual precipitation at three of the four stations (Figure 2.4, Table 2.3), with only White Ridge (+167mm) marginally non-significant (*P* = 0.072). The most westerly stations, Double Waters and Princetown, experienced the steepest annual increases; 331mm (+18%) and 289.7mm (+15%) respectively. There was no change in annual precipitation over the same period (1961 – 2015) at the lowland station Plymouth (+5%, *P* = 0.360) (Table 3).

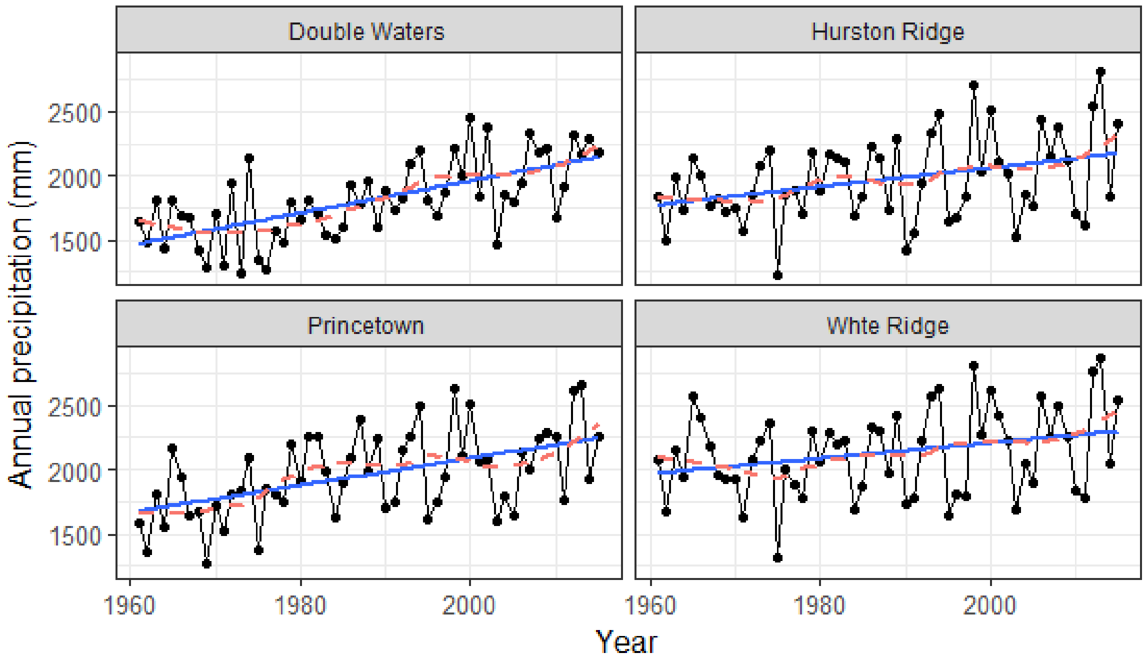

Figure 2. 4 – Total annual precipitation recorded on upland Dartmoor stations: Double Waters, Hurston Ridge, Princetown and White Ridge between 1961 – 2015. Black dots represent total annual precipitation recorded. The blue line is the least squares fit linear trend. The red line is a LOESS (local regression) smoothing curve (span = 0.5).

Examination of seasonal changes in upland and lowland sites (1961 - 2015) (Table 2.3) showed no significant changes in spring precipitation. While marginally non-significant, summer precipitation increased with the most western upland Dartmoor station (Double Waters) experiencing a significant increase (+83mm, +23%, *P* = 0.009). All sites had increasing precipitation in autumn and winter seasons, Double Waters and the other western upland station (Princetown) experienced significant increases ($P \leq 0.05$) in autumn (20%, 15%) and winter precipitation (21%, 17%).

Table 2.3 – Annual and seasonal trends in monthly precipitation totals in lowland Plymouth and upland Dartmoor stations between 1961 – 2015. PLY = Plymouth, DBW = Double Waters , HRR = Hurston Ridge , PRT = Princetown , WHR = White Ridge .Values show observed change (mm and % change) from the mean, calculated by subtracting the mean for 1961 - 2015 from the 2012 trend (linear least squares fit). Statistically significant $P \leq 0.05$ linear trends using the seasonal Mann Kendall test are denoted in bold (* $P \leq 0.001$).

	Lowland		Upland							
	PLY		DBW		HRR		PRT		WHR	
Season	mm	%	mm	%	mm	%	mm	%	mm	%
Spring	-11	-5	21	6	-6	-2	26	7	-15	-4
Summer	26	14	**83**	**23**	40	13	75	19	47	13
Autumn	22	8	**106***	**20***	56	10	**81**	**15**	49	8
Winter	18	6	**121***	**21***	98	14	**106**	**17**	85	11
Annual	52	5	**331***	**18***	**208**	**11**	**290***	**15***	167	8

2.3.2. *Observed vs projected trends*

The interquartile range (IQR) of UKCP18 twenty-five km projections for the 2040 – 2069 period (Table 2.4) suggests the season with the greatest variability around the median is summer, with reductions in mean total precipitation of between 34% - 11% and 32% - 10% for grids covering lowland and upland stations respectively. Spring, autumn and winter seasons had a much lower variability, suggesting higher confidence than summer projections with moderate decreases in spring and increases in autumn precipitation by the 2040 - 2069. Winter projections suggest increases of between 2 – 18% increase in rainfall across locations and climate change scenarios.

Table 2.4 – IQR of projected changes (UKCP18 - 25km resolution) in average seasonal precipitation totals (%) by 2040 - 2069 for one ‘lowland’ (Plymouth) and two ‘upland’ locations (Cowsic Valley, Deabcombe Farm). PLY = Plymouth, Cowsic Valley = COW, Deancombe Farm = DCF. The IQR shows the middle 50% of projected changes between reference 30yr average (1981 – 2010) and future average 60 years ahead or by 2040 – 2069 under RCP 2.6, 4.5 climate change scenarios. Projected data cover three 25km grid cells covering each station: Plymouth (50.439794:-4.2897746), Cowsic Valley (50.670882: -3.9471840), Deancombe Farm (50.446188:-3.9379437). ▲ denotes an increase, ▼ a decrease in precipitation totals.

	Lowland		Upland			
	PLY		COW		DCF	
Season	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5
Spring	▼12 - 0	▼11- ▲1	▼11 - ▲1	▼11 - ▼2	▼11 - ▼1	▼11 - ▲1
Summer	▼31- ▼9	▼34 - ▼11	▼28 - ▼8	▼32 - ▼10	▼29 - ▼8	▼32 - ▼10
Autumn	▼2 - ▲8	▼1 - ▲9	▼2 - ▲8	▼1- ▲9	▼2 - ▲9	▼1 - ▲9
Winter	▲2 - ▲15	▲2 - ▲16	▲1 - ▲12	▲2 - ▲13	▲2 - ▲16	▲3 - ▲18
Annual	▼2 - ▲3	▼2 - ▲3	▼2 - ▲1	▼2 - ▲1	▼1 - ▲3	▼1 - ▲4

Deviation tables for 2040 - 2069 (Table 2.5) show that spring and summer yield the highest deviation between observed and median projected precipitation under both RCP 2.6 and 4.5 climate change scenarios, especially for upland locations (circa 24% for both seasons at Cowsic Valley). Autumn and winter projections whilst not completely consistent, suggest increases but with lower anomalies. Projections for lowland Plymouth in autumn are most consistent with observations.

Table 2.5 – Deviation between 'observed' and median 'projected' (UKCP18 - 25km resolution) changes (%) in average annual and seasonal precipitation totals by the 2050s for lowland and upland locations (observed change (%) - projected change (%)). Observed changes use climate records from one 'lowland' (Plymouth) and two 'upland' stations (Cowsic Valley, Deabcombe Farm) and refer to recorded changes in mean total seasonal precipitation between the reference 30yr average (1981 – 2010) and the 30yr average 60 years previously (1920 – 1949) (reference – past). 'Projected' changes represent median difference between reference 30yr average (1981 – 2010) and future average 60 years ahead or by 2040 – 2069 under RCP 2.6 and 4.5 climate change scenarios. ▲ denotes a positive, ▼ a negative anomaly between observed – projected changes.

	Lowland		Upland			
	PLY		COW		DCF	
Season	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5
Spring	▲ 17	▲ 17	▲ 24	▲ 24	▲ 23	▲ 23
Summer	▲ 19	▲ 21	▲ 22	▲ 24	▲ 20	▲ 22
Autumn	0	▼ 1	▲ 12	▲ 11	▲ 8	▲ 7
Winter	▼ 7	▼ 8	▲ 9	▲ 8	▼ 3	▼ 4
Annual	▲ 3	▲ 3	▲ 14	▲ 13	▲ 8	▲ 8

In common with 2040 - 2069 projections, the IQR of projections for 2070 - 2099 scenarios (Table 2.6) suggests the season with the greatest variability is summer. Reductions in total mean precipitation of 10 – 42% and 10 – 39% are projected in lowland and upland areas respectively between 2070 - 2099 under RCP 2.6 and 4.5 climate change scenarios. There is lower variability around for spring, autumn and winter seasons with moderate decreases projected for spring and moderate increases for autumn precipitation totals. The range of projections for winter suggest increases in total precipitation of between 3 – 26% across locations and emissions scenarios.

Table 2.6 – IQR of projected changes (UKCP18 - 25km resolution) in average seasonal precipitation totals (%) by 2070 - 2099 for one ‘lowland’ (Plymouth) and one ‘upland’ location (Cowsic Valley). Details as for Table 2.4, but refers to 2070 – 2099.

	Lowland		Upland	
	PLY		COW	
Season	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5
Spring	▼9 - ▲2	▼9 - ▲ 2	▼9 - ▲ 1	▼9 - ▲ 1
Summer	▼36 - ▼10	▼42 - ▼14	▼33 - ▼10	▼39 - ▼14
Autumn	▼1 - ▲8	0 - ▲10	▼1 - ▲7	▼1 - ▲8
Winter	▲5 - ▲8	▲9 - ▲26	▲3 - ▲14	▲6 - ▲20
Annual	0 - ▲4	0 - ▲5	▼2 - ▲3	▼2 - ▲3

Deviation tables for 2070 - 2099 projections (Table 2.7) suggest spring, summer and autumn are the seasons with the greatest divergence between observations and latest UKCP18 projections, with divergence higher at the upland (Cowsic Valley) than the lowland site (Plymouth). Deviation is as high as 30%, 33% and 31% for spring summer and autumn respectively under RCP 4.5 for 2070 - 2099 in upland sites compared to 15%, 18% and 9% in the lowlands. Median projections for winter precipitation change are more consistent with observations than other seasons, but while observations are above projected trajectories for the upland location, they fall below for the lowland site. The seasonal difference between the upland and lowland sites means that although annual precipitation deviation between observations and projections is negligible for the lowland site (+ 1%) under both emissions scenarios, it is considerable for upland Cowsic Valley (+ 24%).

Table 2.7 – Deviation between 'observed' and median 'projected' (UKCP18 - 25km resolution) changes (%) in average annual and seasonal precipitation totals by 2070 - 2099 for lowland and upland locations (observed change (%) - projected change (%)). Details as for Table 2.5, but refers to 2070 – 2099. Observed changes use climate records from one 'lowland' (Plymouth) and one 'upland' station (Cowsic Valley). DCF is outside the time-period of analysis.

	Lowland		Upland	
	PLY		COW	
Season	RCP 2.6	RCP 4.5	RCP 2.6	RCP 4.5
Spring	▲15	▲15	▲30	▲30
Summer	▲14	▲18	▲30	▲33
Autumn	▲9	▲9	▲32	▲31
Winter	▼12	▼18	▲15	▲10
Annual	▲1	▲1	▲24	▲24

2.4. Discussion

Long term (>130 years) precipitation records from SW England evidence significant anthropogenic forcing, which is more pronounced in upland sites. This study is fortunate to use one of the longest pair of upland and lowland precipitation records in Western Europe and the dependence of seasonal trends on the time-period analysed, highlights the importance of long-term climate observations (Burt & Holden 2010). The differences between time-periods underscore the difficulty of linking shorter term (<50 years) climate records to anthropogenic climate change, as trends may be confounded by natural multi-decadal atmospheric and/or oceanic cycles (Parker et al. 2007; Bindoff et al. 2013).

Elevated autumn, winter and annual precipitation trends in the UK uplands have previously been linked to a 'double orographic enhancement', associated with positive North Atlantic Oscillation (+NAO), linked to stronger maritime airflow and high atmospheric moisture content (Burt & Holden 2010; Burt & Howden 2013). Upland sites experience enhanced precipitation via susceptibility to the 'seeder-feeder' process, which involves raindrops in upper level clouds washing out droplets within lower level 'feeder' clouds, which form over hills, producing higher rainfall intensities (Bergeron 1965; Hill et al. 1981; Lee et al. 2000). Other mechanisms can occur through primary (sea salt and other organics) and secondary (ocean-released dimethyl-sulphide) marine aerosols, which can drive cloud formation and increase Cloud Condensation Nuclei (CCN) (Hudson et al. 2011; Ovadnevaite et al. 2011; Sanchez et al. 2018). Therefore, while the ‘double orographic enhancement’ has been linked to +NAO associated with periods of maritime weather and south-westerly winds (Burt & Howden 2013; Burningham & French 2013), it is perhaps interaction between the seeder-feeder process and oceanic derived CCN that underpins the mechanism of increased upland precipitation change. This interaction would become stronger during +NAO and could explain enhanced precipitation noted for west coast UK upland sites (Burt & Howden 2013). Observed precipitation trends in upland, windward stations may reflect this process, and explain recorded amplification of the rain-shadow effect by +NAO (Burt & Howden 2013).

A better understanding of the interaction between oceanic-atmospheric processes and upland climate mechanisms is therefore important for accurately modelling future climate changes for upland sites in the NE Atlantic and other oceanic influenced upland regions. The sensitivity of upland precipitation to atmospheric and oceanic cycles may additionally have important implications for understanding the ecological dynamics, conservation priorities, and planning for effective climate mitigation in these areas (Morecroft et al. 2009; Brocket et al. 2019; Lunt et al. 2019).

Records of seasonal precipitation from upland SW England suggest significant divergence between observed trends and recently released UKMO climate projections. Although increases in winter precipitation are broadly consistent with a range of climate model scenarios; records for spring, summer and autumn precipitation show no signs of projected drying (Murphy et al. 2018), with deviation greatest in upland locations.

Using observed changes in precipitation to infer confidence in projected changes has its limitations, namely the uncertainty of future emissions pathways, many of which are non-linear); our methods did not explicitly seek to determine model validity as climate models consider many and varied processes when generated. There are considerable limitations in downscaling projections to the scale used in this study; however, projections for grid cells used, reflect their intended application as a useful starting point for risk assessments and to represent the uncertainty present in existing climate models (Murphy et al. 2018). It was felt vital to contextualise projected trends, considering the likely applicability of these projections in land management decisions, particularly when projected changes in future precipitation are so variable and the range of outcomes high (Murphy et al. 2018). The timeframes for comparison (60 and 90 years) were chosen to avoid being confounded by natural cycles such as AMO and NAO, but this restricted the number of suitable stations. RCP 2.6 and RCP 4.5 climate change scenarios were used in our analysis as these are the most conservative RCPs, which were judged more suitable for comparison. Probabilistic projections for RCPs 6.0 and 8.5 climate change scenarios show similar deviation to observed trends seen for RCP 2.6 and 4.5 (Table A2.2, A2.3) but with elevated magnitude in these more extreme climate change scenarios.

There is presently considerable interest focussed on understanding ecological patterns and process within the context of climate projection data (Parmesan & Hanley 2015; Suggit et al. 2017; Smith et al. 2018). Results highlight the need for caution when examining the future response of upland organisms and ecosystems to projected changes in growing season precipitation totals and that ecologists must actively explore uncertainty in all aspects of climate data before making inferences about biological response (Suggit et al. 2017).

This uncertainty is greatest in summer (Murphy et al. 2018), as drying is predicated on large scale changes in the placement of anti-cyclonic pressure systems (Belleflamme et al. 2015), linked to a natural downturn of the Atlantic Sea Surface temperatures (SSTs), yet confidence levels for these large scale changes is relatively low (Rowell & Jones 2006). The emergence of an Atlantic SST tri-pole pattern and an enhanced meridional SST gradient could lead to increased storminess in the Atlantic, associated with intensifying atmospheric baroclinicity (Frajka-Williams et al. 2017). It is interesting to note that without a changed position of anti-cyclonic systems in the North Atlantic, blocking flow from the Atlantic Ocean, some models (HadAM3PEur) project a net increase in rainfall in the UK and Scandinavia due to the enhanced moisture content of the warmer atmosphere (Rowell & Jones 2006).

Other uncertainties in summer precipitation rest on the uncertain influence of variations in local SSTs on evaporation behaviour (Long & Xie 2015), the downscaling of regional and global models (Rowell 2006), and the large observed seasonal variation in lapse rates (Holden & Rose 2011; Burt & Howden 2013). Consequently, changes in short duration (sub daily) summer events are unclear as projections are less reliable at these scales (Fowler et al. 2007). Improvements in the accuracy of summer projections may be available with the use of 'convection permitting' models, run at high resolution (<5km) to project more localised high impact rainfall events (Kendon et al. 2014, Kendon et al. 2017).

Recent increases in summer precipitation coincide with a move from the negative to the positive phase of the AMO and are supported by long-term UK river flow monitoring data, that show no reduction in summer flow rates (Hannaford 2013). Given the evidenced influence of SSTs on summer precipitation (Dong et al. 2013, Osso et al. 2017) and pressure patterns (Belleflamme et al. 2015), future interaction between natural AMO and background anthropogenic SST warming is likely to prove important. This interaction could be influential in determining the temporal and spatial pattern of future precipitation trends in SW England and more widely for NW European upland coastal sites.

Winter projections are more robust, associated with enhanced atmospheric water vapour content and increased precipitation (Held & Soden 2006, Schaller et al. 2016). Atmospheric Rivers (ARs) are expected to increase in strength and frequency in the UK and Europe wide under multiple global climate model (GCMs) simulations, resulting in heavier precipitation and greater flood risk (Lavers et al. 2013; Ramos et al. 2016). Increases in total monthly precipitation are likely to result in higher soil moisture and the earlier saturation of soils (Blöschl et al. 2017). Higher rainfall totals during single rainfall events, alongside more saturated soils from increases in cumulative monthly rainfall totals, heightens the volume of water and reduces attenuation via soil infiltration and storage. This may result in the rapid transfer of rainfall (via runoff) to river channels, a steeper hydrograph (greater rising limb), and higher flood risk. Increased precipitation in northwest Europe has resulted in increased flood risk (Blöschl et al. 2019).

Precipitation observations support other records from paired upland and lowland sites and highlight that upland locations are particularly sensitive to recent changes in climate (Burt & Holden 2010; Burt & Ferranti 2012). The study provides support for local winter projections (Murphy et al. 2018), underlines the significant potential for future winter flood risk and suggests the damaging floods experienced in the UK between 2007 – 2015 may have set a precedent for future changes.

Results signpost significant increases in spring, autumn, winter and annual precipitation for upland SW England between 1879 and 2012. Moderate increases in summer precipitation represent a deviation from the drier summers predicted with current and previous climate models. Deviation between observed and projected precipitation trends were greatest in upland locations. Taken together, the results highlight the uncertainty between predicted and observed climate trends, particularly for summer precipitation totals and evidence the need for caution when making assumptions on climate impacts based solely on predictive models (Parmesan et al. 2018). The study also highlights the value of long term upland climate monitoring and the importance of model projections at appropriate spatial scales (Watts et al. 2015) to better enable policy makers and practitioners to deliver ‘future proofed’ decisions for the delivery of multiple ecosystem services in the uplands of NW Europe (Reed et al. 2013; Brown & Everard 2015).

Chapter 3.

Native woodland establishment improves soil hydrological functioning in UK upland pastoral catchments

Abstract:

Extreme rainfall and flood events are predicted to increase in frequency and severity as a consequence of anthropogenic climate change (ACC). In upland areas, historical over-grazing and associated soil compaction have further exacerbated peak flood levels and flood risk along many river catchments. As a result, the reinstatement of upland woodland is increasingly seen as pivotal to an integrated suite of options forming part of Natural Flood Management (NFM) associated with a 'public money for public goods' approach to European agriculture. Nevertheless, understanding the impact of native woodland establishment on upland soil hydrology remains relatively poor. This study compares physical and hydrological properties from the surface soils of establishing woodland and grazed pasture across four flood vulnerable upland headwater catchments in Dartmoor National Park, SW England. We show upland native woodland establishment is a viable soil recovery option, with a doubling of soil saturated hydraulic conductivity, increased 'wetness threshold' and reduced surface soil compaction and bulk density within 15 years of establishment. The study supports the establishment of native woodland as an effective tool to improve the hydrological functioning of soils in upland pastoral catchments and the provision of flood mitigation 'ecosystem services'. However, land managers and policy makers must consider past and present management, soil type and catchment location when planning new NFM schemes if environmental benefits are to be maximised and 'public money for public goods' are to be commensurate with outcomes.

3.1. Introduction

Much of the widespread scientific concern about the environmental threat posed by anthropogenic climate change (ACC) stems from acute, extreme events rather than longer-term chronic change (Rahmstorf & Coumou 2011; Vasseur et al. 2014; Parmesan & Hanley 2015). Of the many extreme climate challenges, major shifts in the intensity of extreme precipitation and concomitant increases in regional flooding along river catchments are perhaps the most pressing (IPCC 2014b; Bevacqua et al. 2019). Globally, severe freshwater flooding has long been seen as a major economic problem for agriculture, and one that poses an additional threat to human well-being (Page & Williams 1926; Mirza 2002; Chau et al. 2015).

Like many regions, the United Kingdom (UK) has experienced notable summer and winter flood events in recent years, resulting in significant economic and environmental damage along river catchments (Marsh & Hannaford 2007; Chatterton et al. 2010, 2016; Marsh et al. 2016; Schaller et al. 2016). The UK is set to see an increase in flood events due to projected increases in winter, spring and autumn precipitation (Lavers et al. 2013; Murphy et al. 2018; Bevacqua et al. 2019). The 'uplands', typically >250 – 300m in the UK (Bunce et al. 2018a), are uniquely vulnerable and important for managing this risk. Not only have these areas experienced greater increases in precipitation compared to lowland sites (Burt & Holden 2010; Murphy et al. 2019), but as the source of 68% of the UK's freshwater, they represent the principle areas of river flow generation (Van der Wal et al. 2011; Robinson et al. 2013).

Historic degradation of upland areas (Bardgett et al. 1995; Bunce et al. 2018a) is therefore, of particular concern. A legacy of soil compaction from long-term over-grazing has left many upland soils in poor condition (Sansom et al. 1999; Holden et al. 2007ab). Structural degradation and soil compaction results in the loss of macro-porous structures within the soil profile, of key importance for flood risk management (Palmer & Smith

2013; Alaoui et al. 2018). Indeed, whilst macro-pores typically consist of 10-15% of the soil volume they account for 74-100% of the water movement (Aloui & Helbling 2006). The loss of connectivity between near surface and subsurface macro-pores and the alteration of pore distribution, changes the water saturation states of soils, subsequent runoff, and hydrographic characteristics after rainfall events (Meyles et al. 2003; O'Connell et al. 2007; Dixon et al. 2016). Heavily grazed, compacted areas can become 'active source areas' for runoff generation by lowering the threshold between dry and wet soil states ('wetness threshold') (Meyles et al. 2006; Holden et al. 2007c). Increased runoff leads to unnaturally high flows in wet periods and decreased river base-flow in dry periods (Sansom et al. 1997; Shuttleworth et al. 2019), representing a significant challenge for mitigating the impacts of future seasonal precipitation regimes expected with ACC.

As part of a move towards natural flood management (NFM) solutions, woodland creation is increasingly seen as a way to deliver flood mitigation and attenuate peak river flows (Nisbet et al. 2011; Dadson et al. 2017; Lane 2017; Stratford et al. 2017). Natural flood management attempts to deliver multiple ecosystem services and public benefits including, carbon sequestration, habitat creation, water purification and public health benefits, whilst minimising the social, environmental and economic costs (Iacob et al. 2014; Burgess-Gamble et al. 2017; Lane 2017). Trees offer NFM potential via three potential mechanisms; 1) greater water use 2) increase in hydraulic 'roughness' and 3) amelioration of soil structure (Robinson et al. 2003; Nisbet & Thomas 2006; Nisbet et al. 2011; Birkinshaw et al. 2014).

It is potential impacts on soil properties which are of most relevance for the mitigation of extreme flood events. Evidence from the Pontbren catchment (Wales, UK), suggests woodland creation in former pasture systems had significant and rapid (<10 years) impacts on soil infiltration properties and flood risk (Carroll et al. 2004; Marshall et al.

2014). Nonetheless, our knowledge of how applicable results are to other upland catchments is limited (Burgess-Gamble et al. 2017) and our understanding of how trees affect soil hydraulic properties more generally, surprisingly poor (Archer et al. 2013; Rogger et al. 2017; Stratford et al. 2017; Chandler et al. 2018). This knowledge seems particularly pertinent given the recent commitment by the UK government to plant 11 million trees by 2050 (DEFRA 2018a), a move which is part of a growing interest in native woodland restoration more widely, linked to a 'public money for public goods' approach to European and UK agricultural policy (Bateman & Balmford 2018; Baldock et al. 2019). Consequently, there is a pressing need for improved understanding on the impact native woodland creation has on soil infiltration and physical properties, especially in the upland pastures where they look set to be established.

In this study we test the hypotheses that woodland establishment is associated with; a) lower surface soil compaction b) higher soil water infiltration c) increased soil macro-porosity. We examined the impact of woodland establishment (7 – 15 years without grazing) on infiltration and compaction properties in valley side and valley bottom (podzolic and gley soils) soils on four flood vulnerable pastoral catchments in Dartmoor National Park (DNP), SW England.

3.2. Methods

3.2.1. Study sites

Dartmoor National Park (DNP), covering an area of over 900 km^2, is the largest upland area (highest point - 621m a.s.l) in the southern part of the British Isles (Figure 3.1). Woodland in this area was cleared in prehistory since when the area has primarily been used for grazing livestock. Consequently, vegetation in DNP is dominated by acid grassland and Atlantic heath with relatively sparse tree cover over most of the area (Mercer 2009). In addition to this long history of (over) grazing and associated soil compaction (Sansom et al. 1999), the area naturally receives high levels of precipitation, with extreme rainfall events set to increase into future decades associated with ACC (Fowler & Wilby 2010; Murphy et al. 2019). The many small streams and rivers that rise on the open moorland form ‘flashy’ catchments, naturally vulnerable to spate flooding (Perry 2014). Indeed, the recent flood events in this area (Devon County Council 2013, 2014) coupled with low woodland cover (12%) similar to the UK average (13%) (DNPA 2017; EUROSTAT 2019; Forestry Commission 2019), make DNP an ideal location to test the impact of woodland establishment on soil compaction and water infiltration rates.

Four newly established woodland areas with adjacent grazed pasture (acting as a ‘control’ treatment) were identified (Figure 3.1, Table 3.1) on the basis of available background information (when and how densely trees were planted, former land use etc.), and position within the catchment (i.e. relevance for NFM flood risk mitigation). Three of the four sites were formerly grazed sheep, cattle and deer pasture, recently planted with native trees (*Quercus robur, Quercus petraea, Fraxinus excelsior, Corylus avellana, Sorbus aucuparia, Betula pubescens, Crataegus monogyna*). The fourth (Higher Piles, Erme catchment), is abandoned pasture now left to natural tree colonisation supplemented with additional planted trees. All establishing woodland areas were protected from grazing by fenced exclosures (Table 3.1). Pasture areas were grazed with a mix of sheep, cattle and deer. Grazing intensity was quantified (Table A3.1) after discussion with respective landowners, and animal to Livestock Unit (LSU) conversion followed standard UK format (Natural England 2013).

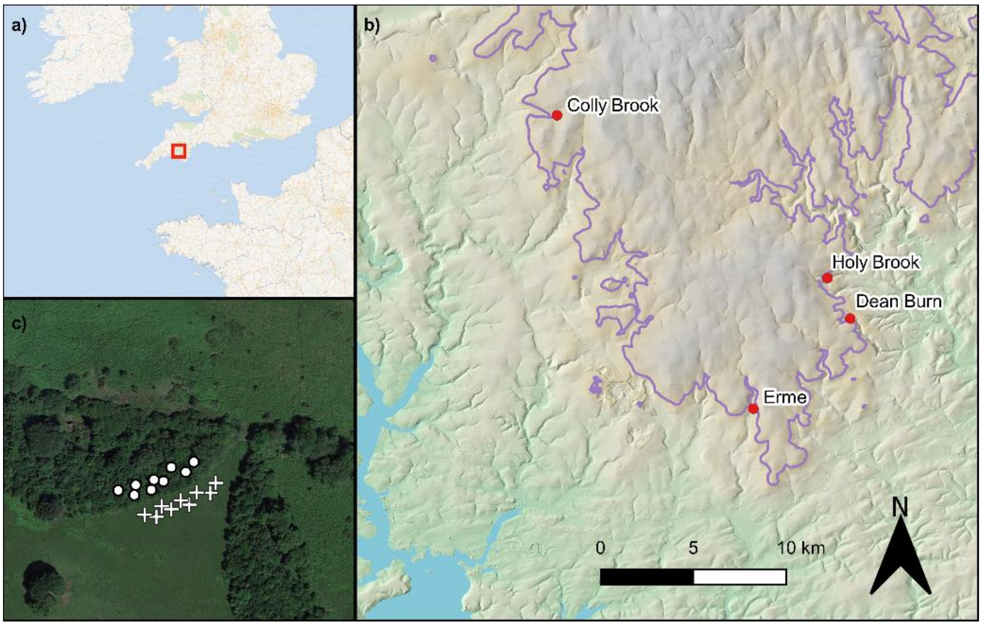

Figure 3. 1 – a) Location of study area (Dartmoor National Park, southwest England) within north-western Europe. b) Locations of catchment sites in relation to the 300m 'upland' isoline. c) Example (Holy Brook) of sampling approach to compare soil hydrological and physical properties in establishing woodland (circles) and pasture areas (crosses).

Table 3.1 – Site information for four river catchments located on Dartmoor, SW England, used to assess the impact of establishing woodland on soil hydrology. Details include location (latitude:longitude), time since planting (woodland age) and composition (tree density and species, planting method). Soil series and descriptive information were classified using field soil pit observations and 'The Soils Guide' (Cranfield University 2019).

	Catchment			
	Colly Brook	**Dean Burn**	**Erme**	**Holy Brook**
Location (Lat:Long)	50.5779: -04.0657	50.4831: -03.8391	50.4382: -03.9110	50.5024: -03.8575
Tree density (ha^{-1})	945	686	1083	1557
Altitude (m)	319m	286m	250m	281m
Woodland age (years)	10	11	7	15
Dominant tree species	Oak	Oak	Oak	Oak & Ash
Method of establishment	Planted	Planted	Natural colonisation with planting	Planted
Position within catchment (Slope angle °)	Valley bottom (0)	Valley slope (7.0)	Valley bottom (0)	Valley slope (9.1)
Soil series	Wilcocks 2	Denbigh	Laployd	Manod
Soil description	Stagnohumic gley soils	Brown Earth, Podzolic	Stagnohumic gley soils	Brown earth, Podzolic.
Natural Hydrology	Seasonally waterlogged	Freely draining	Seasonally waterlogged	Freely draining

3.2.2. Hydraulic conductivity and soil compaction

Differences in water infiltration capacities between adjacent establishing woodland and grazed pasture areas were examined over five-weeks between September and early October 2018. Eight to fourteen sample locations were selected for each establishing woodland and pasture area within catchment sites (sample number matched for each pair)(Figure 3.1). Micro-topographic slope variation between sample pairs, an important variable of hillslope runoff (Thompson et al. 2010; Marshall et al. 2014) was minimised (within 5^{o} range) and recorded using an electronic spirit level. Saturated hydraulic conductivity (Ksat) of soils was quantified using a portable, single ring infiltrometer (100mm x 130mm) inserted 6cm into the soil surface (Carroll et al. 2004). Soil water infiltration was measured until a ‘steady state’ (Ksat) was reached (i.e. <10% difference between three consecutive readings) (Eijkelkamp 2018), with minimal possible time gaps between comparable readings. The ‘wetness threshold’ (Meyles et al. 2003), defined as the volume of water (cm) required for soils to transition from a ‘dry state’ (see soil moisture readings) to a ‘wet state’ (Ksat), was calculated.

Ten surface soil compaction (0 – 10 cm) and 8 to 14 soil moisture (%) measurements (upper 6cm) were taken in each area per location using an impact sheer vane (SL8 10) (19mm head) and theta probe kit (AT ML2X ; www.delta-t.co.uk) respectively.

3.2.3. Soil physical analysis

Six soil cores (60mm x 55mm) were collected from establishing woodland and grazed pasture areas at all four catchments using a Pittman corer (0200 Soil Core Sampler ; www.soilmoisture.com) in December 2018. Cores were divided into upper (2 – 5cm) and lower (6 – 9cm) sections using a sharp knife, to avoid smearing. Separate cores were then saturated for three days, before being weighed and placed on sand suction tables at

0.05bar (- 50cm pressure head) until constant mass was reached; i.e. defined as no more than 100mg between readings (Hall et al. 1977). Samples were re-weighed before drying at 100^{o}C for 24 hours, and reweighed afterwards. The particle density of fine earth soils from each core was determined using the density bottle method (British Standards 1990). Porosity was then determined:

Porosity (% of total sample) = (1 – (bulk density / particle density)) x 100

Subtracting '0.05 bar' porosity from 'saturated' porosity was used as a measure of macro-porosity or 'transmission' porosity (British Standards 1990). Samples were dry sieved to separate fine (<2 mm), small stone (> 2mm, < 16mm) and large stone (> 16mm) fractions. Organic matter (%) from a subsample of the <2mm fraction, was determined using loss on ignition (LOI) (400^{o}c for 18 hours).

3.2.4. Soil classification

The upper soil layers (0 – 25cm) were classified by digging a hexagonal-shaped pit (40 – 50cm deep), and slices of undisturbed soil used to assess structural condition (Figure 3.2)(Palmer & Smith 2013). Soil structure is characterised by the shape, size, and degree of development of primary soil particles into naturally or artificially formed structural units, as well as the presence of voids (pores) between and within aggregates (see Hodgson [1997]). Structural degradation assessment was paired to surface compaction readings for improved confidence in sheer vane methodology (Table A3.2). Samples were assigned to a 'soil series' (Clayden & Hollis 1987) by inspection of surface and subsurface layers within pits and a 5cm wide Edelman auger to assess deeper layers.

Figure 3. 2 – Visual assessment of soil structure in livestock grazed upland pastures and adjacent establishing (10 years since planted) native mixed oak woodland (Dean Burn) in Dartmoor, southwest England. Soils were categorised as having A) poor; B) moderate and C) excellent soil structure. See Table A3.2 for relationship between soil compaction and visual assessment of soil structure.

3.2.5. Statistical analysis

A Shapiro-Wilks normality test and Levene test for homogeneity of variance were performed, despite marginally breaking normality and variance assumptions for some variables (initial infiltration, wetness threshold) parametric testing was applied but results treated with caution (Dytham 2011). Differences between the establishing woodland and pasture areas ('land use'), between catchment and for interacting catchment vs 'land use' impacts were assessed via two-way ANOVA.

Statistics were performed using R studio (R Core Team 2017) and graph production and statistical packages 'GGplot2' (Wickham 2009), 'cowplot' (Wilke 2017) and 'Car' (Fox and Weisberg 2011) respectively.

3.3. Results

Ksat, initial infiltration and 'wetness threshold' were higher in establishing woodland than grazed pasture areas ('Land Use' effect $P < 0.001$ for all responses) (Table 3.2). For Ksat and initial infiltration, the impact of woodland establishment was dependent on catchment site (i.e. found a significant 'Land use' × 'Catchment' interaction), mostly relating to higher pasture infiltration and lower woodland infiltration at the Holy Brook. The elevated wetness threshold in woodland areas was however ubiquitous across all catchment sites (Figure 3.3), with no 'Land use' × 'Catchment' interaction. 'Dry state' surface soil moisture (EW mean 29.6, SE = 4.8, GP mean = 30.4, SE = 2.0) did not vary with land use.

Table 3.2 – The influence of newly established woodland on surface soil hydrological properties along four river catchments (Colly Brook, Dean Burn, Erme, Holy Brook) located in Dartmoor, SW England. Mean (±SE) values of saturated hydraulic conductivity (cm $^{-hr}$)('Ksat'), initial infiltration rate (cm $^{-hr}$) ('I infiltration'), Wetness Threshold (cm^{-hr}) ('W threshold'), and surface soil moisture (%) of soils in establishing 'woodland' sites are compared with control grazed 'pasture' areas using two way ANOVA with significant (P < 0.05) differences denoted in bold font.

				Results of Two-way ANOVA: Land use (df = 1)		Catchment (df = 3)		Interaction (df = 3)	
Soil property	**Land use**	**Mean**	**SE**	***F***	***P***	***F***	***P***	***F***	***P***
Ksat (cm $^{-hr}$)	Woodland	1035.2	288.5	**15.2**	**< 0.001**	**3.7**	**0.014**	**6.9**	**< 0.001**
	Pasture	574.1	134.5						
Infiltration (cm $^{-hr}$)	Woodland	1778.5	444.4	**35.4**	**< 0.001**	**3.9**	**0.011**	**6.6**	**< 0.001**
	Pasture	693	137.0						
W threshold (cm)	Woodland	29.4	2.3	**24.1**	**< 0.001**	2.0	0.124	1.8	0.164
	Pasture	18.8	1.3						
Soil moisture (%)	Woodland	29.6	4.8	0.9	0.330	2.2	0.094	2.2	0.100
	Pasture	30.4	2.0						

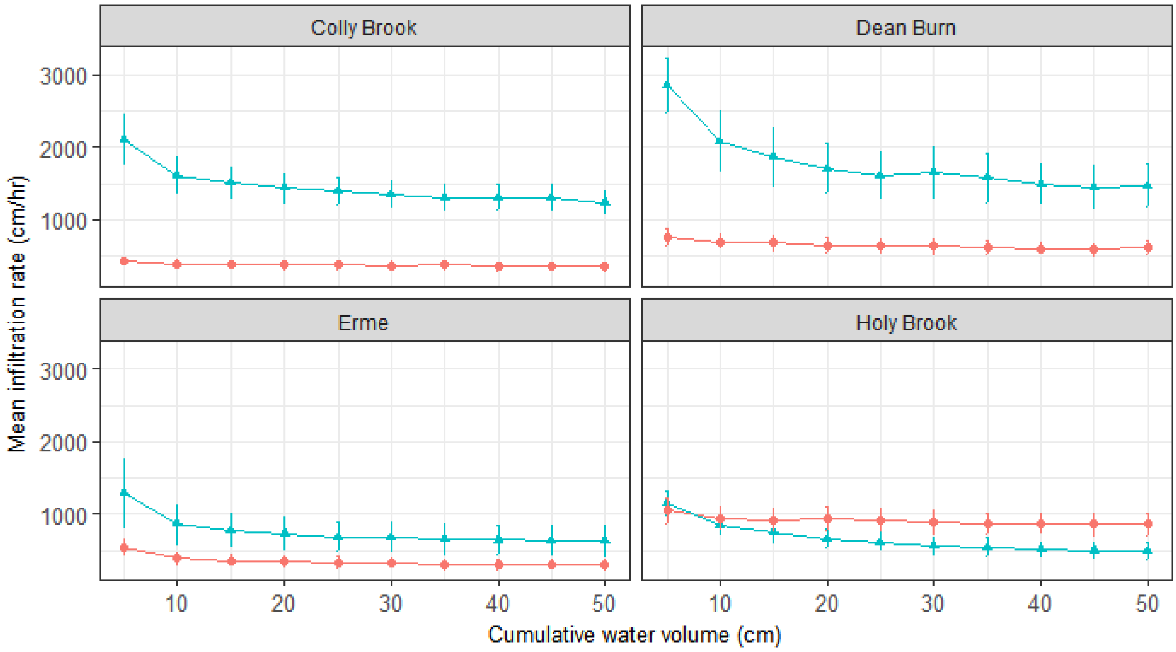

Figure 3. 3 – The influence of newly established woodland on surface soil hydrological properties along four river catchments (Colly Brook, Dean Burn, Erme, Holy Brook) located in Dartmoor, SW England. Mean (±SE) infiltration rate (cm^{-hr}) by cumulative water volume of soils in establishing woodland sites (blue) compared with control grazed pasture (red) areas. The first point on each graph represents 'initial infiltration' (the first 5cm), a flat line (<10% difference between three consecutive readings) represents 'Ksat' and the 'wetness threshold' is the cumulative water volume between initial infiltration 'dry state' and Ksat.

Soil surface soil compaction (Kpa) and bulk density (g cm^{-3}) (BD) were significantly higher in pasture areas ('Land Use' effect $P < 0.001$ for both responses) (Table 3.3). The impact of woodland establishment on soil compaction (i.e. BD, M porosity and SOM) varied between catchments as differences in soil physical properties between establishing woodland and pasture were minimal at Holy Brook, where SOM and M porosity were comparatively low (Figure 3.4), small stone percentage highest (Table A3.4), and historic stock density higher (Table A3.1). The impact of woodland establishment in lowering surface soil compaction was greatest where SOM was higher (i.e. Colly Brook and Dean Burn) but the site with the youngest establishing woodland (Erme) evidenced the most marked changes in BD, SOM and M porosity (i.e. lower BD and increased SOM and M porosity in establishing woodland areas). For SOM and M porosity catchment differences resulted in no overall ‘land use’ impact for these soil properties. Differences in compaction, BD, percentage of small stones (%), macro-porosity (M porosity) (%) and organic matter content (SOM) of surface soils were observed between catchments (Table 3.3).

Table 3.3 – The influence of newly established woodland on surface soil physical properties along four river catchments (Colly Brook, Dean Burn, Erme, Holy Brook) located in Dartmoor, SW England. Mean (±SE) values of surface soil compaction (Kpa), bulk density with stones (g cm^{-3})(BD), macro-porosity (%)(M porosity), percentage of small stones (%) and organic matter (%)(SOM) of soils in establishing ‘woodland’ sites are compared with control grazed ‘pasture’ areas using two way ANOVA with significant (P < 0.05) differences denoted in bold font.

Soil properties	Land use	Mean	SE	Land use (df = 1) *F*	Land use (df = 1) *P*	Catchment (df = 3) *F*	Catchment (df = 3) *P*	Interaction (df = 3) *F*	Interaction (df = 3) *P*
Compaction (Kpa)	Woodland	21.8	6.8	**194.3**	**< 0.001**	**3.9**	**0.011**	**18.9**	**< 0.001**
	Pasture	52.0	2.7						
BD (g cm^{-3})	Woodland	0.672	0.046	**22.6**	**< 0.001**	**10.8**	**< 0.001**	**6.1**	**0.001**
	Pasture	0.795	0.060						
M porosity (%)	Woodland	9.8	1.0	2.4	0.128	**34.5**	**< 0.001**	**10.5**	**< 0.001**
	Pasture	9.3	0.9						
Small stones (%)	Woodland	32.4	11.2	0.6	0.458	**229.1**	**< 0.001**	2.2	0.108
	Pasture	33.5	11.4						
SOM (%)	Woodland	15.4	1.2	2.4	0.129	**21.9**	**< 0.001**	**6.4**	**0.001**
	Pasture	14.3	2.3						

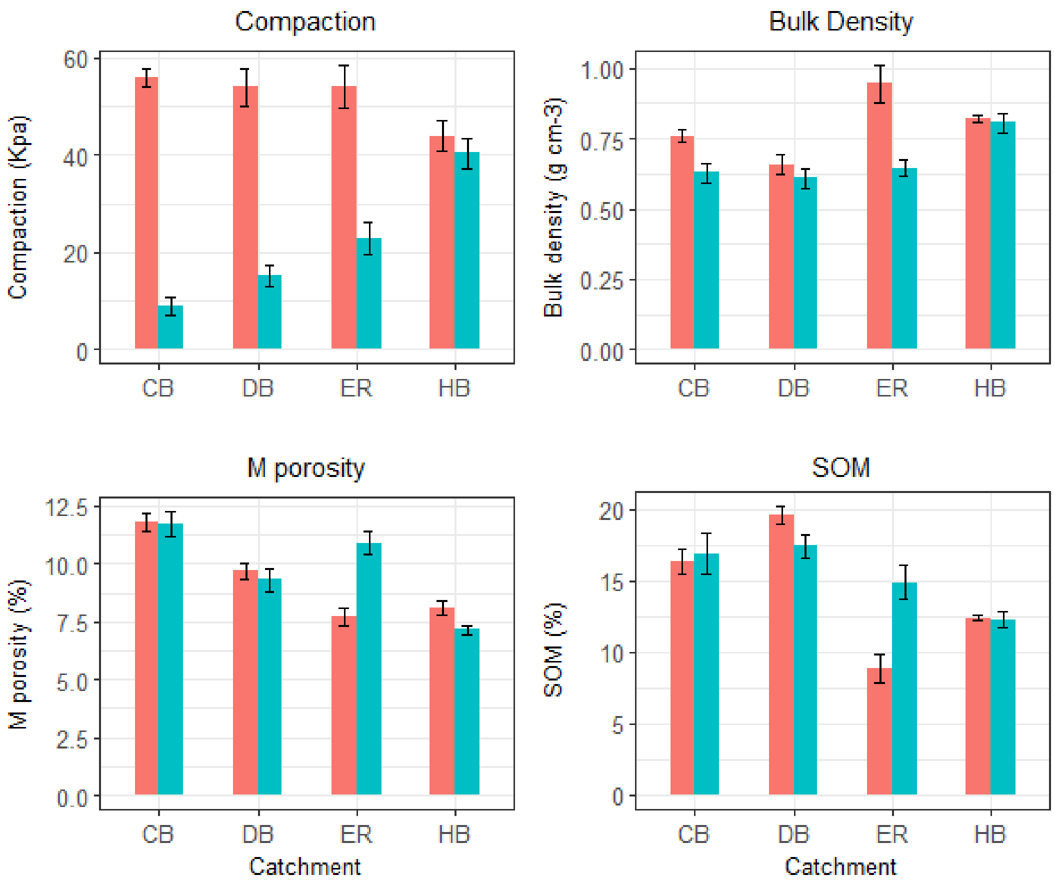

Figure 3. 4 – Site-specific difference in surface soil physical properties between establishing woodland and grazed pasture areas in upland catchments (Colly Brook, Dean Burn, Erme, Holy Brook) in Dartmoor, SW England. Values show the mean (±SE) surface soil compaction (Kpa), bulk density (g cm-3), macro-porosity (%) ('M porosity) and organic matter (%) ('SOM') recorded in establishing woodland (blue) and grazed pasture (red) areas.

Results show differences in surface soil compaction in areas of different vegetation (Figure 3.5). In all three catchments surface soil compaction is significantly lower in gorse (*Ulex europaeus*) and bracken (*Pteridium aquilinum*) dominated areas than under grass (*Poaceae spp*) swards. Mean surface soil compaction under grass dominated areas is between twice and three times greater than for gorse and bracken. Whilst soil compaction is lowest under gorse there is no significant difference between compaction under gorse and bracken vegetation. Surface soils under vegetation associated with early stages of woodland establishment (Bracken and Gorse) can be considered to have an 'excellent' to 'good' soil structure compared to the 'moderate' soil structure under grass dominated areas (see Table A3.2).

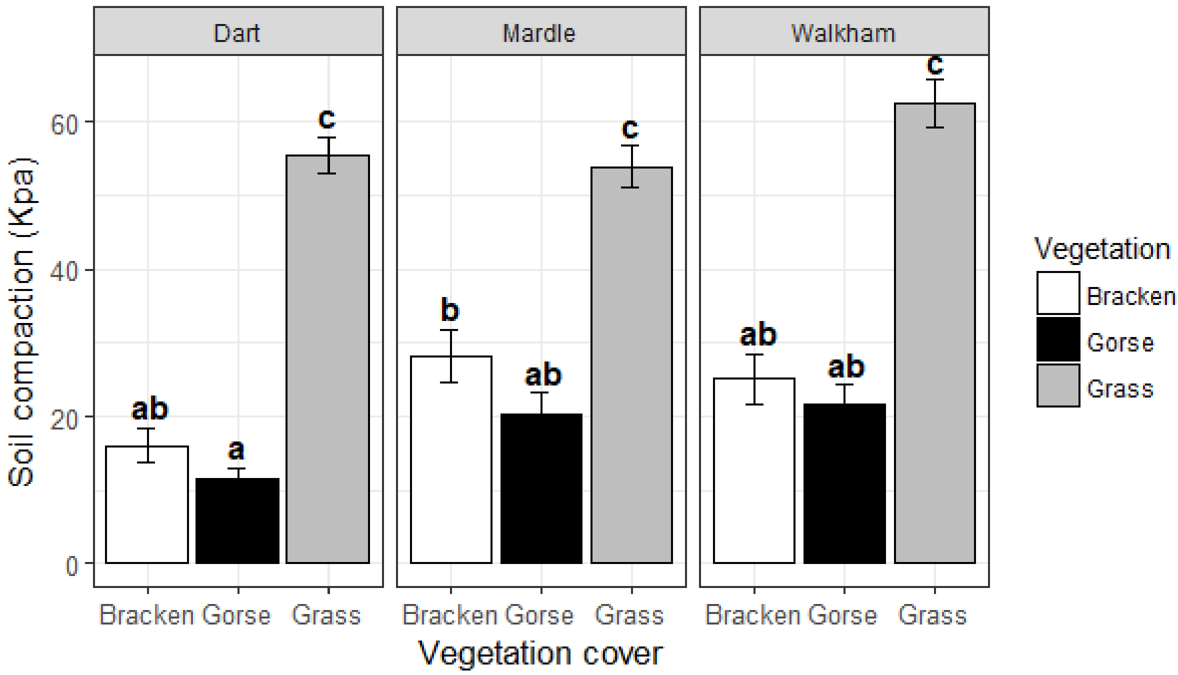

Figure 3.5 – Mean (±SE) soil compaction under different vegetation types in four upland catchments (Dart, Mardle, Walkham) located in Dartmoor, SW England. Details show mean (±SE) values of surface soil compaction (Kpa) recorded under bracken (Pteridium aquilinum), gorse (Ulex europaeus) and grass/graminoid vegetation types along three study catchments (Dart, Mardle, Walkham) in Dartmoor, SW England (n = 50). A two-way ANOVA and TukeyHSD test was performed and significant difference ($P \leq 0.05$) denoted using letters (a, b, c etc.).

3.4. Discussion

The degraded nature of soils in many UK upland pastoral catchments (Sansom 1997; Holden et al. 2007c), alongside elevated precipitation trends in these areas (Murphy et al. 2019) highlights the importance of hydrological integrity and soil recovery in flood risk management. Our results show that native woodland establishment in upland pasture areas offers a viable, and potentially rapid (7 – 15 years) means to reduce surface soil compaction and bulk density with concomitant benefits to Ksat and 'wetness threshold' (i.e. soil water holding capacity).

Difference in wetness thresholds have considerable impact on the steepness of the hydrograph peak, with wet state 'active source areas' quickly converting rainfall into either saturated overland flow or subsurface flow runoff (Meyles et al. 2003). During this 'wet state', the water at a hillslope scale can become highly connected, with topography and slope angle dominating (Table A3.3). This connectivity results in the rapid conversion of water to stream discharge via a network of ephemeral channels and rapid flow pathways, often associated with animal tracks and areas of high compaction (Meyles et al. 2006). Establishing woodland where livestock has been excluded therefore offers effective NFM by reducing the number of wet source areas, the connectivity of hillslope moisture, and the conversion of rainfall to stream discharge.

Although not as high as the 12-fold increase in Ksat reported by Chandler et al. (2018), this studies average 2.2-fold increase in establishing woodland versus grazed pasture areas was broadly similar to Marshall et al. (2009) (2.5-fold) and Archer et al. (2013) (4.5-fold). Nonetheless, catchment-specific differences highlight the importance of local soil conditions and corroborate the view that the positive impact of trees on soil permeability (Ksat) and flood risk is dependent on a range of interacting factors (Chandler & Chappell, 2008).

In real terms, mean steady state infiltration recorded in surface soils at woodland (10,352 mm hr^{-1}) and grazed pasture (5,741 mm hr^{-1}) sites was far in excess of values recorded at ungrazed woodland (1,239 mm hr^{-1}) and grazed pasture sites (32 mm hr^{-1}) by Chandler et al. (2018). The very high water infiltration rates in this study may reflect large preferential flow paths (large cracks) deep in the soil profile due to the exceptionally dry summer immediately preceding the recording period (late summer/early autumn 2018). Seasonal and climate factors are thought to play a large role in defining temporally dynamic changes in soil structure (Wheater et al. 2008), and further understanding of the seasonal impact of soil recovery mechanisms are required.

Whilst absolute infiltration values at the time of recording were far in excess of any potential rainfall totals, heightened infiltration rates and reduced compaction and bulk density properties of soils in livestock excluded woodland suggests these areas represent important areas of soil recovery when catchments are more saturated. In these areas, heightened storage potential or 'wetness threshold' mean that surface soils are able to accept more rainfall, and run off from naturally saturated soils. In decreasing surface soil compaction and increasing water storage, livestock excluded woodland establishment will reduce the saturation of surface soils in winter where naturally freely draining soils have been damaged. Reduced surface soil saturation is associated with enhanced acceptance of water to lower soil horizons and attenuation during heavy rainfall events and may aid in natural flood management.

The ability of soils to accept rainwater is highly dependent on soil type, with less permeable ('stagnant') soils reaching 'wet state' quickly, and freely draining soils such as brown earth podzols, rarely reaching saturation if in good condition (Brady and Weil, 2008). Indeed, the catchment specificity of results, specifically the negligible recovery of Ksat for the site with highest past grazing intensity (Holy Brook), suggests soils can reach a 'point of no return' if the elastic limit is exceeded. The resistance (vulnerability) and resilience (recovery) of soils to compaction are affected by both management impacts and natural soil properties (Brady and Weil 2008; Gregory et al. 2009), involving a complex interaction between clay content (%), soil organic matter (SOM), water content, soil texture, biological activity and past and previous management (Gregory et al. 2009; Bonetti et al. 2017).

The most noticeable beneficial effect of woodland establishment on Ksat occurred where SOM was highest (i.e. Colly Brook and Dean Burn), supporting the view that higher SOM is linked to increased soil resilience (Bonetti et al. 2017). This study therefore suggests, at least in the short term (<15 years), woodland NFM schemes will be most effective in areas where soils are more resilient. Heavily degraded soils with low resilience likely require remediation if the benefits of woodland establishment are to be maximised. The Holy Brook catchment site, where historic stock density was highest (Table A3.1), showed no recovery in steady-state water infiltration (Ksat) following woodland establishment, with negligible treatment impacts on bulk density, compaction and macro-porosity, despite the greater age and density of planting. This finding highlights the important role of historic stock density, soil type and management in determining potential woodland NFM outcomes and soil remediation requirements. Moreover, it should not be assumed that woodland creation will always improve soil health, hydrology, and peak flows (Soulsby, Dick, Scheliga, & Tetzlaff, 2017). Indeed, whilst long-term evidence from upland catchments typically links higher tree cover to reductions in river discharge (Robinson et al., 2003; Birkenshaw, Bathhurst, & Robinson, 2014; Evaristo & McDonnell, 2019), records for effective attenuation of peak flows for the most severe river flooding by woodland at catchment scale is limited (Burgess-Gamble et al., 2017; Dadson et al., 2017; Soulsby et al., 2017). Consequently, it is important that realistic NFM expectations are communicated to the public and policy makers.

Our study demonstrates the potential of native woodland restoration in upland pasture systems to improve the hydrological functioning of soils needed to mitigate the increasing flood risk expected with ACC. Establishment of native woodland where naturally freely draining soils have suffered long-term soil compaction through (over) grazing offers the highest potential increases in infiltration rates. These compacted soils are typical of mid-slope valley pastures in UK catchment headwaters. Results however do not differentiate the impact of absence of livestock from the addition of trees, with areas of bracken and gorse associated with significantly reduced compaction compared to grass dominated areas despite the absence of trees. Indeed, the specificity of soil recovery mechanisms require further investigation if ecosystem service provision associated with native woodland establishment on extensive unenclosed pastoral systems is to be accurately assessed, and land management priorities identified. Results from other catchments indicate the effect of trees may be additional to the impact of reduced grazing pressure on soil recovery (Marshall et al. 2014; Chandler et al. 2018). Some of the potential relationships determining the impact of woodland establishment on soil recovery and natural flood management are explored in Figure 3.6

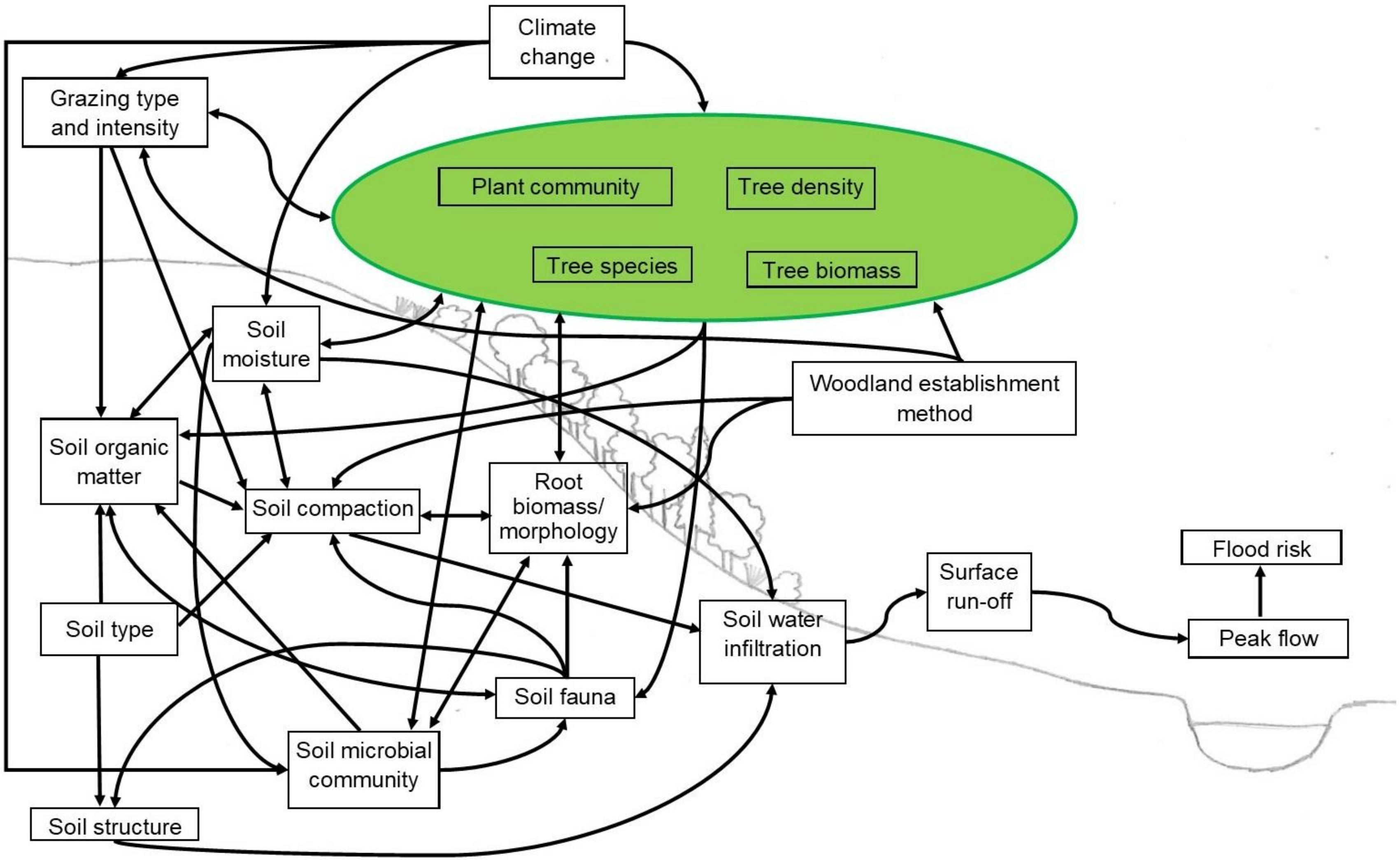

Figure 3. 6 – Relationships between mechanisms impacting on the effectiveness of woodland establishment for soil recovery and natural flood management. Arrows indicate the direction of the hypothetical causal relationship. Double-headed arrows indicate potential two-way association.

Despite the likelihood that upland land-use policy will increasingly promote the establishment of woodland within pasture systems to mitigate lower-catchment flooding, it is vital that land managers and policy makers consider the context in which NFM outcomes are expected. Consultation and co-operation with farmers and land managers with local soil knowledge will be essential if environmental benefits are to be maximised. In addition, despite the potentially important benefits of woodland establishment to carbon sequestration (Perks et al. 2010; Uri et al. 2017), changes in land management will likely throw up trade-offs between ecosystem service benefits (Iacob et al. 2014; Evans et al. 2015; Mitchell et al. 2017; Garcia & Fraser 2019). In this broader context, NFM research must not only consider the seasonality and individuality of soils, but also the impact on other ecosystem services to ensure 'public money for public goods' are commensurate with outcomes.

Chapter 4.

Too much of a good thing? – Impact of soil saturation on the survival, performance and development from acorn of UK native oak trees

Abstract:

As a key variable in determining plant viability and productivity, soil moisture (SM) is of fundamental importance in understanding the response of biological systems to global anthropogenic climate change (ACC). There is growing interest in woodland (re-)establishment for climate mitigation (linked to carbon sequestration), natural flood management (NFM) and other ecosystem services. However, understanding the response of trees to climate impacts, such as changes in soil moisture, will be essential for both realising the multiple benefits of woodland restoration and understanding the barriers for implementation. Indeed, there is a pressing need to determine the impact of threshold effects on species' distribution, abundance and productivity. This study uses pot and field experiments to assess the survival and performance of juvenile (< 3 years old) native oak (*Quercus robur*, *Quercus petraea*) to changes in soil moisture in the organic soils typical of upland areas. Pot experiments show *Quercus robur* seedling development was reduced (45%) in soils with high water tables (WTs) (70mm below soil surface) and growth was absent in flooded soils typical of 'active' mire (water table 30mm above soil surface). Surviving seedlings experienced diminished photosynthetic vitality (PI_{abs}), root:shoot ratios and late summer 'lammas' growth in 'high' (- 70mm, 75% SM) and 'medium' (-150mm, 48% SM) water table treatments. Field trials showed that planted juvenile *Quercus robur* were found to be more tolerant of saturated, poorly drained soils than *Quercus petraea*, but growth was highly variable by year, likely due to climatic variability and stress accumulation. The reduction in root:shoot ratios associated with livestock grazing was greater in freely draining soils. Poorly-drained soils with high soil moisture pose a potential constraint on the establishment of oak saplings in upland pastures; however, impacts can only be assessed in combination with other stressors. The high

variation in UK native *Quercus* to soil moisture suggests if upland oak woodland fragments can be connected there is likely to be sufficient diversity for ACC adaption and population expansion.

4.1. Introduction

The (re-)establishment of woodland is important for the mitigation of risks associated with anthropogenic climate changes (ACC), whilst delivering multiple ecosystem services (Griscom et al. 2017; Bastin et al. 2019; Evaristo & McDonnell 2019). However, increased attention on woodland (re)establishment as a mitigation method demands greater attention on the impacts of climate change on the ability of native woodland restoration efforts to provide these services (Sgrò et al. 2011; Thomas et al. 2014). Indeed, the feasibility of woodland (re)establishment and ecosystem service provision offered depends fundamentally on its response to ACC.

Changes in the amount and character of precipitation with ACC are likely to alter soil moisture characteristics, a key variable in determining the response of plant productivity to increases in temperature and atmospheric carbon (Collins et al. 2018; Stocker et al. 2018; Lunt et al. 2019). The global role of soil moisture in determining the terrestrial carbon uptake is increasingly recognised (Seneviratne et al. 2010; Green et al. 2019) with differences in soil moisture changing the distribution of semi-natural communities and the success of plant generation from seed (Walck et al. 2011; Le Roux et al. 2013). Deviation from optimum environmental conditions can result in impairment of plant growth, reduced fecundity, and sometimes increased mortality. Impacts are determined by tolerance to both excess and deficiency of resources and the interaction with other stressors (Niinemets 2010).

Whilst water is a key requirement for plant growth (Aranda et al. 2012), excess soil moisture can starve soils of oxygen (hypoxia), potentially damaging plant performance via reductions in respiration and photosynthesis (Parent et al. 2008). Soil compaction reduces macro-pores, increasing sensitivity to oxygen deficiency in comparison to loose, well-aggregated soils (Brady & Weil, 2008). Chronic lack of oxygen (anoxia) can facilitate the accumulation of carbon dioxide and toxic metabolites, limiting the growth of existing roots and causing decay (Parent et al. 2008; Kozlowski 1997). Oxygen starvation also impacts on redox potential and the availability of certain nutrients for plant uptake, potentially causing nutrient deficiency and/or toxicity (Brady & Weil, 2008). Waterlogged (anaerobic) soils can impair macro nutrient uptake by root systems, the transportation of products of photosynthesis, and can make plants more susceptible to pathogens (Gravatt & Kirby 1997).

Deficiency of soil moisture generally reduces stomatal conductance, CO_2 uptake and the growth of trees (Lévesque et al. 2013). Severe deficiency or drought are typically associated with reduced photosynthesis, and hydraulic and metabolic failure in plants (Saiki et al. 2017). Drought can also inhibit root assimilation of nutrients and reduce the microbial mineralisation of soil nutrients (Kreuzwieser & Gessler 2010). Soil moisture levels have the capacity to influence plant nutrition indirectly via impacts on the soil microbial community and the behaviour of mycorrhizal fungi (Cavagnaro 2018, Brockett et al. 2012). Consequently, an understanding of the response of trees to soil moisture is essential for realising the multiple benefits of woodland restoration and natural flood management.

The response of oak (*Quercus* spp) regeneration to soil moisture is particularly relevant given this species is showing signs of decline throughout its range, linked to changes in climate (Denman et al. 2014), including increases in rainfall and soil saturation along Atlantic coasts (Rozas & García-González 2012a; Rozas & Sampedro 2013). The future colonisation of native oak (*Quercus robur*, *Quercus petraea*) in the UK uplands (Bunce et al 2018a) is of heightened significance given evidenced increases in precipitation (Burt

& Holden 2010; Murphy et al. 2019), and their key role within ecosystem functioning (Mitchell et al. 2019). Upland oak woodlands are recognised as internationally important for nature conservation and are highlighted under the European habitats directive due to their fragmented distribution and support of specialist lower plant (ferns and bryophytes), lichen and animal assemblages (Baarda 2005; JNCC 2014; Lamacraft et al. 2018). Upland oak woodlands are characterised by woodland NVC W11 and W17, which are termed 'Atlantic' rainforests when they occur along upland oceanic coasts (Rodwell 1991; Baarda 2005). These woodlands have the richest bryophyte cover in Europe, possibly the world, due to their high humidity and number of available niches (Rothero 2005).

While the benefits of oak woodland establishment in upland pastures for soil water recovery and reduced flood risk is increasingly recognised (Marshall et al. 2014; Murphy et al. *submitted*), knowledge on establishment in compacted (often waterlogged), organic soils which typify UK upland pastures would be particularly prescient. Previous studies have investigated the response of native UK oaks to waterlogging, finding *Quercus robur* is more tolerant to moisture excess than *Quercus petraea* (Dreyer 1991; Dapardeu et al. 2015). The tolerance of *Quercus robur* is mainly conferred by its capacity to produce adaptive features, such as adventitious roots and hypertrophied lenticels, but also via the maintenance of fermentative pathways (Le Provost et al. 2012, Le Provost et al. 2016).

However, whilst the short-term (< 6 weeks) binary (waterlogging vs non-waterlogged) impact of soil saturation on native UK oak is well studied, there is little understanding of the temporal and quantitative thresholds determining establishment, an area identified as crucial in climate change studies (Suggit et al. 2015). In addition, whilst the regeneration stage of plant development is typically the most vulnerable and important life history phase, the impact of climate change on this stage is still poorly understood (Fenner & Thompson 2005; Parmesan & Hanley 2015).

This study sets the following hypotheses: 1) oak seedling development and performance from acorns will progressively diminish with higher surface soil moisture in waterlogged organic soils; and 2) the performance of planted juvenile (2-year-old) native oak will be reduced in poorly drained soils typified by mire (M6) communities in comparison to freely-drained acid grassland pasture.

4.2. Methods

4.2.1. Impacts of water table on Quercus robur seedling development from acorn – (pot experiment)

A randomised block pot-based experiment was set up at Plymouth University research facility Scardon Garden (Lat: 50.377030 Long: -4.1376585) (Figure 4.1). Pots (rectangular - 22 litres) were filled with un-amended peat (*Bord na mona*) to 5cm below the pot rim. The surface of each pot was seeded with vegetative propagules of a *Carex echinata-Sphagnum* mire vegetation (NVC - M6) dominated by *Sphagnum papilosum.* Local provenance *Quercus robur* acorns (collected at New Bridge, Dartmoor – Lat: 50.524544 Long: -3.8198192) were checked for viability using floatation testing. Viable acorns were left in a seed tray of damp leaves until germinated. One hundred and thirty germinated acorns were inserted 2cm deep into the soil (5 acorns per pot) in November 2016 at the top of the soil profile (Below mire vegetation) and covered. Pots were subjected to four water table (WT) treatments. Water table depths are expressed relative to the acorn planting level, consisting of no drainage holes ‘flooded’ (35mm above acorn), ‘high’ (70mm below acorn), ‘medium’ (153mm below acorn) and ‘low’ (223mm below acorn) water table treatments. There were six replicate pots for each treatment (30 acorns per treatment).

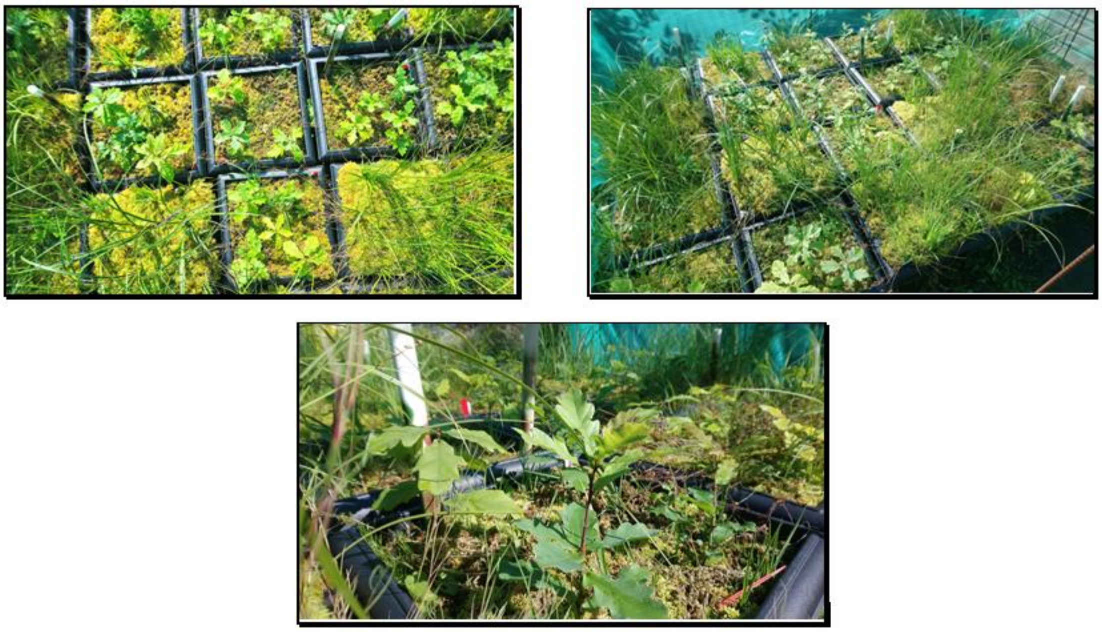

Figure 4. 1 – Pot experiment testing the impact of water table depth and soil moisture on the first year development of planted acorns of native oak (*Quercus robur*) collected on Dartmoor (New Bridge - Lat: 50.524544 Long: -3.8198192), southwest England. The pot experiment was conducted at Scardon Garden, Plymouth University between November 2016 and October 2017.

The number of germinating seedlings and shoot emergence date of seedlings in pots was recorded and shoot height was measured fortnightly. Floral surveys of companion plants were conducted at the start (November 2016) and end of the experiment (October 2017)(Table A4.1). The growth from randomly selected *Sphagnum papillosum* was recorded between January and November 2017.

4.2.2. Impact of soil moisture on establishment of planted native oak saplings in upland pastures - (field experiment)

One hundred and forty four juvenile (two-years-old) native oak saplings were 'slot planted' in an upland pasture area of Dartmoor (Dendles Waste – Lat: 50.452875 Long:-3.9511210), southwest England. All trees (*Quercus robur* (72 trees), *Quercus petraea* (72 trees)) were of local provenance (*Quercus robur* from New Bridge (Lat: 50.524544 Long: -3.8198192), *Quercus petraea* from Hembury (Lat: 50.503279 Long: -3.7992586), Dartmoor). Three areas of distinct soil structure were identified (Figure 4.2): 1) Freely-draining (FD) podzolic soils with U4 (*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland) vegetation community; 2) Seasonally-waterlogged (SW) soils of U4 grassland but dominated by *Agrostis capillaris* and *Anthoxanthum odoratum*; 3) Waterlogged (W) (permanently) soils characterised by M6 (*Carex echinata-Sphagnum fallax*) vegetation (Figure 4.3, Table A4.2). These communities are typical of many upland pastoral sites and distributed over large areas of the UKs uplands (Averis et al. 2004). A random stratified technique was used to select six sites within each of the three areas where oak saplings were planted (18 sites in total). Half of all saplings were protected with fenced exclosures ('Gengards', New Woods Forestry, Norwich, UK) in groups of eight, with nine of these groups protected and nine left open to livestock grazing (see Table A5.3) (n = 9).

Figure 4. 2 – Soil profile of A) freely draining (FD), B) seasonally waterlogged (SW) and C) waterlogged (W) (permanently) soils located in the upland pastures (Dendles Waste) of Dartmoor, southwest England.

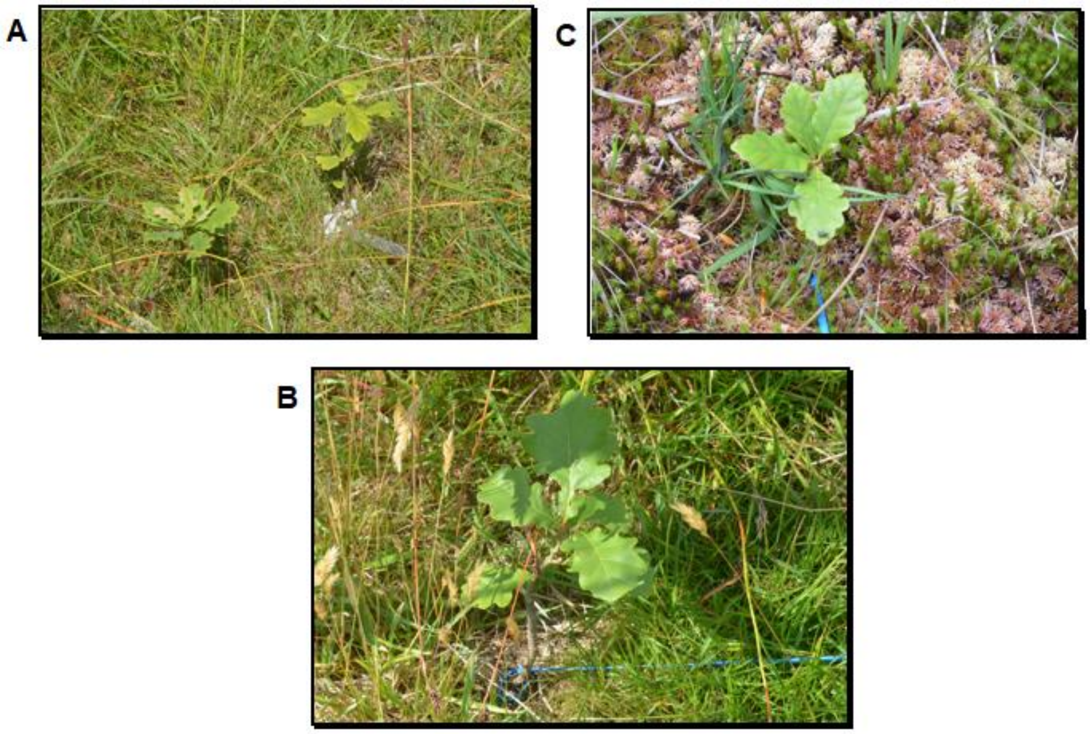

Figure 4. 3 – Juvenile (two-years-old) native oak (*Quercus robur*, *Quercus petraea*) saplings planted (spring 2018) in: A) freely draining (FD)(podzolic) soils characterised by U4 grassland. B) Seasonally waterlogged (SW) soils also of U4 grassland but dominated by *Agrostis capillaris* and *Anthoxanthum odoratum.* C) Waterlogged (W) (permanently) soils characterised by mire communities (NVC - M6) in the upland pastures (Dendles waste) of Dartmoor, southwest England.

The emergence date, current year's shoot growth of pasture planted oaks were recorded throughout the experiment (April 2018 – October 2019), and the companion plants that were surrounding saplings (15 cm^2) recorded in August 2018.

4.2.3. Stem diameter vs soil moisture of natural colonising juvenile (two-years-old) oaks

In addition, soil moisture immediately surrounding naturally colonising native oak saplings and their stem diameter were measured in upland pastures of Dartmoor (Dartmeet (lat: 50.5481, long: -3.8750) n = 21, Merrivale (lat: 50.5492, long: -4.0458) n = 16).

4.2.4. Evaluation of plant stress using chlorophyll fluorescence – (both pot and field based experiments)

Chlorophyll fluorescence (CF) analysis (Photosynthesis Efficiency Analyser [PEA]) (Hansatech Instruments Ltd 2019) was used to measure the response of trees to changes in soil moisture. CF is a rapid, non-destructive, and objective form of photosynthesis measurement (Silva et al. 2007), used to measure the response of plants to environmental change (Murchie & Lawson 2013). CF is re-emitted light or 'fluorescence' from chloropyll-a molecules within leaves which reveals information on the efficiency of photochemistry and heat dissipation used to provide energy and reducing power for CO_2 assimilation (Murchie & Lawson 2013). All readings were taken from the upper surface of three replicate leaves from each sampled tree between 7.00 – 9.00am *(GMT/UTC +0)* in the morning after dark adaption (30 minutes), in accordance with good practice guidance (Murchie & Lawson 2013).

The most commonly used indicator is the Fv/Fm ratio, which is inversely proportional to the damage of photosystem II (PSII) reaction centre in chlorophyll modules within leaves (Farquhar et al. 1989). The more stressful the environment, the greater the reduction in the maximum quantum efficiency of PSII (lower photosynthetic potential) and the lower the Fv/Fm number (Favaretto et al. 2010). This provides a direct measure of the 'optimal quantum efficiency' of the plant (Ritchie 2006) and is commonly used for quantifying stress in leaves (Murchie & Lawson 2013).

Performance Index (PI_{abs}) is an integrative parameter used as a measure of plant 'vitality' (Mehta et al. 2010). PI_{abs} reflects the functionality of both photosystems I and II, providing quantitative information on the current state of plant performance under stress conditions (Strasser et al. 2004). PI_{abs} is shown to be more sensitive to changes in plant performance resulting from altered water availability than Fv/Fm (Živčák et al. 2008; Silvestre et al. 2014).

4.2.5. Measurement of soil moisture and water table – (both pot and field based experiments)

In both pot and field experiments, CF readings were taken alongside soil moisture readings. The moisture content (%) in soil surface (top 6cm) immediately surrounding each tree was measured using a theta probe (AT Delta-T Devices, HH2 moisture meter). For pots, the WT depth was measured (dip well and water probe) at fortnightly intervals to check levels were constant. All pots were watered with harvested rainwater throughout the experiment to maintain water tables.

4.2.6. Measurement of growth using dry weight – (both pot and field based experiments)

All trees in pots and half of the surviving trees (equal number of *Quecus robur* and *Quercus petraea*) in the field experiment were removed in autumn 2017 and 2018, respectively. After removal, soil was washed from the roots and trees were oven dried at 80°C for five days. Plants were separated into individual plant parts and the dry weight mass (g) of shoots, leaves, main root, and fine roots determined.

4.2.7. Statistical analysis

Analyses were performed using R studio (R Core Team 2017). All variables were tested for normality using Shapiro-Wilks tests. Differences in mean dry weight of surviving oak seedlings were normally-distributed and so tested using analysis of variance (ANOVA). Tukey HSD test was used for post hoc analysis. In the case that variables showed departure from normality, differences between treatment were assessed using Kruskal Wallis tests applied in 'R' using the conover.test package (Dinno 2017). Non-parametric correlation analyses were applied to non-normal soil moisture, CF and shoot growth data using Kendall rank correlation coefficient and 'kendall' package (McLeod 2011).
Multivariate statistics were used to compare the relationships between soil moisture, plant community, *Sphagnum papillosum* growth and oak seedling survival in pots.
Multivariate analysis was conducted in a two stage process: 1) A constrained redundcy

analysis was used (after confirming data linearity [< 2 gradient axis] with a detrended correspondence analysis [DCA]) to determine the relationship between soil moisture and water table depth (explanatory variables) with likely response variables plant community and *S.papillosum* growth. 2) An unconstrained principle component analysis (PCA) was then used to determine the relationship between plant community and *S.papillosum* growth with oak survivorship. Multivariate statistics were carried out using the 'vegan' package (Oksanen et al. 2019). All graphs were produced using 'GGplot2' (Wickham 2009) and 'cowplot' (Wilke 2017) packages.

4.3. Results

4.3.1. Impact of water table depth on seedling survivorship and development from acorn

4.3.1.1. Oak seedling emergence and survival

There was significant difference in mean WT depth and soil moisture throughout the experiment across treatments (Figure 4.4). No native oak recruits emerged in the 'flooded' treatment, significantly more (45%) emerged in the 'high' WT treatment with higher survivorship occurring at medium (77%) and low (83%) WT treatments. In contrast, *Sphagnum papillosum* growth was significantly highest in the flooded treatment and lowest in the low WT treatment.

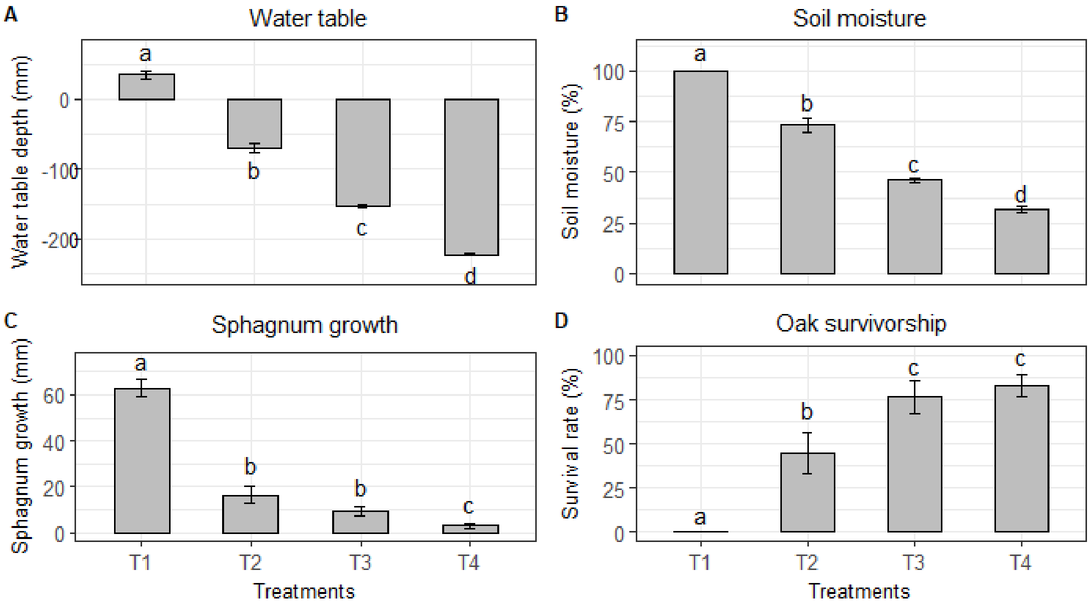

Figure 4. 4 – Mean (±SE) A) water table (WT) depth (cm above or below the soil surface) B) surface soil moisture (% in top 10 cm) C) Sphagnum growth (mm) and D) Survivorship or 'recruitment success' rate of oaks planted as acorns in four pot based soil hydrology treatments. T1 = 'Flooded' (+35mm WT), T2 = 'High' (-69mm WT), T3 = 'Medium' (-153mm WT), T4 ='Low' (-223mm WT) water tables. Soil moisture represents mean average surface (top 10cm) volumetric soil water content (%) between May - August 2017. Sphagnum growth represents growth (mm) between January and November 2017. 'Oak recruitment success' refers to the number of surviving oak seedlings as a percentage of the acorns planted. Significant difference between individual treatments ($P < 0.05$) via Kruskal-Wallis and Conover-Iman test, denoted using different uncapped letters (a,b,c etc).

A constrained redundancy analysis (RDA) showed soil moisture and water table depth explained only 24% of variance in the plant community present and the growth of *Sphagnum papillosum*, however a permutation test showed water table and soil moisture were significant explanatory variables of variance ($F = 3.340$, $p = 0.001$, $df = 2$). An ordination plot shows there is positive association between explanatory variables soil water and water table with *Sphagnum papillosum* growth and the cover of *Eriophorum angustifolium* along the first axis (Figure 4. 5). There is negative association between soil water and water table with the cover of *Viola palustris*, and a weak negative association with *Molinia caerulea.*

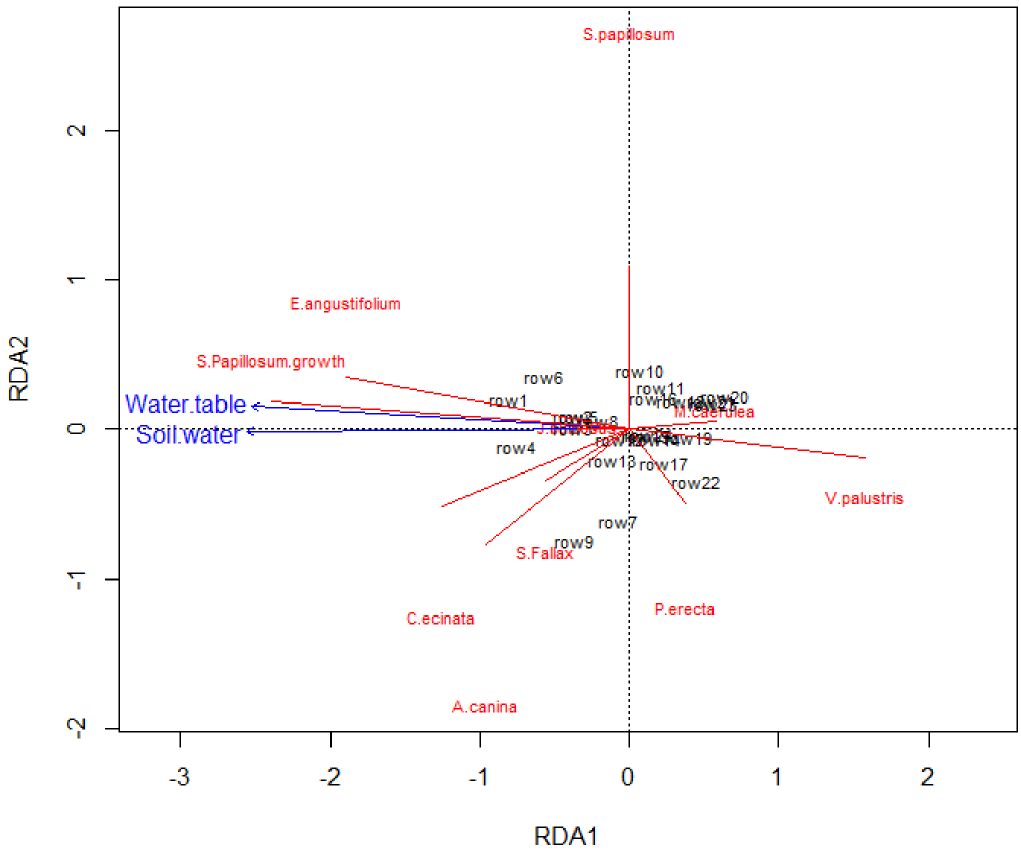

Figure 4. 5 – Triplot of constrained redundency analysis (RDA) between response variables Sphagnum papillosum growth and plant cover scores (red arrows) with explanatory variables soil water (%) and water table depth (mm)(blue arrows) in experiment pots located at Plymouth University research facility (Scardon Garden). RDA 1 explains 21% of the variance and RDA 2 just 3%.

A subsequent unconstrained principal component analysis (PCA) and regression model of plant community and sphagnum growth found a significant relationship ($F = 16.07$, $p < 0.001$, adjusted $R^2 = 0.663$) to oak survivorship (%) along principle components one (T value = 5.49 , $p < 0.001$), three (T value = 2.85, $p = 0.010$), and seven (T value = -3.15, $p = 0.005$) explaining 47% of total variance. PCA regression model coefficients showed *Sphagnum papilossum* growth (-21.9), *Eriophorum angustifolium* (-13.3), and *Molinia caerulea* cover (-10.2) had the strongest negative relationship to oak survival, and *Viola palustris* cover (7.4) the strongest positive relationship.

4.3.1.2. Performance of surviving Quercus robur seedlings in pots

Oak seedling total shoot growth (mm) was greater in low than high WT treatments, but there was no significant difference with the medium treatment (Figure 4.6). There was significantly lower late summer (July – August) or 'lammas' shoot growth in high as opposed to medium and low WT treatments. However, the proportion of seedlings with 'lammas' shoot growth for both high (17%) and medium (38%) treatments was less than in the low (81%) WT treatment. Root collar diameter was significantly smaller in the high WT treatment than low and medium WTs.

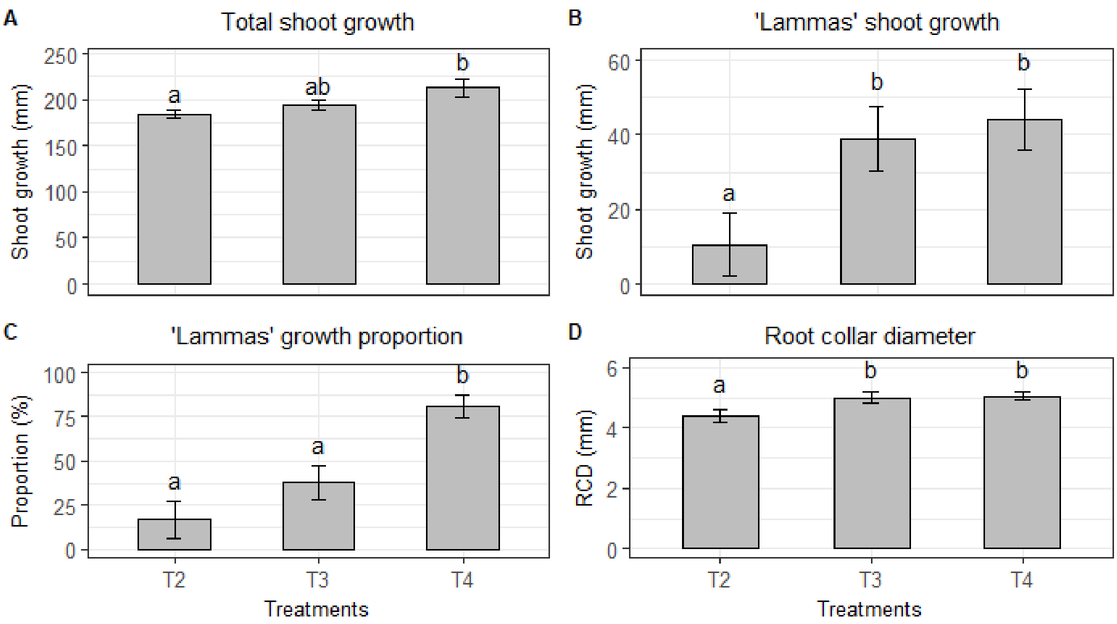

Figure 4. 6 – Mean (±SE) A) total shoot growth (mm) B) late summer 'lammas' shoot growth (mm) C) Lammas growth proportion (%) D) root collar diameter (RCD) (mm) of surviving *Quercus robur* seedlings across treatments (T2,T3,T4). Proportion with late summer (July – Auhust) 'lammas' growth refers to the % of the total surviving seedlings with 'lammas' growth. T1 = 'Flooded' (+35mm) , T2 = 'High' (-69mm), T3 = 'Medium' (-153mm), T4 ='Low' (-223mm) water tables. Significant difference between individual treatments ($P < 0.05$) via Kruskal-Wallis and Conover-Iman test, denoted using different uncapped letters (a,b,c etc).

4.3.1.3. Chlorophyll fluorescence of Quercus robur seedlings in pots

Average photosynthesis vitality (PI_{abs}) was found to be significantly greater in the low water table (-223mm) treatment than both medium (-153mm) and high (-69mm) WTs (Table 4.1). Interestingly, despite the lower soil moisture (-26%) and WT (-84mm), oaks in the medium treatment experienced no significant difference in mean average leaf photosynthetic vitality (PI_{abs}) compared to seedlings in the high WT treatment. No difference in seedling leaf Fv/Fm was found between any treatment.

Table 4.1 – Mean (±SE) photosynthetic efficiency of leaves from surviving *Quercus robur* seedlings measured using CF parameters (PIabs, Fv/Fm) across water table treatments (T2, T3, T4) over a 12 week period between 30 May – 15 August. Significant difference between individual treatments (P < 0.05) via Kruskal-Wallis and Conover-Iman test, denoted using different uncapped letters (a,b,c etc).

	Photosynthetic efficiency of oak					
	T2 'High' WT		**T3 'Medium' WT**		**T4 'Low' WT**	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**
Performance Index (PI_{abs})	1.472 a	0.220	1.556 a	0.149	2.320 b	0.245
Fv/Fm	0.780 a	0.011	0.780 a	0.009	0.791 a	0.006

Comparison of weekly leaf CF readings with soil moisture and air temperature between May – August indicates photosynthetic vitality (PI_{abs}) had a significant negative correlation with soil moisture and a positive relationship with maximum and higher minimum temperature (Figure 4.7). Fv/Fm ratio of oak leaves had a strong positive relationship to maximum, higher minimum temperature, but no correlation with soil moisture (Table 4.2).

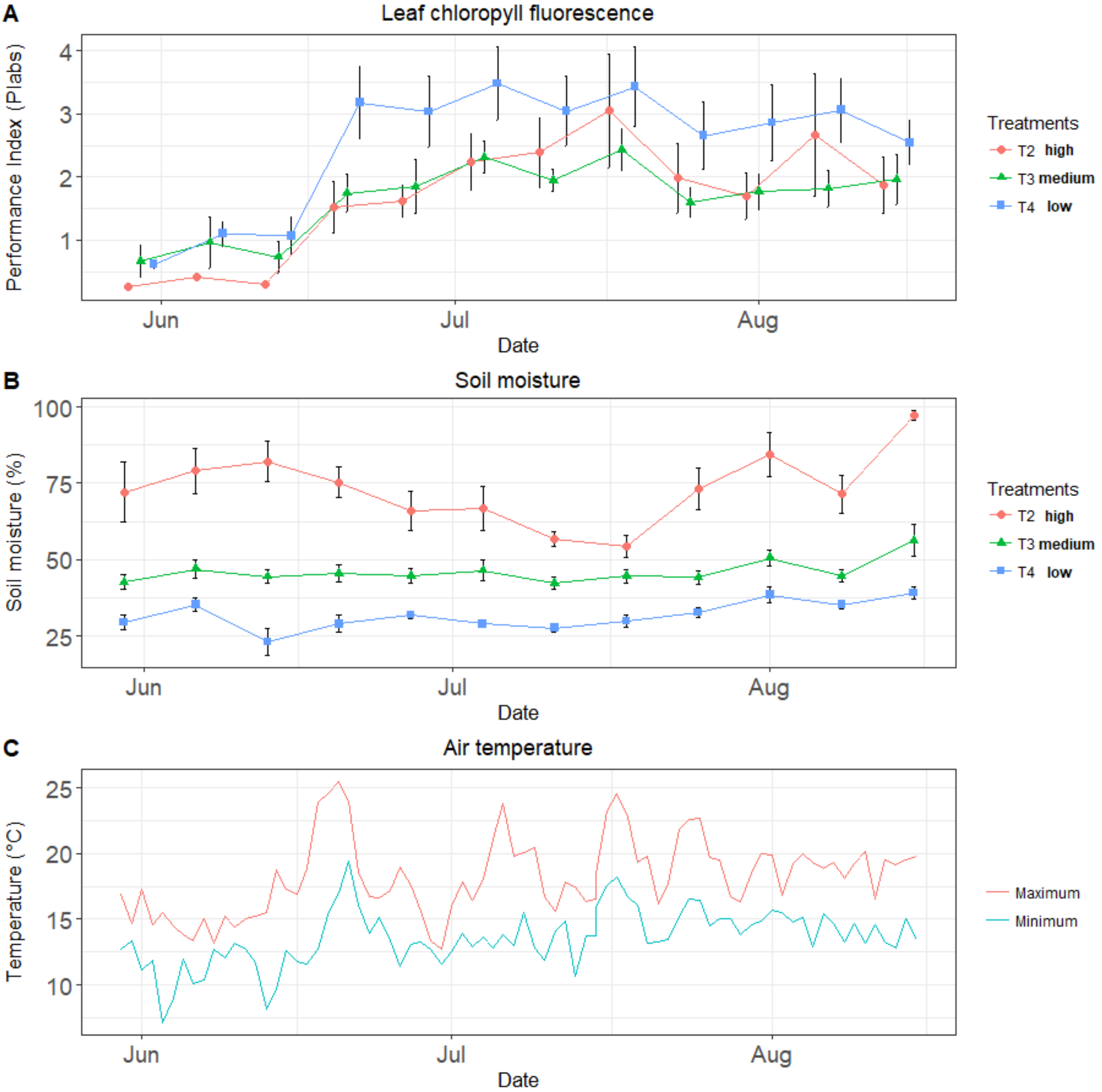

Figure 4. 7 – A) Photosynthetic vitality PI_{abs} from the leaves of *Quercus robur* seedlings growing in high (T2 - 69mm), medium (T3 -153mm) and low (T4 – 223mm) WT treatments in pots at Plymouth research facility (Scardon Garden). PI_{abs} and soil moisture were recorded alongside each other recorded over a twelve-week period between 30 May – 15 August 2017. The 24-hour mean maximum and minimum air temperatures (°C) recorded in Plymouth Mountbatten between 9am the day before and 9am *(GMT/UTC +0)* the morning of CF readings (Met Office 2012).

Table 4.2 – Correlation between leaf chlorophyll fluorescence (CF) readings (Performance index [PI_{abs})], Fv/Fm) of native oak (*Quercus robur*) seedlings growing in high (T2 - 69mm), medium (T3 -153mm), and low (T4 – 223mm) WT treatment pots, with surrounding surface soil moisture (%), and maximum and minimum temperatures (^{o}C). PI_{abs} and soil moisture were recorded alongside each other recorded over a twelve-week period between 30 May – 15 August 2017. The 24-hour mean maximum and minimum air temperatures (°C) recorded in Plymouth Mountbatten between 9am the day before and 9am *(GMT/UTC +0)* the morning of CF readings (Met Office 2012). The strength (TAU value) and significance (*P* value) of correlations was assessed via Kendall rank order correlation.

	Photosynthetic efficiency of oak			
	PI_{abs}		**Fv/Fm**	
	TAU	***P***	**TAU**	***P***
Soil moisture (%)	-0.190	≤ 0.001	-0.074	0.062
Maximum air temperature (°C)	0.222	≤ 0.001	0.305	≤ 0.001
Minimum air temperature (°C)	0.267	≤ 0.001	0.391	≤ 0.001

4.3.1.4. Dry weight of surviving Quercus robur seedlings in pots

Shoot, leaf, root, and total tree dry weight (g) of oak recruits was significantly lower in the high WT treatment than both medium and low WT treatments, where there was no difference (Figure 4.8). The mass of the main root (tap root) was significantly higher in the low WT treatment than the medium WT, which was significantly lower than the high WT treatment. The mass of oak fine roots was greatest in the medium WT treatment, significantly greater than fine roots in the high WT treatment. The root:shoot ratio of oak seedlings was significantly lower in 'high' (-69mm) than both 'medium' (-153mm) and 'low' (-223mm) water table treatments; however, the low WT treatment had the highest fine root:main root ratio (Table 4.3).

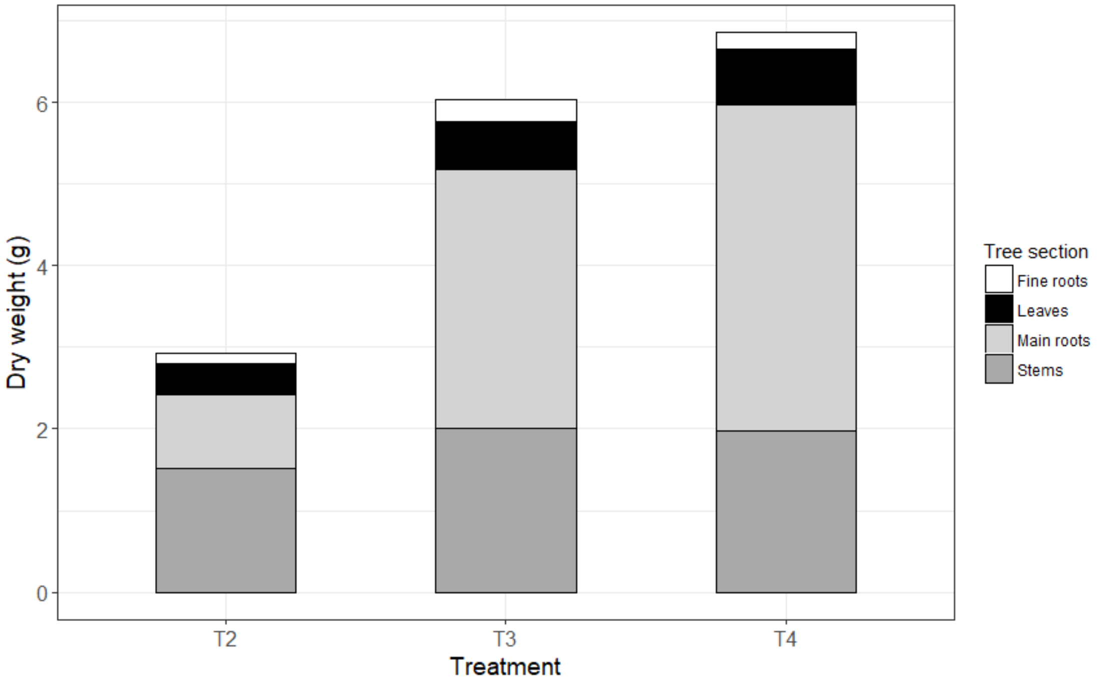

Figure 4. 8 - Mean (±SE) dry weight (g) of year old surviving *Quercus robur* seedlings across water table treatments (T2,T3,T4). T2 = 'High' (-69mm), T3 = 'Medium' (-153mm), T4 = 'Low' (-223mm) water tables. One-way Analysis of Variance (ANOVA) and Tukey HSD used to determine significant difference (P ≤ 0.05) between treatments.

Table 4.3 – Mean dry mass (g) (± SE) of different parts of surviving *Quercus robur* recruits per pot (N=6) across treatments. T2 = 'High' (-69mm), T3 = 'Medium' (-153mm), T4 = 'Low' (-223mm) water tables. Significant difference between individual treatments (P ≤ 0.05) via One-way Analysis of Variance (ANOVA) and Tukey HSD, denoted using different uncapped letters (a,b,c, etc.).

	Dry mass of oak					
	T2 'High' WT		T3 'Medium' WT		T4 'Low' WT	
	Mean	SE	Mean	SE	Mean	SE
Total mass	2.924 a	0.343	5.938 b	0.441	6.850 b	0.342
Shoot mass	1.518 a	0.119	2.012 b	0.125	1.983 b	0.114
Leaf mass	0.380 a	0.058	0.580 b	0.028	0.676 b	0.042
Root mass	1.026 a	0.231	3.347 b	0.324	4.191 b	0.340
Root: shoot ratio	0.516 a	0.090	1.288 b	0.091	1.600 b	0.153
Main root mass	0.899 a	0.227	3.165 b	0.253	3.986 c	0.318
Fine root mass	0.127 a	0.017	0.276 b	0.036	0.205 ab	0.038
Fine root: main root ratio	0.182 a	0.045	0.084 b	0.008	0.053 c	0.007

4.3.2. Impact of soil moisture on juvenile native oak saplings planted in upland pastures

4.3.2.1. Survival and performance of planted native oak saplings

There was no difference in the survival rate of native oaks between areas of freely draining (91.7%), seasonally waterlogged (87.5%) and permanently waterlogged soils (100%). There was no significant difference in mean shoot growth between native oak species in 2018, 2019 and for combined years. However, whilst in the first growing season after planting (2018), for both native oak species (*Quercus robur*, *Quercus petraea*) there was a positive but non-significant relationship between shoot growth and surface soil moisture; in the following year (2019), there was a significant negative relationship (TAU = -0.362 , *P* = 0.05) between soil water and *Quercus petraea* shoot growth (Figure 4.9). When the shoot growth for both years was combined, there was a significant positive relationship between *Quercus robur* shoot growth and soil moisture, but no significant relationship for *Quercus petraea* (Table 4.4).

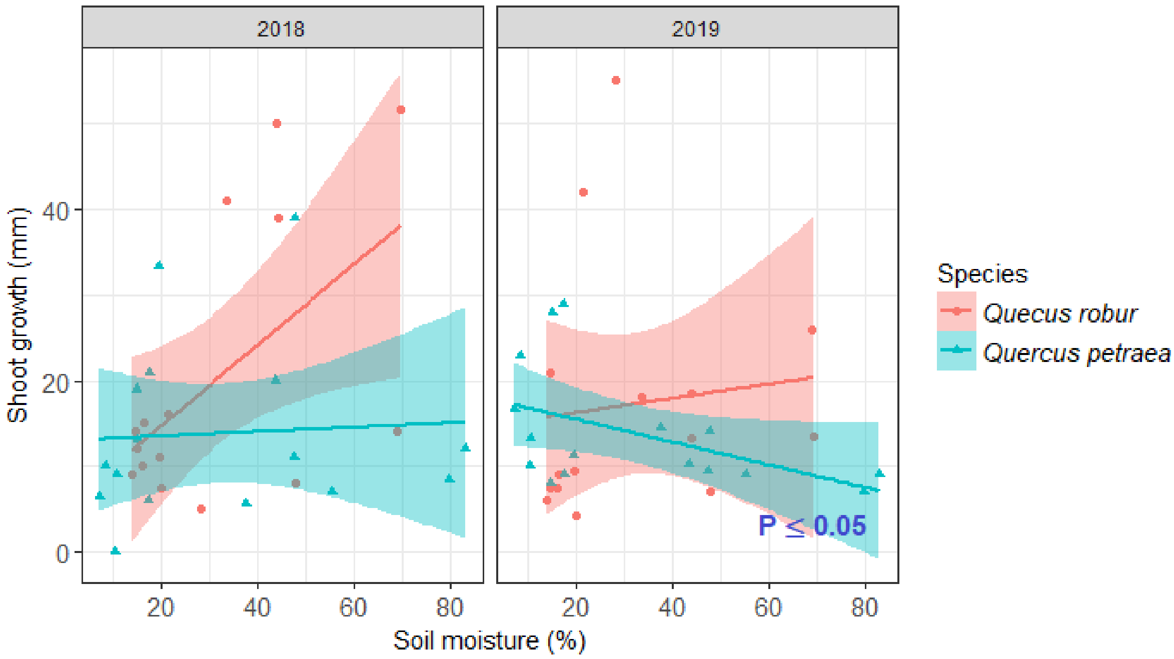

Figure 4. 9 - Correlation (±SE) between soil moisture (%) and annual shoot growth (mm) of juvenile (two-year-old) native oak (Quercus robur, Quercus petraea) planted in the upland pastures (Dendles Waste) of Dartmoor, southwest England (n = 16). All saplings sampled were protected from grazing. The strength (TAU value) and significance (P value) of correlations in 2018 and 2019 were assessed via Kendall rank order correlation.

Table 4.4 – Correlation between soil moisture (%) and annual shoot growth (mm) of juvenile (two-year-old) native oak (*Quercus robur*, *Quercus petraea*) planted in an upland pastoral site in Dartmoor, southwest England (n = 16). All saplings sampled were protected from grazing. Reported are the strength (TAU value) and significance (*P* value) of correlations in 2018, 2019 and for combined years assessed via Kendall rank order correlation.

	Soil moisture vs shoot growth			
	Quercus robur		***Quercus petraea***	
Year	**TAU**	**P value**	**TAU**	**P value**
2018	0.287	0.137	0.200	0.305
2019	0.287	0.137	-0.362	0.051
Total	0.382	0.047	0.083	0.690

4.3.2.2. Chlorophyll fluorescence of planted native oak saplings

There was significant positive relationship between photosynthetic vitality (leaf PI_{abs}) of native oaks and surface soil moisture (Figure 4.10). Planted *Quercus robur* had a stronger positive response to moisture during the growing season (TAU = 0.346, P = 0.000) than *Quercus petraea* (TAU = 0.231, P = 0.001) (Table 4.5). *Quercus petraea* reached optimal performance at lower soil moisture than *Quercus robur*, before steep reductions in photosynthetic vitality at 75% soil moisture. Yet, overall (June – August 2018) planted *Quercus petraea* had higher mean photosynthetic vitality (PI_{abs} = 3.37) (W = 2352.5 , P = < 0.001) than *Quercus robur* (PI_{abs} = 1.92) saplings. Only with significant rainfall (+60mm) recorded at the beginning of August during the very dry summer of 2018 were there notable increases in surface soil moisture and PI_{abs} of planted saplings (Figure 4.11).

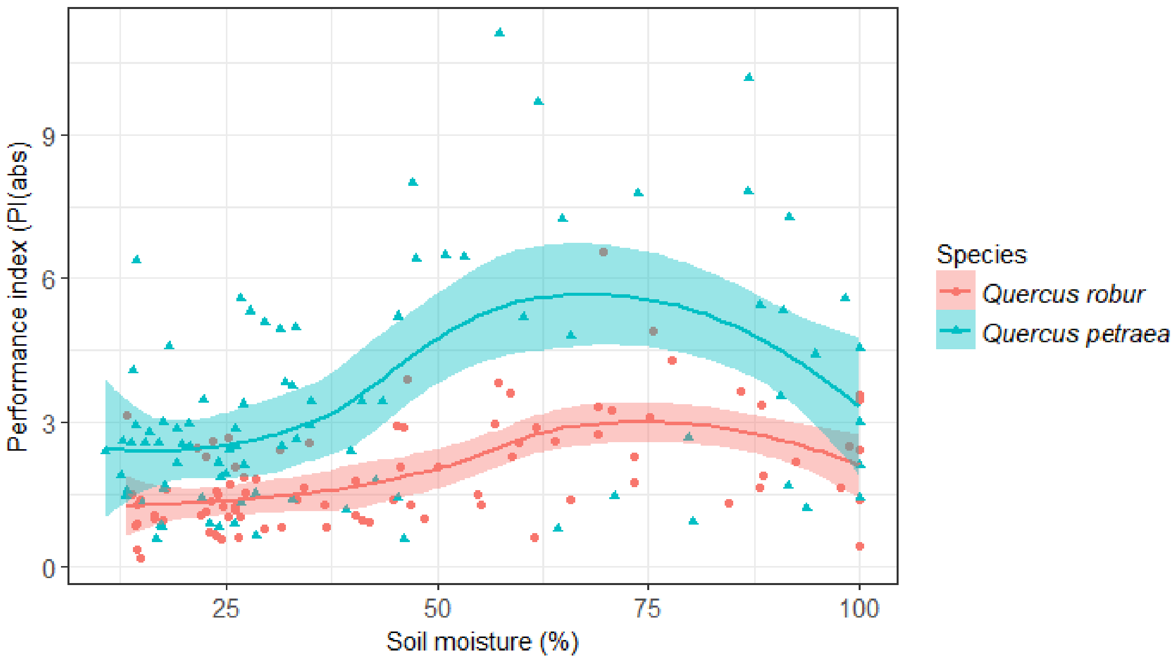

Figure 4. 10 – Correlation between the leaf photosynthetic vitality (Performance index [PI_{abs}]) of juvenile (two-year-old) native oak (*Quercus robur*, *Quercus petraea*) saplings and surrounding surface soil moisture (%) planted in upland pastoral catchments of Dendles Waste, Dartmoor, southwest England. Each point reflect mean leaf PI_{abs} from two-year-old *Quercus robur* (New Bridge) and *Quercus petraea* (Hembury woods) saplings and surrounding surface soil moisture (%) between June and August 2018 (n = 89). All saplings sampled were protected from grazing. A LOESS (local regression) smoothing curve was fitted.

Table 4.5 - Correlation between surface soil moisture (%) and mean photosynthetic vitality (PI_{abs}) of juvenile (two-year-old), local provenance (Dartmoor) native oak (*Quercus robur*, *Quercus petraea*) saplings planted in the upland pastures (Dendles Waste) of Dartmoor, southwest England (n = 89). All saplings sampled saplings were protected from grazing. The strength (TAU value) and significance (*P* value) of linear relationships were assessed via Kendall rank order correlation.

Oak vitality (PI_{abs}) vs soil moisture

Quercus robur		*Quercus petraea*	
TAU	**P value**	**TAU**	**P value**
0.346	0.000	0.231	0.001

**note: correlation tests assessed the linear relationship and do not capture the full monotonic variation.*

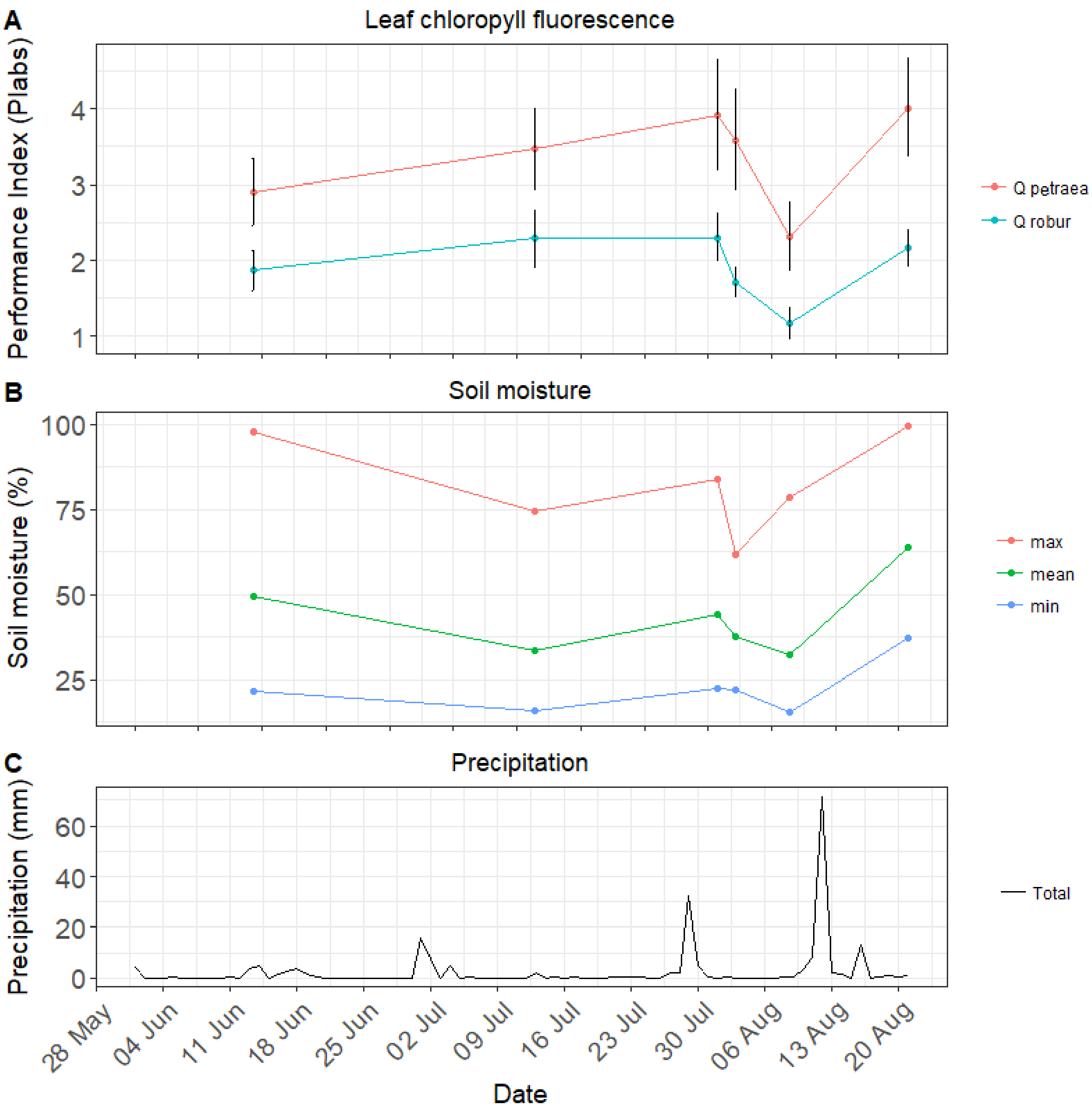

Figure 4. 11 – A) photosynthetic vitality PI_{abs} of juvenile native oak (*Quercus robur*, *Quercus petraea*) saplings planted in upland pastures of Dartmoor, southwest England; B) surface soil moisture (%) surrounding saplings; and C) Daily total precipitation between June – August 2018. PI_{abs} and soil moisture measurements were taken together. Daily precipitation was obtained from the nearest climate station, Cornwood (lat: 50.4182, long: -3.9595 accessed via Met Office 2012).

4.3.2.3. Dry weight of planted native oak saplings

The study finds the difference in main root dry weight between trees in livestock 'exclosures' and 'open' grazing treatments was greatest in more freely drained (FD) soils, with lowest difference between main root dry weight in exclosure and livestock grazed treatments found in the permanently waterlogged soils (W) (Figure 4.12). Interestingly, the fine root mass of planted trees was greatest for protected trees in freely-draining soil and lowest for livestock grazed areas in seasonally waterlogged soils. Whilst the root:shoot ratios of planted trees was significantly higher in exclosure plots for freely-draining, and seasonally-waterlogged soils, livestock grazing made no difference to root:shoot ratios in permanently waterlogged soils (Figure 4.13).

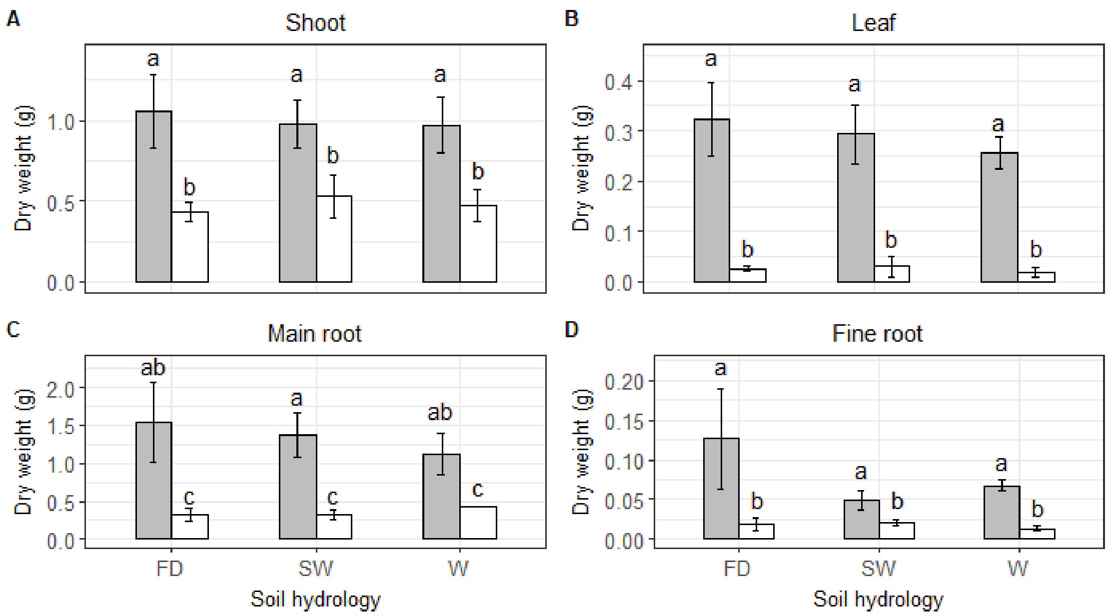

Figure 4. 12 – Mean (±SE) dry weight (g) of A) shoots B) Leaves C) Main roots and D) Fine roots of juvenile (two-year-old) native oak planted in livestock 'exclosures' (grey) and pastures 'open' (white) to grazing (n = 3) in the uplands (Dendles waste) of Dartmoor, southwest England. Trees were planted in April and removed in September 2018. Soil hydrology: FD = freely draining, SW = seasonally waterlogged, W = waterlogged (permanently). Significant difference between individual treatments ($P < 0.05$) via Kruskal-Wallis and Conover-Iman test, denoted using different uncapped letters (a,b,c, etc.).

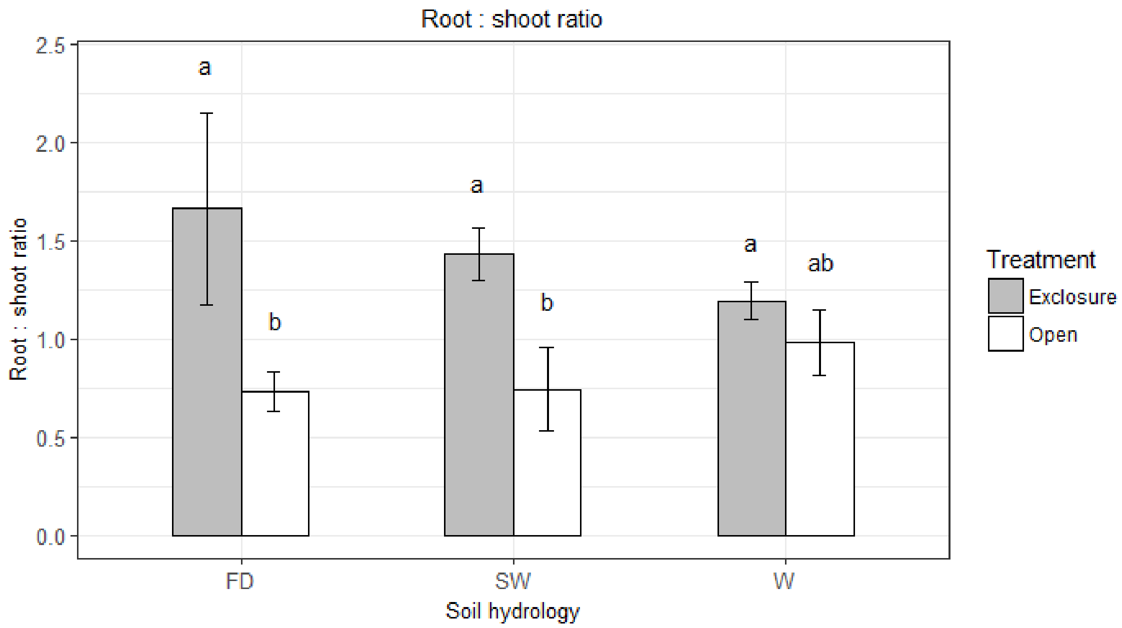

Figure 4. 13 - Mean (±SE) root: shoot ratio from dry weight of 2 year old native oak planted in livestock 'exclosures' and pastures 'open' to grazing (n = 3) in the uplands (Dendles waste) of Dartmoor, southwest England. Trees were planted in April and removed in September 2018. Soil hydrology: FD = freely draining, SW = seasonally waterlogged, W = waterlogged (permanently). Significant difference between individual treatments ($P \leq 0.05$) via Kruskal-Wallis and Conover-Iman test, denoted using different uncapped letters (a,b,c, etc.).

4.3.3. Naturally colonising, juvenile oak (two-year-old) - Stem diameter vs soil moisture

The stem diameter of naturally colonising juvenile (two-years-old) oak saplings at Dartmeet is significantly negatively related to the soil moisture content of surface soils (TAU value = *-0.46, P value = 0.03*) (Figure 4.14). The stem diameter of trees at Merrivale are very marginally non-significantly (TAU value = -0.46, *P* value= 0.070) negatively related to soil moisture content. When locations are combined, there is significant negative (TAU value = -0.43, *P* value = 0.007) relation to soil moisture.

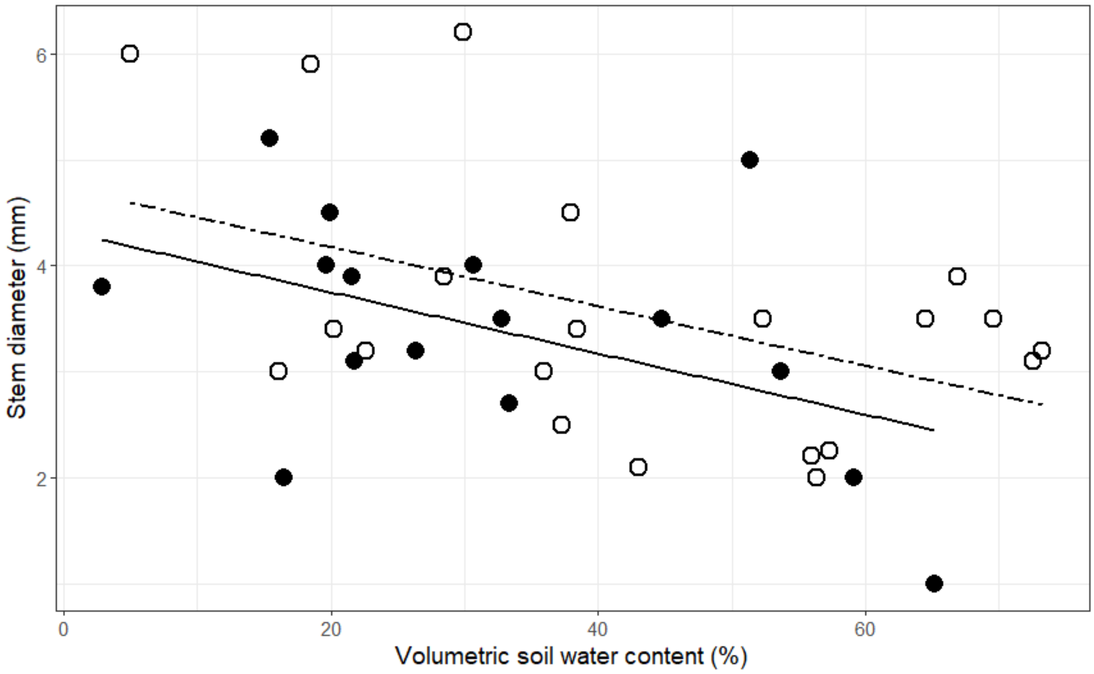

Figure 4. 14 – Correlation between soil moisture and stem diameter of juvenile (two-year-old) naturally colonising native oak (*Quercus robur*, *Quercus petraea*) sapling in the upland pastures of Merrivale ([n = 16] = black circles) and Dartmeet ([n = 21] = white circles) in Dartmoor, southwest England. The strength (TAU value) and significance (P value) of correlations were assessed via Kendall rank order correlation.

4.4. Discussion

The response of native oak trees to elevated soil moisture and changing plant communities will be essential for both realising the multiple benefits of native woodland establishment in UK upland areas and understanding the barriers for implementation (Thomas et al. 2014, Sgrò et al. 2011). The study shows that whilst *Quercus robur*, particularly at very early development stages (0 - 1 years), have a relatively high tolerance to soil moisture and flooded soils, oak seedlings are unable to establish in 'active' mire or blanket bog sites, typified by high (flooded) water tables and a functioning acrotelm (Lindsay 2010). Despite large seeds (acorns) confering significant performance benefits to the establishment of first-year seedlings, and reducing competition stress from surrounding vegetation (Löf & Welander 2004; Palmer et al. 2004), surviving seedlings in waterlogged soils experienced diminished photosynthetic vitality (PI_{abs}) and late summer 'lammas' growth. Diminished lammas growth represents a significant disadvantage for oak seedlings competing with surrounding vegetation (Jensen et al. 2011a,b; Annighöfer et al. 2015). Additionally, the severely diminished root systems and lower root:shoot ratios of surviving seedlings in more waterlogged (anaerobic) soils reduces their capacity to obtain water, nutrients, and escape below ground competition from surrounding vegetation (Harmer & Robertson 2003; Mokany et al. 2006; Parent et al. 2008). Indeed, the elevated fine root mass and reductions in leaf PI_{abs} of seedlings in medium compared to low water tables suggests that elevated, below-ground competition for nutrients limited by anoxic conditions could be partly responsible for the observed reduction in 'lammas' shoot growth. Consequently, results show that whilst acorns allow the development of oak seedlings in unfavourable poorly drained soils, surviving seedlings will be at significant disadvantage once acorn reserves are used up (Jensen et al. 2011a,b; Annighöfer et al. 2015). Consequently, the relatively high oak seedling survivorship in ‘high’ (45%) and ‘medium’ (77%) water table treatments is likely an overestimation of future sapling survival.

The interaction between seasonal variation in soil moisture and changes in the development response of roots is critical for tree nutrition and successful establishment (Harmer & Robertson 2003; Mokany et al. 2006; Brunner et al. 2015). Results demonstrate that in poorly drained, flat, or over compacted upland pasture sites, increases in soil moisture and/or water tables may reduce the development, performance, and future competitive ability of oak seedlings (Parent et al. 2008). Indeed, the observed inverse relationship between *Sphagnum* growth and oak seedling survivorship forwarns us that changes in soil moisture and the subsequent response of upland plant communities will be integral in determining the character of afforestation in the uplands and the provision of ecosystem services.

The performance of planted juvenile native oak in poorly drained to freely draining soils was highly divergent between native oak species, confirming the enhanced tolerance of *Quercus robur* to waterlogging compared with *Quercus petraea* (Dreyer 1991; Dapardeu et al. 2015). There was however, no drop in survival or mean photosynthetic performance in waterlogged soils, perhaps reflecting that mortality from the accumulation of stresses may often only happen after multiple years (Kelly et al. 2002; Niinemets 2010). Indeed, reduced *Quercus petraea* shoot growth in waterlogged soils was only apparent in the second year after planting. Differential performance between years was also a symptom of the higher rainfall totals during summer 2019 (seventh wettest in UK since 1910) compared to the previous summer (fifth driest summer in England since 1910) (Met Office 2018b; Met office 2019). Such factors demonstrate the importance of long-term experimentation in ecological research if ACC impacts on tree regeneration are to be accurately assessed (Parmesan & Hanley 2015; Palmer et al. 2017).

The ability of trees to successfully establish will depend on their morphological and physiological response to initial stresses (such as low oxygen and enhanced competition) during early development as well as their capacity to modify their environment over time (Pärtel & Helm 2007; Mitchell et al. 2012; Murphy et al. 2020). Consequently, root morphological response to ACC associated changes in annual and seasonal soil moisture may prove crucial for the future composition of woodlands and their ecosystem functioning. Whilst soil moisture is a critical factor, it is not the only one, and the pronounced negative impact of livestock on oak root mass in freely draining soils compared to waterlogged ones highlights tree performance and successful establishment is dependent on a complexity of multiple stressors (Niinemets 2010).

Future research should test the long-term impact of multiple drivers on early oak tree establishment (Parmesan & Hanley 2015). Considering the policy impetus for afforestation and evidenced changes in climate in the UK uplands (Burt & Holden 2010; DEFRA 2018a, 2019a; Committee on Climate Change 2019; Murphy et al. 2019); there is pressing need to test the response of native tree genotypes to increases in temperature and atmospheric CO_2 along both soil moisture and herbivory gradients. Results would elucidate the cost implications and policy changes needed to ensure desirable ESS impacts, and clarify the specifications for woodland planting schemes. Improved understanding is particularly warranted considering the substantial ESS trade-offs between land uses (Iacob et al. 2014; Evans et al. 2015; Mitchell et al. 2017), the relative uncertainty, particularly of summer precipitation in the uplands (Murphy et al. 2019), and the paucity of research on native compared to exotic conifer woodland (Burton et al. 2018).

This study shows large seeded tree species such as UK native oak are at increased vulnerability to waterlogging stress in the period immediately following seedling development, after the loss of acorn reserves which are able to buffer impacts from environmental stressors (Brookes et al. 1980). Evidenced increases in precipitation over the compacted surface soils of UK upland pastures, (Burt & Holden 2010; Murphy et al. 2019) resulting in elevated soil moisture, particularly in flatter, poorly drained hill top sites has the potential to be a significant constraint on native oak establishment, particularly along western ‘Atlantic’ upland coasts. Valley slope sites with naturally better drained soils should be prioritised for native oak establishment. In these freely-draining soils elevated rainfall, would likely benefit oak woodland establishment over grassland and heath competitors (Löf & Welander 2004; Harmer & Robertson 2003).

Nonetheless, the differential waterlogging tolerance between UK native oak species shows there is a high-degree of variation within native UK *Quercus* to differential soil moisture levels, confirming oaks high intra-specific diversity (Arend et al. 2011). If sufficient connectivity between fragmented upland oak woodland populations can be provided, there is likely to be sufficient diversity for ACC adaption and future population expansion even on poorly drained and/or compacted pasture slopes.

Chapter 5.

Optimising oak woodland expansion into upland pastoral systems

Abstract:

The establishment of woodlands is receiving considerable attention due to their potential for carbon sequestration, biodiversity, natural flood management (NFM) and other ecosystem services. In NW Europe, native Atlantic oak (*Quercus* spp) woodlands have been cleared from upland areas and replaced by low-diversity grazing pastures, reducing floodwater retention in the headwaters of river catchments. Large-scale planting is expensive, but the conditions under which rapid natural colonisation of large seeded tree species is possible, largely unknown. Where and when we can rely on natural colonisation is an important question with serious cost implications for woodland expansion. This study assessed the location and performance of young (<12 years) conspecific Fagaceae species (*Quercus robur, Quercus petraea*) in the upland pastoral catchments of Dartmoor, southwest (SW) England. Sapling survival and growth was assessed throughout early ontogeny in extensive, enclosed and former pasture systems and using long- and short-term grazing exclusion experiments. Colonisation was largely confined to 20m of the nearest mature tree and largely restricted to freely draining, west facing, acid pasture slopes. Although density of the youngest (0 – 3yr, 4 – 7yrs) saplings did not vary between livestock 'exclosure' and lightly grazed 'open' plots, overall density of older recruits (8 – 12 years) was greater in 'exclosure' plots. Saplings planted into exclosures also had higher survival, and leaf, shoot, root dry weight after just 7 months compared to those in grazed plots, similar to naturally recruiting saplings which were taller and less damaged by grazing. The natural regeneration potential of large-seeded tree species such as oak in open, upland areas is highly constrained by grazing and the absence of key seed dispersal agents. Rapid establishment for NFM delivery is only viable if oaks are planted within fenced exclosures strategically located within headwater and valley slope pastures. In the

largely treeless UK uplands, valley areas could act as foci for further re-colonisation and the timely provision of key ecosystem services such as climate mitigation.

5.1. Introduction

Woodland (re-)establishment is widely advocated as an effective means to mitigate anthropogenic climate change (ACC) with the potential to sequester a total of 3 petagrams of CO_2 equivalent a year ($PgCO_2e\ y^{-1}$) globally by 2030 (Griscom et al. 2017; Bastin et al. 2019). The creation of woodlands in upland catchments may also prove an effective tool for natural flood management (NFM), reducing the risk of flood damage associated with ACC at both local and regional scales (Marshall et al. 2014; Evaristo & McDonnell 2019; Murphy et al. *submitted*). Benefits are associated with enhanced water interception, soil infiltration, storage, and soil recovery, with a reduction in surface run-off and attenuation of peak river flows (Nisbet et al. 2011; Marshall et al. 2014; Murphy et al. *submitted*). Consequently, woodland creation offers multi-faceted climate change mitigation potential whilst providing additional ecosystem services (ESS) and public benefits, including biodiversity, water purification and soil health improvements (Iacob et al. 2014; Griscom et al. 2017).

Historically, large areas of native oak (*Quercus spp*) woodland were cleared as part of agricultural expansion across Europe (Woodbridge et al. 2014; Roberts et al. 2018). In the UK especially, upland areas are typified by very low woodland cover (Bunce et al. 2018a). Subsequent and extensive agricultural 'improvement', in the form of burning, drainage and heavy grazing to maximise livestock productivity, has converted these areas to grassland and heathland vegetation (Fyfe & Woodbridge 2012; Fyfe et al. 2014). Historic degradation has resulted in significantly diminished conservation and carbon storage potential (Bardgett et al. 1995; Sansom et al. 1999) and poor management, particular overgrazing by sheep and deer, has severely limited any woodland regeneration. In addition, soil compaction resulting from historically high livestock densities when coupled with ACC-driven precipitation increases in the uplands (Sansom et al. 1997, Holden et al. 2007ab, Murphy et al. 2019), constitutes a very real threat to downstream communities from elevated run-off and enhanced flood risk. With an increase of 1 billion ha of woodland globally, necessary to limit global warming to 1.5°C by 2050 (IPCC 2018), upland valley slopes and catchment headwaters constitute prime candidates for native woodland creation in the UK and beyond (Burgess-Gamble et al. 2017; Evaristo & McDonnell 2019; Murphy et al. *submitted*). The maintenance of productive upland pasture is strongly dependent on agricultural subsidy, and consequently, is likely to experience considerable environmental changes if policy and land-use priorities shift (Reed et al. 2013; Bunce et al. 2018b; Sandom et al. 2018). In the UK for example, government commitments to mitigate climate change (Committee on Climate Change 2019; Defra 2019b) place considerable emphasis on prioritising land management policies to maximise ecosystem service benefits in marginal agricultural areas. In this context, there is growing interest in what is loosely termed 'rewilding', 'wilding' and other forms of ecological restoration (Jepson 2015; Sandom et al. 2018), at the vanguard of the movement towards a 'Natural Capital' led approach to agricultural policy (Bateman & Balmford 2018; Baldock et al. 2019).

Like other potential woodland creation sites globally, the UK's upland areas have multiple agricultural, social and environmental sensitivities (Holden et al. 2007a, Bonn et al. 2009; Bonn et al. 2014). Woodland creation must carefully weigh up existing conservation interests including species rich grassland, heath and wetland habitats, whilst satisfying agricultural and societal needs (Iacob et al. 2014; Mitchell et al. 2017; Burton et al. 2018). Tree planting is likely to prove controversial, expensive and logistically difficult (Commons Act 2006; Strengers et al. 2008) but the capacity for natural colonisation in these often heavily grazed areas is poorly understood. The (re-)establishment of oak (*Quercus spp*) woodland is of heightened significance given its decline in NW Europe, and potential loss of ash trees (*Fraxinus excelsior*) through 'ash dieback' (*Hymenoscyphus fraxineus*) (Denman et al. 2014; Broome et al. 2019; Mitchell et al. 2019). Upland 'Atlantic' oak woodlands are highlighted under the European habitats directive due to their fragmented distribution and support of specialist plant (lichen and bryophyte) and animal assemblages (Baarda 2005; JNCC 2014; Lamacraft et al. 2018).

Although the regeneration of upland oak woodland (dominated by *Quercus robur* and *Q petraea*) has long been studied (Watt 1919, Shaw 1968), we know comparatively little about what limits and shapes oak regeneration in the open, non-forest environments (Bobiec et al. 2018) that typify upland pastures. Successful oak colonisation depends however, on multiple, interacting biotic and abiotic factors (Worrell & Nixon 1991; Bobiec et al. 2018; Hanley et al. 2019) and it seems likely that in the treeless and grazed uplands, seed dispersal, competition with grassland plants, and herbivory represent the most important constraints. Indeed, whilst the potential usefulness of woodland creation is increasingly recognised, effective implementation will require improved understanding of the practical measures needed for its establishment. Consequently, this study asked the following questions; 1) What is the extent of sapling recruitment outside the existing woodland edge 2) How does grazing by livestock impact recruitment and does this change with sapling age and surrounding vegetation?

5.2. Methods

5.2.1. Study location

Dartmoor National Park (DNP), in southwest England (approximately 50° N 00° W) is the largest upland area (953km^2 and up to 621m a.s.l) in the southern part of the British Isles (Perry et al. 2014). Following extensive woodland clearance and conversion to sheep grazing, and following high and increasing precipitation trends here (Murphy et al. 2019); DNP represents a perfect location to examine constraints to native oak woodland restoration within a context of climate mitigation. Less than 4% of the deciduous woodland cover remains (Mercer 2009; Fyfe et al. 2013; DNPA 2017) restricted to fragments such as three small, isolated Atlantic oakwoods (Simmons 1965; Barkham 1978). DNP is now characterised by upland blanket bog, valley mire, heathland and acid grassland habitats and is grazed by three livestock species; i.e. (sheep – 133,000, cattle – 35,000, and ponies 1,300) on open access 'commons' and enclosed farmstead pastures (Dartmoor Commons Act 1985; Mercer 2009; Silcock et al. 2012). The number of grazing animals on Dartmoor as with other upland sites increased dramatically between the 1950s and 2000 (particularly sheep – x7 fold increase) in response to market trends and common agricultural policy (CAP) support payments (Baldock et al. 2002; Sansom et al. 1999). However, since the turn of the century, numbers have stabilised and are now in decline (Silcock et al. 2012).

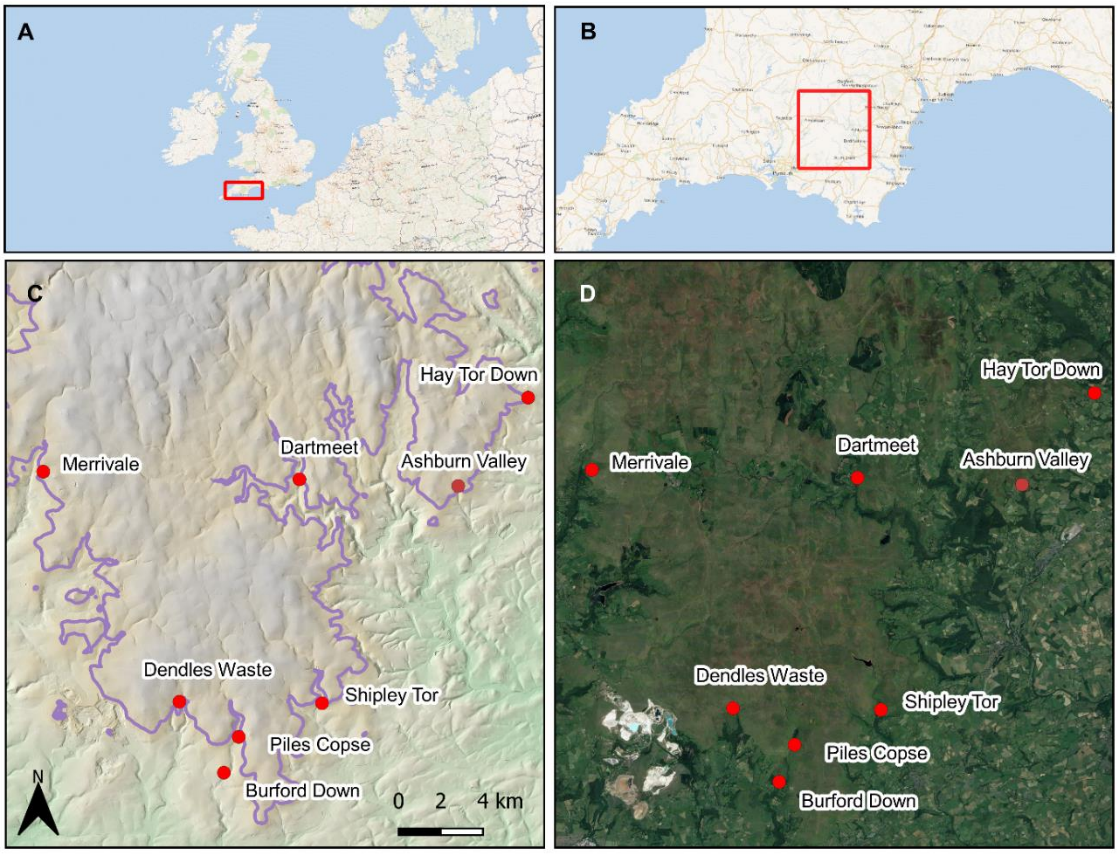

Figure 5.1 – A) Location of study area (southwest England) within north-western Europe. B) Locations of sites of Dartmoor south west England. Sites of natural colonising native oak (*Quercus robur*, *Quercus petraea*) saplings and experimentally planted juvenile oak (Dendles Waste) within upland pastures of Dartmoor, southwest England in relation to: C) Topography and 300m isoline. D) Satellite imagery.

5.2.2. Extent of sapling recruitment?

A desktop search was conducted using satellite data (Google Maps 2017) to identify upland areas (>250 - 300m) experiencing woodland/scrub encroachment (Figure 5.1, A5.1). Identified areas were then visited to determine presence of mature native oak trees and recruits (winter - spring 2017). The search revealed six pasture sites experiencing natural oak colonisation alongside an additional site (Piles Copse), with evidence of oak colonisation within fenced exclosures (Figure 5.2, Table 5.1).

Each site was walked to a distance of 100m from the woodland edge to visually locate a subset of the population (i.e. every other sapling) of all oak saplings (trees <12 years old) present. Sapling age (using bud ring scars - Clark & Hallgren [2004]), root collar diameter

(RCD) and surrounding vegetation cover (%) in the immediate vicinity (50 x 50cm area) of each tree were recorded. The distance of saplings to the trunk of the nearest mature conspecific (i.e. most likely seed source) was also quantified (see Harmer & Morgan 2007). No distinction was made between *Quercus Robur* and *Quercus petraea* individuals in analysis due to widespread hybridisation, a common occurance for these 'species' (Petit et al. 2003).

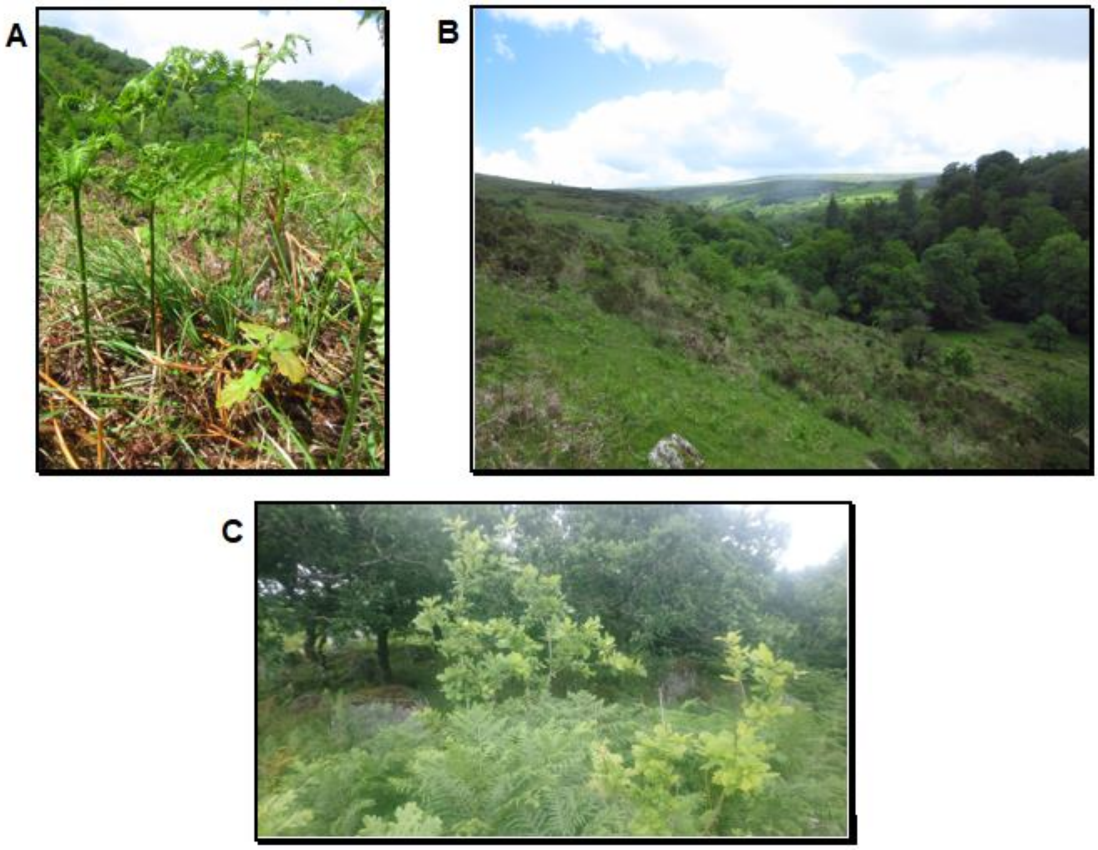

Figure 5. 2 – Sites identified as experiencing natural colonisation of native oak (*Quercus robur*, *Quercus petraea*) saplings in the extensive (pictures A,B - Dartmeet) and enclosed (picture C – Merrivale) upland pastures of Dartmoor, southwest England.

5.2.3. Impact of grazing on sapling recruitment and growth

The study subsequently (summer 2018) focussed on three sites where natural oak colonisation was considerable (>50 saplings) - these were the extensive pasture at Dartmeet, enclosed pasture at Merrivale, and a former pasture at Piles Copse (fenced in 2011) (Figure 5.3, Table 5.1).

The density and age class (0 – 3 years, 4 – 7 years, 8 – 12 years) of colonising oak saplings was recorded in 10 x 10 m areas (at Piles Copse the size of fenced exclosures were used), up to 20m from the woodland edge.

Sites were also walked to a distance of 20m from the woodland edge to visually locate all saplings between 1 – 7 years old. These ages were chosen as oak sapling performance can decrease in the years immediately following the first year, when seedlings use up their acorn energy store (Brookes et al. 1980; Palmer et al. 2004). A subset of the population (i.e. every other sapling), were tagged and the age, height, condition, early summer and late summer 'lammas' (i.e. July – August) shoot growth of each individual, and the cover and height of surrounding ground flora (within 50 x 50cm) recorded.

The density of oak colonisation in fenced exclosures (Piles Copse) erected in 2006 (3 replicates) and 2011 (1 replicate) (Howell 2013) were compared with adjacent grazed pasture areas (Figure 5.3, A5.3, Table A5.2) for three different age classes (0 – 3years, 4 – 7 years, 8 – 12 years). Within exclosures not all trees were natural colonisers, for recruitment density calculations the estimated number of trees planted in each exclosure (after discussion with landowner) were excluded from the analysis. Bracken controlling Asulox herbicide was applied in the 2006 exclosures, potentially providing additional benefit to oak saplings.

Figure 5. 3 – Livestock exclosures (fences) established in 2006 (B, C) and 2011 (A) protecting naturally colonising and number of planted native oak (*Quercus robur*) saplings in the upland pastures (at Piles Copse) of Dartmoor, southwest England.

A livestock exclusion experiment was established at Dendles Waste (Figure 5.1) (Lat: 50.452875, Lon: -3.9511210). Three areas of distinct soil structure were identified: 1) Freely-draining (FD) podzolic soils with U4 (*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland) vegetation community; 2) Seasonally-waterlogged (SW) soils of U4 grassland but dominated by *Agrostis capillaris* and *Anthoxanthum odoratum*; 3) Waterlogged (W) (permanently) soils characterised by M6 (*Carex echinata-Sphagnum fallax*) vegetation. One hundred and forty four juvenile (two-year-old) native oak trees (*Quercus robur* (72 trees), *Quercus petraea* (72 trees)) were 'slot planted' into exclosures in spring 2018. All trees were of local provenance (*Quercus robur* from New Bridge (Lat: 50.524544 Long: -3.8198192), *Quercus petraea* from Hembury (Lat: 50.503279 Long: -3.7992586), Dartmoor). Half of the trees (arranged in groups of 8 individuals) were protected with fenced exclosures ('Gengards', New Woods Forestry, Norwich, UK) and nine groups protected and nine left open to sheep and pony livestock grazing (Figure 5.4, Table A5.3). The survival, shoot growth, leaf area, and condition of trees was monitored throughout summer 2018 and 2019.

Figure 5. 4 – Livestock 'gengard' exclosures (New Woods Forestry, Norwich) planted with juvenile (two-years-old) native oak (*Quercus robur*, *Quercus petraea*) saplings (A), in the upland pastures (Dendles Waste) of Dartmoor, southwest England in spring (March) 2018. Half of the trees (arranged in groups of 8 individuals) were protected with fenced exclosures ('Gengards', New Woods Forestry, Norwich, UK) and nine groups protected and nine left open to sheep (B) and pony (C) livestock grazing (Table A5.3).

A random selection of trees (at Dendles Waste) in each exclosure and open plots were removed in Autumn 2018. After soil was washed from the roots, trees were oven dried at 80^{o}C for five days and dry weight biomass of shoots, leaves, and main root and fine roots determined.

5.2.4. Statistical analysis

Data analysis for the relationship between natural colonisation and surrounding ground flora were analysed across sites (data within sites homogenised). For planted trees the data from 144 tree individuals were aggregated into 9 replicates, (homogenised within groups of 8 as in field set-up). All statistical analyses were performed using R studio (R Core Team 2017). Data were assessed for normality via Shapiro-Wilks test, all analysis had multiple non-normally distributed data so non-parametric statistical tests were utilised. Kendall rank order correlation ('Kendall' package (McLeod 2011) examined correlation between height and RCD of naturally colonising trees and ground flora cover. This test was used to determine the strength and significance of relationship between tree age and tree height, grazing damage, shoot growth, late summer 'lammas' shoot growth proportion and the cover and height of vegetation for extensive, enclosed and former pasture systems. The Wilcoxon exact rank sum test (using shift algorithm (Streitberg & Röhmel 1986) was utilised via the 'exactRankTests' package (Hothorn & Hornik 2017). The test was used to determine variation in vegetation height, and the density, survival, grazing damage and survival of oak recruits between livestock excluded ('exclosure') and 'open' pasture plots.

A Kruskal Wallis test determined significant difference in tree densities, recruit performance and vegetation between age class and site. A Conover Iman test ('conover.test' package [Dinno 2017]) was used to determined significant differences between individual sites. Graphs were produced using 'GGplot2' (Wickham 2009), 'cowplot' (Wilke 2017) packages.

5.3. Results

5.3.1. Sites of natural colonisation by native oak

All sites experiencing oak colonisation were typified by freely draining, podzolic soils (typically Moor Gate soil series) with the majority located on west facing slopes supporting U4 (*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland) and U20 (*Pteridium-Galium*) NVC communities (Table 5.1). Most recruitment was observed at Dartmeet (63 saplings) and Merrivale (35), sites with comparatively low soil pH. Oak recruits were located in areas of extensive (‘commons’) and enclosed pasture. Average sapling age ranged between 2.2 (Hay Tor) and 5.6 years old (Asburn valley) but younger individuals were associated with higher grass cover (NVC – U4). Conversely, larger individuals (i.e. larger root collar diameter) were associated with higher bracken cover (NVC U20) (Table 5.2).

Table 5.1 – Upland pastoral sites located in Dartmoor, southwest England, experiencing native oak (*Quercus robur, Quercus petraea*) colonisation identified by visual satellite image assessment and ground-truth field surveys. All sites were located on steep acid grassland pastures. The location (Latitude: Longitude, altitude), management (pasture system, animal type, grazing intensity) and natural features (soil hydrology, soil pH, soil series, slope aspect and angle) of upland pastoral sites used in the study. At certain sites information was unavailable (-). Management information obtained from landowners, Dartmoor commons authorities, Dartmoor National Park Authority and by direct observation. Information on soil type, natural soil hydrology, habitats (Cranfield University 2019) and pH (Centre for Ecology & Hydrology 2007) was accessed remotely. HSL = higher level stewardship agri-scheme (Natural England 2013). * Bracken (*Pteridium aquilinum*) cut back, a traditional management practice (Averis et al. 2004).

	Sites of native oak colonisation						
	Dartmeet	**Merrivale**	**Ashburn valley**	**Shipley Tor**	**Burford Down**	**Hay Tor Down**	**Higher Piles (Piles Copse)**
Lat:long	50.5481: -3.8750	50.5492: -4.0458	50.5476: -3.7685	50.4537: -3.8550	50.4230: -3.9205	50.5858: -3.7231	50.4384: -3.9111
Altitude (m)	258m	305m	302m	266m	248m	268m	256m
Pasture system	Extensive (‘commons’)	Enclosed	Enclosed (agri-scheme)	Enclosed (agri-scheme)	Enclosed (agri-scheme)	Extensive (‘commons’)	Former (HLS)
Livestock type	Sheep, cattle, ponies	Sheep, cattle	-	Sheep	-	Sheep, cattle, ponies	Cattle, sheep
Livestock density (LSU ha^{-1})	0.400 (winter 0.170)	-	-	-	-	-	0.201 (winter 0.012) (in exclosures = 0)
Dominant NVCs	U4, U20, W23	U4, U20	U20	U4, U20	U4, U20	U20*	U4, U20
Natural soil hydrology (pH)	Freely draining (4.62)	Freely draining (4.62)	Freely draining (6.07)	Freely draining (6.07)	Freely draining (6.07)	Freely draining (6.07)	Freely draining (4.62)
Soil series	Moor Gate (Podzolic)	Moor Gate (Podzolic)	Moor Gate (Podzolic)	Moor Gate (Podzolic)	Moretonhampstead/Moor Gate (Podzolic)	Manod (Podzolic)	Moor Gate (Podzolic)
Aspect of dominant slope (angle °)	West (13)	West (11)	West (5)	West (16)	South East (11)	East (14)	West

Table 5.2 – Relationship between native oak (*Quercus robur* and *Quercus petraea*) sapling performance and surrounding vegetation (% cover). Reported are (Kendall rank order) correlation between mean tree condition (see tree condition scoring – Table A5.1), root collar diameter (RCD), age (years) and grass (*Poaceaea spp*), bracken (*pteridium aquilinum*) and bare ground cover (%) across six upland sites experiencing natural colonisation of native oak in Dartmoor, southwest England. Significant correlations ($P \leq 0.05$) are denoted in bold font. n = 5 for all variables except 'number of ground flora species' where n = 6.

	Native oak colonisation			
	RCD		Age	
Ground cover	**TAU**	***P* value**	**TAU**	***P* value**
Grass cover (%)	-0.800	0.083	**-1.000**	**0.016**
Bracken cover (%)	**1.000**	**0.016**	0.800	0.083
Bare ground cover (%)	0.737	0.076	0.527	0.206
Number of ground flora species	-0.552	0.126	-0.690	0.055

The location of individual saplings in relation to the nearest mature conspecific shows the majority regenerated within 25m (mean 13m, max 75m) of the woodland edge (Figure 5.5).

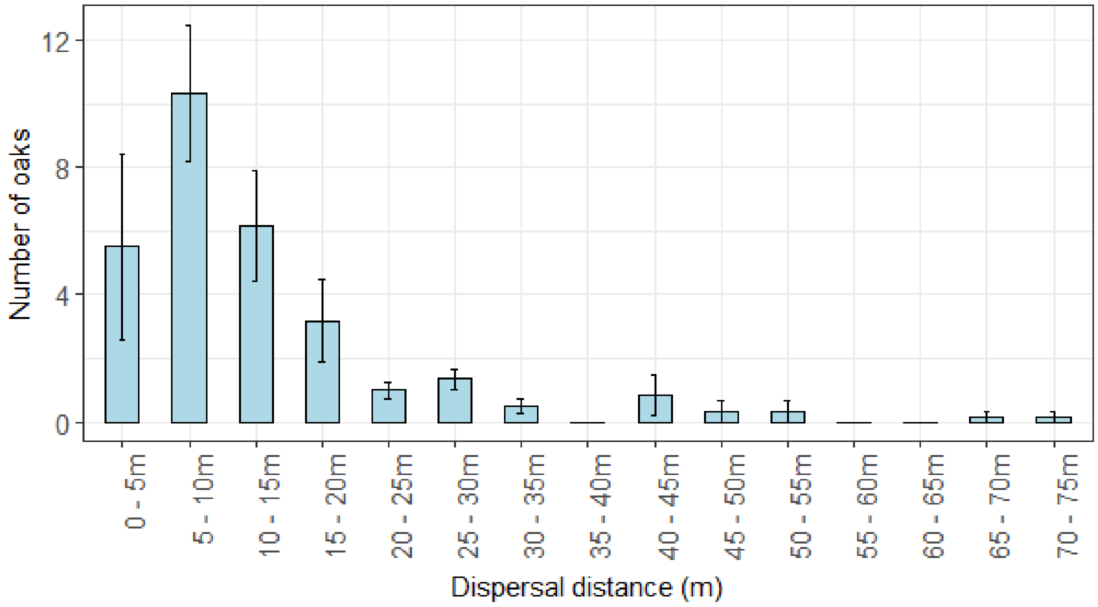

Figure 5. 5 - Frequency classes of mean (±SE) dispersal distance (m) of native oak (*Q. robur, Q petraea*) saplings from the woodland edge (nearest conspecific seed source) in six upland pastoral locations (Dartmeet, Merrivale, Ashburn valley, Shipton Tor, Burford Down, Hay Tor Common) in Dartmoor, southwest England.

5.3.2. Impact of grazing on native oak sapling recruitment and growth

At sites where livestock were allowed to graze (Dartmeet and Merrivale), oak saplings seldom survived more than 8 years, but their exclusion (Piles Copse) resulted in no apparent decline in the density of older oak recruits (Figure 5.6). Sapling growth varied between sites (Table 5.3) and exclusion resulted in increased height, condition and early summer shoot growth. There was considerable ontogenetic deterioration of tree condition at both grazed sites (Dartmeet and Merrivale). However, oak recruits in extensive pastures experienced less ontogenetic deterioration and greater height increases than enclosed pastures, linked to associated increases in the extent of bare ground and grass and bracken height.

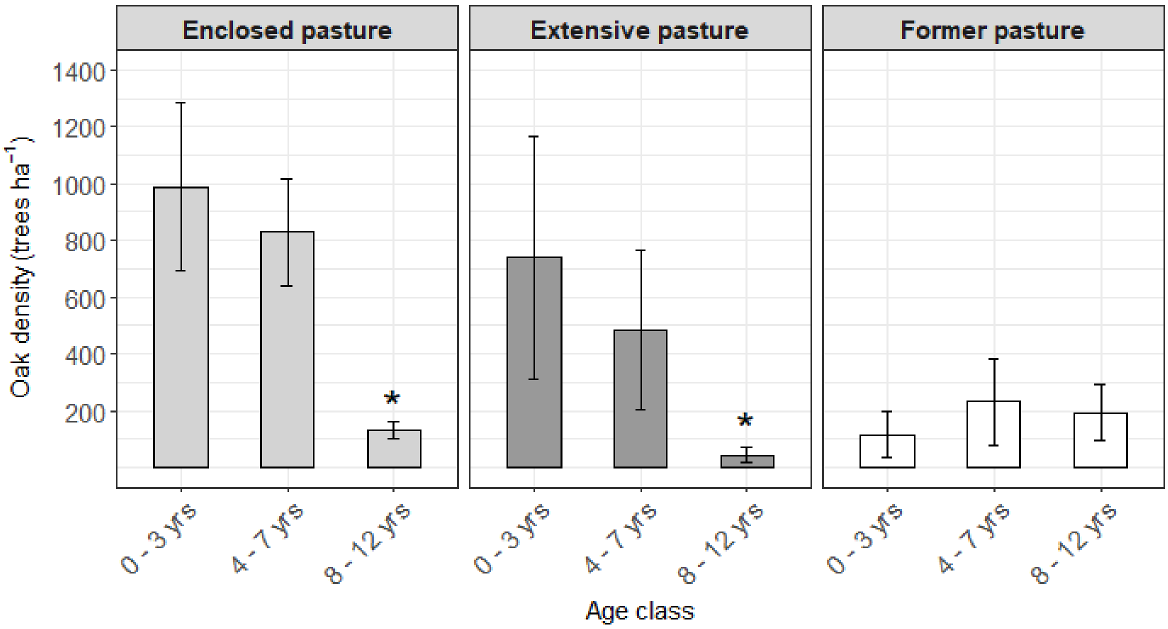

Figure 5. 6 – Mean (±SE) density of oak (*Quercus robur*, *Quercus petraea*) recruits (trees per ha^{-1}) at a) extensive (Dartmeet) b) enclosed (Merrivale) c) former pasture (Piles Copse) sites in Dartmoor, southwestern England. The density of oak recruits was recorded at woodland edges within pasture (3 replicates) and former pasture systems (4 replicates). Oak recruits were divided into age classes: 0 – 3 years, 4 – 7 years and +8 - 12 years using growth scars, and only trees younger than 12 years were included. Significant differences within site age classes within site was determined via Kruskal wallis rank sum test and conover iman test.

Table 5.3 – Details of native oak (*Quercus robur, Quercus petraea*) establishment recorded at three upland pastoral sites. Mean values (± SE) of tree performance (height (mm), current year early summer 'E shoot growth' (mm), current year late summer or 'Lammas growth' (mm), proportion of trees with lammas growth (%), condition = see Table A.1) and surrounding vegetation (grass, bracken and bare ground cover (%), grass and bracken height (mm)). Significant difference between sites is determined via Kruskal wallis rank sum test and conover Iman test between individual sites and denoted with different lower case letters (i.e. a, b, c) . Changes in tree performance and surrounding vegetation with tree age ('vs age') are examined using kendall rank order correlation. + tree condition scoring criteria (Table A5.1). Reported are TAU value (correlation) and significance denoted * ≤ 0.05 , ** P ≤ 0.01 , *** P ≤ 0.001. n = number of oaks surveyed.

	Native oak colonisation					
	Extensive pasture *(Dartmeet) n = 55*		**Enclosed pasture *(Merrivale) n = 76***		**Former pasture *(Piles Copse) n = 75***	
	Mean (SE)	**vs age**	**Mean (SE)**	**vs age**	**Mean (SE)**	**vs age**
Tree age (years)	$4.0^{a} \pm 0.2$		$2.9^{b} \pm 1.0$		$3.5^{a} \pm 0.2$	
Tree height (mm)	$395^{b} \pm 35$	**0.775*** **	$271^{a} \pm 28$	**0.645*** **	$596^{c} \pm 43$	**0.796*** **
Tree condition+	$2.8^{a} \pm 0.2$	**-0.258***	$2.9^{a} \pm 0.1$	**-0.335*** **	$4.6^{b} \pm 0.1$	0.040
E shoot growth (mm)	$33^{a} \pm 4$	0.102	$33^{b} \pm 2$	**0.261** **	$64^{c} \pm 5$	**0.358*** **
Lammas growth (mm)	$22^{a} \pm 3$	0.143	$34^{a} \pm 6$	-0.055	$48^{b} \pm 7$	**0.317***
Lammas proportion (%)	$45.5^{a} \pm 6.8$	0.600	$37.3^{a} \pm 5.6$	-0.200	$45.3^{a} \pm 5.8$	-0.310
Grass cover (%)	$52^{a} \pm 4$	-0.197	$68^{b} \pm 4$	**-0.365*** **	$44^{a} \pm 4$	-0.091
Bracken cover (%)	$30^{b} \pm 4$	0.175	$27^{b} \pm 3$	-0.022	$14^{a} \pm 3$	0.076
Bare ground cover (%)	$31^{b} \pm 4$	**0.231***	$13^{a} \pm 2$	0.177	$16^{a} \pm 3$	**0.225***
Grass height (mm)	$165^{b} \pm 12$	**0.254***	$111^{a} \pm 8$	0.103	$224^{c} \pm 10$	**0.247***
Bracken height (mm)	$580^{a} \pm 27$	**0.228***	$526^{a} \pm 23$	0.148	$772^{b} \pm 21$	0.137

Whilst for grazed sites there is significant positive relationship between sapling height and bare ground and a negative correlation with grass cover, it is only true for older saplings (4 – 7 years) (Table 5.4). In the extensive pasture even the height of younger saplings was negatively associated with grass swards. In the enclosed pasture site, the height of younger saplings was positively related to the height of grass and bracken, and the height of older saplings (4 – 7 years) with the cover of bracken.

Table 5.4 – Correlation between height of oak saplings and the height and cover of surrounding ground flora for younger (1 – 3 years) and older (4 – 7 years) saplings growing in extensive, enclosed and former pasture systems of Dartmoor, southwest England. The strength (TAU value) and significance (*P* value) of correlations was assessed via kendall rank order correlation. * ≤ 0.05 , ** P ≤ 0.01 , *** P ≤ 0.001. n = number of oaks surveyed.

	Sapling height vs ground cover					
	Extensive (Dartmeet) n = 55		**Enclosed (Merrivale) n = 76**		**Former (Piles Copse) n = 75**	
	1 – 3 yr	**4 – 7 yr**	**1 – 3 yr**	**4 – 7 yr**	**1 – 3**	**4 – 7 yr**
Bracken cover (%)	0.003	0.136	0.141	**0.387***	-0.195	0
Grass cover (%)	**-0.446****	**-0.454*****	-0.106	**-0.496****	-0.007	0.0238
Bare ground cover (%)	0.222	**0.398****	0.092	**0.397***	-0.093	0.137
Grass height (mm)	0.003	-0.189	**0.261****	-0.346	0.184	0.122
Bracken height (mm)	0.254	0.241	**0.196***	0.348	-0.055	0.022

Overall, the mean density of oak trees (trees per ha^{-1}) was significantly higher in exclosed compared to open plots (df = 3, W = 16, P = 0.028). Whilst there was no difference in density for younger trees (0 – 3 years P = 0.685, 4 – 7 years P = 0.060), the density of the older oak saplings (8 – 12 years) was higher in ‘exclosure’ (P = 0.028) (Figure 5.7).

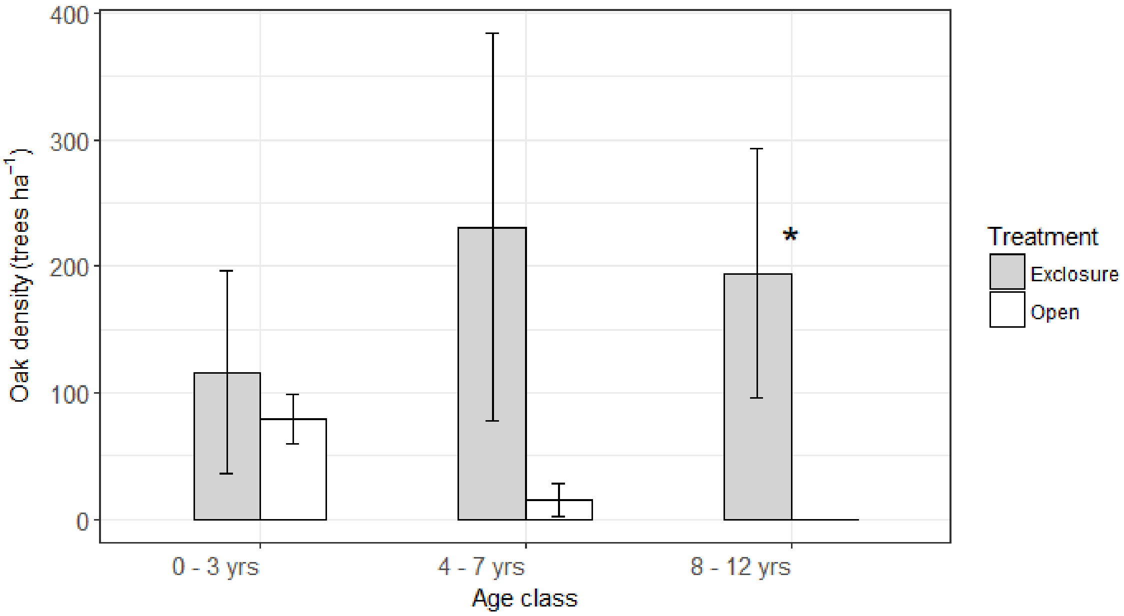

Figure 5. 7 – Mean density (trees per ha^{-1}) of native oak recruits (*Quercus robur, Quercus petraea*) in exclosure and open pasture treatments for 0 – 3, 4 – 7 and 8 – 12 yr age classes at Piles Copse, Dartmoor, southwest England. Exclosure plots represent areas of no stock grazing, open plots were subjected to grazing (summer = 0.201 LSU [ha^{-1}], winter = 0.012 LSU [ha^{-1}]) principally by cattle and sheep. Statistical difference ($P \leq 0.05$) was determined using Wilcoxon exact rank sum test (W). n = 4 (df = 3) and denoted * ≤ 0.05 , ** P ≤ 0.01 , *** P ≤ 0.001.

The survival of planted 2 year old native oak trees in exclosure plots was 55% higher after just 7 months than that observed in open plots (Figure 5.8). Oaks in exclosures experienced higher annual shoot growth but no difference in the occurrence or quantity of late summer 'lammas growth'. Trees in exclosures had a higher average tree condition score and leaf size compared to trees subject to grazing, where the mean sward height was 80mm lower than in livestock excluded plots.

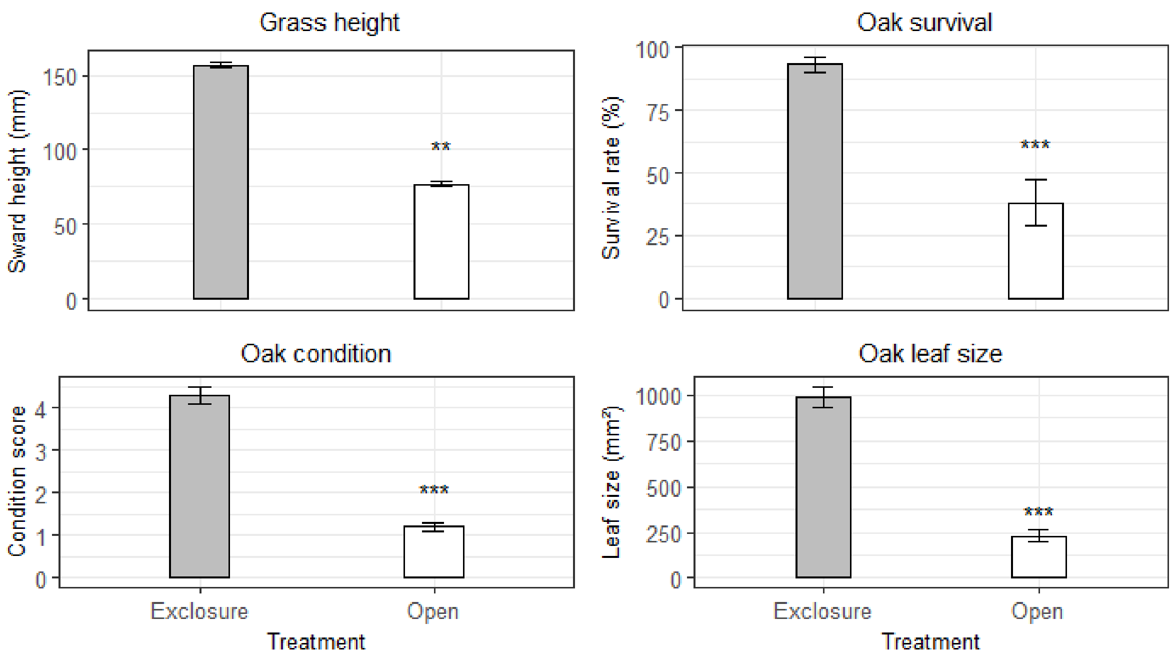

Figure 5.8 – Mean (± SE) survival (%), oak condition (condition score), leaf size (mm^2) and grass sward height (mm) of 2 year old native oak trees (*Quercus robur, Quercus petraea*) planted in 'exclosure' and 'open' pasture plots at Dendles Waste, Dartmoor, southwest England. Exclosure plots represent areas of no stock grazing, open plots were subjected to grazing (0.080 LSU [ha^{-1}]) by sheep, ponies and deer. Oak survival is defined as the percentage % of trees still alive. Leaf size is the length x width at the widest point of three random leaves, only complete undamaged leaves were chosen for this parameter. Grass sward height was measured around each colonising tree ($15cm^2$). Tree condition score (5 = no grazing damage, 1 = severe grazing damage – see table a.1). Grass height, survival, condition and leaf size were recorded in late summer 2018. Statistical difference ($P < 0.05$) was determined using Wilcoxon exact rank sum test. n = 9 and denoted * ≤ 0.05 , ** P ≤ 0.01 , *** P ≤ 0.001.

Oak recruits in exclosure plots experienced significantly greater current year shoot growth than trees in open plots (Figure 5.9). Whilst there was no difference in shoot growth in late spring (May) by August shoot growth in exclosure plots was almost three times that experienced in open plots, where current year shoot growth diminished from the previous month.

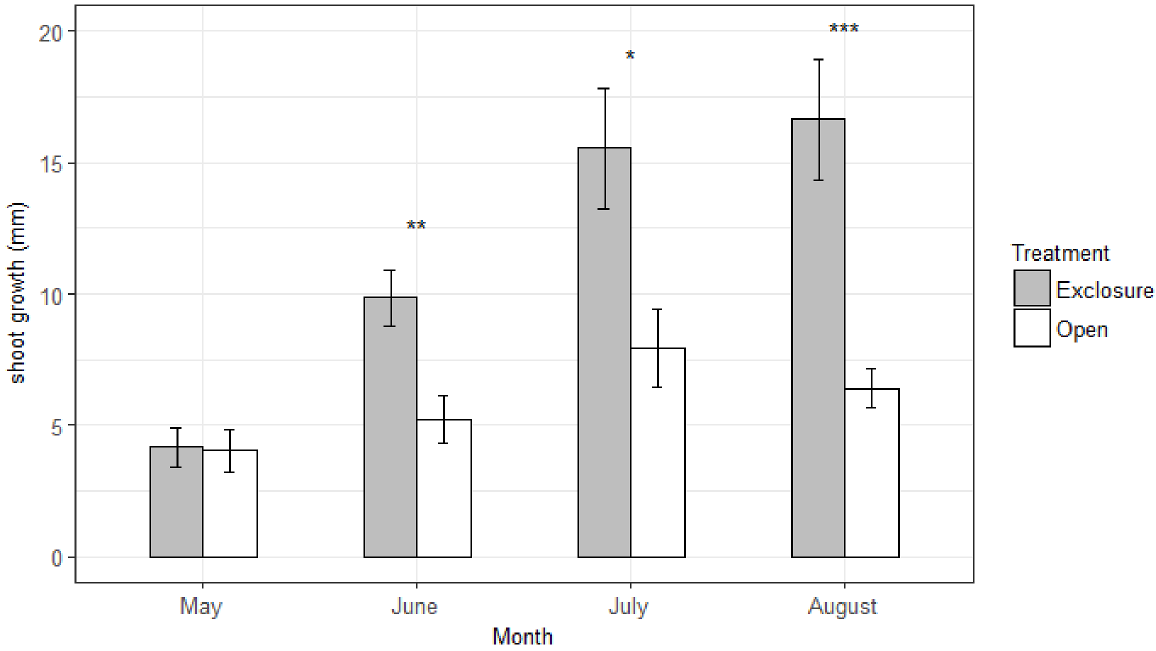

Figure 5.9 – Mean current year shoot growth (mm) of 2 year old planted native oak (*Quercus robur*,*Quercus petraea*) in upland pasture plots ‘open’ to and ‘excluded’ from grazing in Dartmoor, southwest England. Exclosure plots represent areas of no stock grazing, open plots were subjected to grazing (0.080 LSU [ha^{-1}]) by sheep, ponies and deer. Statistical difference was determined using Wilcoxon rank sum test ($P < 0.05$). n = 9 and denoted * ≤ 0.05 , ** $P \leq 0.01$, *** $P \leq 0.001$.

Mean total dry mass of planted 2 year old oak trees was greater in ‘exclosure’ (no grazing) compared to ‘open’ pasture (0.80 LSU ha^{-1}) plots (Table 5.5). Interestingly, the dry mass (g) of all tree parts: i.e. shoot, leaf, main root and fine roots was lower in plots open to livestock. The main root dry weight was four times lower in grazed plots compared to exclosure and resulted in significantly reduced root: shoot ratios.

Table 5.5 – The effect of grazing by livestock on mean dry weight and root:shoot ratio of two year old native oak trees (*Quercus robur, Quercus petraea*) planted in upland pasture at Dendles Waste, Dartmoor, southwest England (n = 9). 'Exclosure' represents areas of no stock grazing, Grazed 'open' areas were accessible to grazing (0.080 LSU [ha^{-1}]) by sheep, ponies and deer. Significant difference ($P < 0.05$) between treatments via Wilcoxon exact rank sum test and denoted in bold.

	Sapling dry weight (g)				
	Exclosure		**Open**		
	Mean	**SE**	**Mean**	**SE**	***P* value**
Total mass (g)	2.715	0.318	0.881	0.066	**<0.001**
Shoots (g)	1.000	0.090	0.474	0.047	**<0.001**
Main roots (g)	1.353	0.159	0.373	0.048	**<0.001**
Fine roots (g)	0.081	0.015	0.017	0.003	**<0.001**
Leaves (g)	0.294	0.032	0.028	0.009	**<0.001**
Root: shoot ratio	1.430	0.162	0.841	0.096	**0.003**

5.4. Discussion

Understanding the practical constraints on native upland woodland establishment is of high priority considering its potential carbon sequestration, NFM and other ESS benefits (Griscom et al. 2017; Nisbet et al. 2011). We observed oak sapling recruitment within upland acid grassland and bracken communities were largely restricted to (west facing) valley slopes with naturally freely draining podzolic soils. Oak saplings were most frequent in the infertile sites, with lower pH, perhaps reflecting lower nutrient (particularly nitrogen) concentrations and reduced competition with grassland swards (Hodge & Harmer 1996). Whilst these upland pasture slopes represent ideal locations for upland afforestation and flood water attenuation (Averis et al. 2004; Murphy et al. *submitted*), results show oaks natural recolonization potential here is severely limited by grazing livestock and dispersal distances.

Vectors of establishment such as jays and squirrels can transport acorns at high densities (400 per ha) and over long distances (0.5 – 1.5km) (Bossema 1979; Worrell et al. 2014). However, little establishment was found more than 25m (25 – 100m) from a putative parent tree, suggesting that either this essential dispersal service was lacking or seedlings are unable to establish in these areas (see also Palmer et al. 2004). Even in the absence of livestock and assuming for earliest oak reproductive ability at 20 years old (Shaw 1974); based on a recolonization distance limit of 75m (furthest sapling) from the parent tree, maximum treeline advancement rate would not exceed 3.75m y^{-1} (i.e. 375m/100 years). This figure moreover, does not account for the well-known impact of climate variation on mast events and reproductive output (Shaw 1974; Hanley et al. 2019). Indeed, viable seed source is the most dominant factor determining oaks establishment (Hodge & Harmer 1996; Harmer et al. 2005). Consequently, it seems highly unlikely that natural oak recruitment could extend woodland cover into upland pastures at the rate currently needed for ACC-mitigation.

The poor performance and reduced survival of oaks subject to grazing by livestock represent additional challenges for woodland establishment in the uplands. Oaks growth form renders saplings particularly vulnerable to complete defoliation by ungulates (Palmer et al. 2004), limiting significantly their regeneration potential in grazed areas (Palmer et al. 2004, Truscott et al. 2004). The study however suggests variation within grazed areas; oak saplings developed faster in extensive (commons) pasture compared with enclosed pasture systems. This is associated with increases in the occurrence and extent of bare ground, and the height of grass and bracken, likely reflecting enhanced protection from bracken (*Pteridium aquilinum*), gorse (*Ulex spp)* and bramble (*Rubus fruticosus)* shrubs present here.

Like other unpalatable species brackens high toxicity may offer some protection from herbivore attack (Vera 2000; Kuiters & Slim 2002; Bakker et al 2004), with grazing low enough within bracken swards for saplings to persist and escape browsing (Barkham 1978). The association between sapling performance and bare ground however suggests, only where clumps of bracken and other shrubs are sufficiently dense to prevent or reduce grazing across seasons is protection effective. Indeed, only in the middle of dense bracken clumps are oak shoots not browsed back in spring when trees are most palatable (Barkham 1978).

Findings suggest the protection afforded to saplings by dense foliage is most beneficial for older saplings (>3 years old). Dense bracken can smother seedlings, reduce light levels and may support higher populations of acorn predators (Humphrey & Swaine 1997; Janzen 1971). Whilst dense foliage may hinder early seedling establishment, evidence from enclosed pasture and short-term livestock exclosure suggests even young (< 4 years old) saplings require some level of protection to survive in grazed swards. Where vegetation is short, unprotected (in 'open' areas) the few surviving planted juvenile (2 years) saplings experienced large reductions in root mass, likely reflecting diminished energy capacity after defoliation (leaves and shoots). Diminished root systems can hamper young saplings ability to escape intense root competition from grasses (Harmer & Robertson 2003). Indeed, whilst the disturbance dynamics afforded by low or moderate grazing can be beneficial for the early establishment of oak saplings, without subsequent protection from grazing, their subsequent survival and performance is severely diminished (Grime 1977; Uytvanck et al. 2010; Bobiec et al. 2018). Consequently the reported positive and negative effects of unpalatable species on oak recruitment (Vera 2000; Kuiters & Slim 2003; Harmer & Morgan 2007), likely reflects oaks ontogenetic dependent relationship with surrounding vegetation.

Results suggest that whilst livestock browsing limits tree survival and subsequent performance, perhaps counter-intuitively, the total absence of browsing livestock may also be unhelpful for initial oak establishment. Dense stands of unpalatable vegetation types (e.g. bracken), associated with grazing cessation, provide no benefit during the earliest life stage (0 – 3 years) of oak. The successful establishment of oak woodland in upland pastures will require careful livestock management specific to tree life-stage requirements. To ensure natural regeneration of oak close to the woodland edge, grazing should be maintained immediately prior to establishment, and once a significant number of oak saplings are present, likely after a mast event and/or the occurance of acorn scatter hoarding by birds and rodents, cease temporarily for a period of at least 12 years to ensure establishment. Planted trees would benefit from careful site selection, with older (4 – 7 years) oak trees in particular planted where tall and dense bracken provide trees with additional performance benefit and protection from livestock grazers. Careful site selection may allow trees to be planted without the need for visually intrusive tree guards, a major barrier to the social acceptance and environmental sensitivity of new woodlands (Farjon & Hill 2019; Crouzeilles et al., 2020).

This study supports earlier recommendations that herbivore exclusion (or at least a major reduction in densities) is an essential prerequisite for oak woodland expansion (Kelly 2002; Truscott et al. 2004). However, perhaps the character of grazing is as crucial as the overall intensity. Temporary cessation in grazing during oaks crucial early development (first 12 years) would aid establishment before livestock could, if required, be returned for ‘wood pasture’ grazing. Such a model recognises the ontogenetic dependence of oak establishment, would allow farmers and grazers to maintain livelihoods and help balance competing agricultural and conservation interests.

In the context of increasing policy impetus for woodland expansion in upland areas (Defra 2018a, 2019; Committee on Climate Change 2019); the limitations to recruitment potential highlighted here, represent significant constraints to native oak woodland establishment. It seems clear that to meet (re-)establishment targets for ACC mitigation, native tree planting schemes could be strategically placed along catchment headwaters of upland river valley slopes. This would not only aid the successful establishment of planted saplings whilst providing rapid flood mitigation (Marshall et al. 2014; Murphy et al. 2020), but together with targeted grazing management, enhance the potential for further natural establishment of native oak along upland valley corridors. Such an approach would maximise oaks regeneration niche whilst recognising its poor advancement within upland areas.

Chapter 6.

General discussion, synthesis, and a new research framework

Anthropogenic climate change (ACC) poses a fundamental and existential crisis for both human society and the natural world (Parmesan & Yohe 2003; IPCC 2014a; Steffen et al. 2018). Successful and effective mitigation demands urgent and improved understanding of both the viability of potential mitigation and the temporal and contextual constraints on implementation (Thomas et al. 2014; Griscom et al. 2017). Natural climate solutions to ACC are increasingly gaining prominence for effective mitigation, due to their lower cost and provision of multiple associated environmental and societal benefits (Iacob et al. 2014; Burgess-Gamble et al. 2017; Griscom et al. 2017; Lane 2017). The (re-)establishment of woodlands is receiving considerable attention due to their potential for carbon sequestration, biodiversity, natural flood management (NFM) and other ecosystem services (ESS) (Iacob et al. 2014; Griscom et al. 2017; Bastin et al. 2019; Evaristo & McDonnell 2019). The UK uplands cover around one third of the UK's land area, and are integral for the delivery of multiple provisioning, regulating and cultural services (Holden et al. 2007; Curtis et al. 2014). The uplands, as source of 68% of the UK's freshwater (Van der Wal et al. 2011), and an estimated minimum 40% of total UK soil carbon stocks (Bradley et al. 2005), represent areas of high climate mitigation potential. The sheer multiplicity of ESS that are, or could be, provided by the uplands means that there is greater opportunity for net gain in ESS in comparison to the lowlands (Bonn et al. 2009; Reed et al. 2009; Curtis et al. 2014). Projected precipitation increases and soil compaction linked to historic degradation, however, means these areas currently pose considerable flood risk to downstream communities, placing growing importance on land management decisions (Sansom et al. 1999; Murphy et al. 2018). As areas of marginal agricultural value, most reliant on public subsidy and with low tree cover (Hanley et al. 2007; Bunce et al. 2018a), UK upland areas represent ideal areas for woodland expansion. Cessation of EU agricultural payments (CAP), alongside relatively ambitious climate change commitments and UK environmental policy, suggest there is considerable and imminent prospect of change in upland management (Bunce et al. 2018b; Defra 2018a; Sandom et al. 2018; Climate Change Committee 2019). Consequently, the largely treeless UK uplands offered an ideal test case to examine the benefits of native oak woodland establishment for ACC mitigation and the constraints posed. The thesis set out (using Dartmoor as a test case) to: 1) Evaluate the impact of oak woodland establishment on the recovery of soils in upland catchments for the potential mitigation of downstream flood risk associated with ACC; and 2) assess the constraints on oak woodland establishment associated with increased soil moisture, livestock grazing, and the potential for oak woodland expansion in UK upland pastures.

6.1.1. Defining the problem – changes in precipitation in the UK uplands

Chapter two examined changes in precipitation trends between multiple upland and a lowland site. The thesis evidenced the enhanced sensitivity of upland sites to ACC (Burt & Holden 2010; Murphy et al. 2019). Significant long term (1879 – 2012) increases in spring and autumn precipitation and no significant change in summer precipitation, represent significant deviations from the future drying projected for summer and growing seasons by the latest probabilistic projections (UKCP18) (Murphy et al. 2018). Greater deviation in upland areas between projected changes (UKCP18) (%) and observed precipitation, highlights the potential uncertainties in future plant productivity and the difficulty in making 'future proof' land use decisions in the UK uplands (House et al. 2010).

Moreover, the study highlights that the interaction between ACC and natural atmospheric and oceanic cycles (such as NAO and AMO) will determine future climate. The evidenced connection between AMO and European climate (Sutton & Dong 2012; Osso et al. 2018), and the amplification of AMO post industrialisation (Moore et al. 2017), suggest a substantial role for Atlantic oceanic temperatures in the character of future ESS provision in the UK uplands. Despite expected shrinkage in the bioclimatic envelope for UK mire, increases in summer precipitation since the 1960s (linked to +AMO), have increased peatland CO_2 sequestration, including in climatically marginal (southwest England) ‘active’ upland mire sites (Billett et al. 2010; Clark et al. 2010; Lunt et al. 2019). Additionally, AMO-NAO coupling is shown to have substantial influence over forest productivity (Wang 2011; Madrigal-Gonzalez et al. 2017). The importance of soil moisture on climate-feedbacks and the terrestrial carbon sink (Seneviratne et al. 2010; Green et al. 2019), means interaction between natural atmospheric-oceanic cycles and ACC will likely determine the relative merits for competing land uses and woodland character over time. Such temporal dynamics exemplifies the need for improved understanding on the influence of natural cycles on upland ACC climate forcing over the next half century, when land use decisions for climate mitigation are so critical (Griscom et al. 2017; Steffen et al. 2018).

The latest climate change models project increases in winter precipitation (Murphy et al. 2018). These models are supported by the findings from observed precipitation trends (Chapter two) along with evidence of increases in river floods in the UK and northwest Europe (Lavers et al. 2011; Blöschl et al. 2017). Increases in river flooding are linked to advancement in the timing of soil moisture maxima (Blöschl et al. 2019), and combined with autumn, winter and spring precipitation trends suggest upland soils, particularly along western coasts will become wetter and for longer. This improved understanding of the seasonal uncertainty within climate projections, set out in chapter two, can be used to help refine the likely direction of climate change pressures on the land management, alongside the soil and hydrological drivers of catchment management.

6.1.2. A natural flood management (NFM) solution?

Chapter three showed that native woodland establishment in upland pasture areas offers a viable, and potentially rapid (7 – 15 years) means to reduce surface soil compaction (2.4-fold) and bulk density (1.2-fold) with concomitant benefits to Ksat (1.8-fold increase) and 'wetness threshold' (1.6-fold increase)(i.e. soil water holding capacity). In improving the soil hydrological functioning of soils, native woodland establishment may offer an effective tool for the natural management of downstream flood risk expected with climate change in the UK uplands. This is the first study to measure comparable differences in the water infiltration rates of soils between establishing native woodland and pasture sites across multiple (more than two) UK upland catchments. Catchment-specific differences highlight the importance of local soil conditions and consideration of past and present management, soil type and catchment location when planning new woodland NFM schemes.

The specificity of hydrological change and the multitude of potential mechanisms on soil hydrology and floodrisk (Figure 3.6) suggests careful site selection and detailed scoping is needed to maximise potential flood-mitigation value. The strategic placement of native woodland will be critical to reduce surface runoff on site, but crucially, 'soak up' runoff generated further up the hillslope (Chandler et al., 2018), and reducing surface run-off generated by both saturation excess (run-off when soil saturated) and infiltration excess (rainfall intensity greater than infiltration rate). Flooding can result from both these processes (individually and in combination), and the flood mitigation potential of native woodland will be defined by its placement (soil type, soil condition, slope angle), character (extent, tree density, tree species, management), and the seasonal climate (rainfall patterns, evaporation potential) at respective catchments. Long term monitoring of river flows in upland catchments should be conducted to clarify and refine realistic NFM outcomes associated with different types of woodland establishment.

Site choice is likely to be particularly important and difficult in the UK uplands, considering the multiple stakeholder interests and ecosystem service trade-offs (Bonn et al. 2009; Reed et al. 2009). Further to this, the dominant impact of land use on soil hydrology indicated by this and previous studies, suggests careful management and communication will be required to ensure that NFM benefits are realised for new woodland schemes established on agricultural land. Indeed, the rapid soil recovery recorded in this study was from establishing woodland where livestock were excluded. Soil recovery and potential NFM is lower in wood pasture compared to livestock excluded woodland, particularly where animals are enclosed and/or kept in high densities (Sharrow 2007; Chandler et al. 2018). The dominance of land-use is highly relevant considering the desired integration of woodlands and forestry within agriculture and farming, and the future implementation of new environmental land management schemes (Defra 2018a; Burton et al. 2019; Rayment 2019). Impacts will be particularly significant in marginal upland areas, where management decisions rely on interaction between policy and farm profitability (Hanley et al. 2007; Pakeman et al. 2018). Moreover, results in this study suggest the most degraded sites with highest soil compaction may require mechanical pre-treatment remediation, suggesting native woodland establishment may not always be the cheap or simple option typically characterised (Lane 2017). Consequently, authorities and land managers should consult both woodland and soil expertise as an essential component of the scoping exercise before woodland NFM schemes. Such consultation would help define remediation requirements, maintenance costs and management recommendations for schemes. Adoption and uptake of schemes by farmers and landowners however will require incentivisation, financial aid, and in certain circumstances the maintenance of agricultural activity to maintain income.

In the largely unenclosed UK uplands, the creation of 'wood pasture' by leaving areas to succeed to unpalatable vegetation such as bracken and gorse 'scrub' could exclude grazing livestock and protect developing trees. The NFM benefits (soil recovery) of such an approach, alongside compromises between agricultural and conservation outcomes, could allow for a 'new pastoralism' (Jepson 2019) in the uplands. A dynamic woodland pasture model would leave room for multiple stakeholder interests, provide NFM and help balance the provision of competing ESSs.

In summary, chapter three advances potential catchment management through improved understanding of the viability, and variability of land-use change effects on soil systems for hydrological change. In particular, the thesis furthers knowledge on the impacts of upland native woodland establishment and scrub development on soil compaction, macro-porosity, structure, organic matter, water saturation, and water infiltration; critical components of soil systems and mechanisms of hydrological change for driving flooding hydrology within catchments.

6.1.3. Soil moisture and the future resilience of upland oak woodlands

Findings from chapter four suggest UK native oak (*Quercus robur* and *Quercus petraea*) are constrained by saturated soil conditions in the period immediately following acorn germination. In flatter areas, plateaux, or often poorly drained upland sites, the increased rainfall projected with ACC and observed in this study (Chapter two) suggest conditions will increasingly favour mire and wet woodland development over oak woodland establishment (Lunt et al. 2019; Murphy et al. 2019). Impacts will be most pronounced on windward western upland coasts where precipitation increases have been greatest (Burt & Holden; Murphy et al. 2019). Findings show naturally freely draining valley slope sites, where surface soil compaction has increased surface soil run-off, should be prioritised for upland oak establishment. On freely draining sites increases in precipitation will likely be positive for oak establishment, where competition for water by grasses can be a significant constraint on sapling performance and survival (Hodge & Harmer 1996; Löf & Welander 2004; Collet et al. 2005).

The importance of soil moisture on oak establishment suggest that increases in upland rainfall will be a key driver of future ESS provision in the UK uplands (Curtis et al. 2014; Murphy et al. 2019). The variability in soil moisture tolerances between oak provenances from different European regions and countries (Jensen & Hansen 2010; Arend et al. 2011) suggest mixed-origin oak in planting schemes would improve future resilience (Sgrò et al. 2011; Breed et al. 2013). However, the differential waterlogging tolerance between UK native oak species suggests there is a high-degree of variance within local provenance native UK *Quercus*. Although predictive provenancing for new woodland planting schemes is considered a last resort by some, due to limitations of selection criteria and uncertainties in future climate (Thomas et al. 2014; Whittet et al. 2017); new woodland schemes should use both native oak species (*Quercus robur* and *Quercus petraea*) from a range of local provenances, alongside a high mix of other native tree species to improve the capacity for adaption. This strategy would maintain both local adaptation to maritime climatic conditions and genetic diversity, and conserve the potential of upland 'Atlantic' oak woodlands to face future climate changes. Such an approach offers an ecologically sound step towards increasing the future resilience of oak woodlands (Mitchell et al. 2019). Focussing on connecting existing woodland fragments and ensuring a high species mix within new woodlands would also improve resilience (Sgrò et al. 2011; Dawson et al. 2013; Thomas et al. 2014).

In chapter four, the likely impacts of climate driven changes in soil hydrology on land/management were explored by examining native oak tree ecological and physiological soil moisture requirements. Oak seedlings were remarkably tolerant to waterlogging, with moderately successful first year establishment (45% survival) recorded at an average watertable depth of just 70mm below acorns. High oak seedling survival (77%) occurred when water tables were on average just 150mm below acorns. In clarifying the soil hydrological thresholds determining the establishment of oak in UK upland pasture, this chapter helps refine and define the likely success, spatial extent, character, and future pressures on native woodland establishment for NFM in upland catchments.

6.1.4. Constraints to oak establishment?

There is growing scepticism amongst some conservationists to tree planting over concerns on the character placement of potential afforestation schemes (Tree 2018; Farjon & Hill 2019). Concerns over tree provenance, tree species mix, waste associated with tree guards, and the impact on other nature conservation priorities (i.e. semi natural grasslands), raise legitimate questions over the future form and function of new woodlands (Burton et al. 2018; Farjon & Hill 2019; Morss 2019). However, chapter five shows that we cannot rely on natural regeneration for rapid establishment of oak woodland in the UK uplands given current conditions, which are typified by low oak cover and isolated seed source, low number of seed vectors, insufficient protection from livestock grazing and infrequent masting (Table A5.2). Although observed sapling densities close to existing woodlands were high enough to satisfy requirements of UK woodland creation grants (Defra 2018c), our results suggest there may be only limited potential for natural colonisation of native oak into UK upland pasture beyond existing woodland edges (< 20m).

Even allowing for reductions in grazing, absence of the vectors of acorn dispersal (corvids such as jays - *Garrulus glandarius*), and their navigation structures (trees), mean natural oak regeneration in upland pastures is severely constrained (Bossema 1979; Kollmann & Schill 1996). Indeed, it is important to note that the relatively rapid post-glacial advancement of oak in Europe (400m y^{-1}), was likely partially facilitated by humans (Haws 2004; Kremer 2015; Gieseke et al. 2017). It is recommended that oak trees should be planted (along with other native species) in livestock exclosure in upland slope sites at the headwaters of catchments to provide rapid NFM. Only where oak trees occur along valley corridors, may planting be supplemented by naturally colonising oak.

These findings are highly significant for woodland expansion and the implementation of UK climate mitigation policy whilst the UK commercial nursery sector has insufficient capacity to meet expected demand for trees (Whittet et al. 2016). Moreover, despite the growing agenda for afforestation in the UK (Climate Change Committee 2019; Defra 2018a, 2019a), there is a consistent gap between policy aspiration and actual levels of woodland planting (Burton et al. 2018). Native woodland creation in still an unattractive option for landowners. Just 13,000 hectares of woodland were created in 2018/2019, the majority quick-growing exotic conifers (Forestry Commission 2019). Money for woodland has to compete with other grant systems (Slee et al. 2007; Slee et al. 2014). Additionally, high implementation costs, reductions in land value, and loss of agricultural income make native woodland afforestation schemes particularly unattractive to economically marginal upland farms (Hanley et al. 2007; Strengers et al. 2008; Burton et al. 2018). In extensive upland pastures, the loss of pasture and restrictions against fenced exclosures in unenclosed and/or ‘common’ areas represent a significant impediment to woodland creation (Dartmoor Commons Act 1985; Commons Act 2006).

The use of protective, unpalatable (bracken) or thorny vegetation (gorse, bramble) and companion trees (blackthorn – *Prunus spinosa*, hawthorn – *Cretaegus monogyna*) may shelter developing oak trees from livestock (Vera 2000) and aid recovery of soils; it has long been quoted, “the thornbush is the mother of oak” (Authur Standish, fl. 1611 – 1615). However, results from this study suggest the protection afforded to oak saplings by dense stands of unpalatable vegetation types such as bracken is only beneficial for older saplings (4 – 7 years) in grazed pasture systems. The impact of vegetation on sapling development being specific to development stage highlights the dynamic nature of ecological processes, and the disturbance requirements for natural woodland establishment.

The establishment of woodland pasture systems, through targeted tree planting and temporary livestock exclosure to protect natural regenerating trees would offer a compromise between conservation and agricultural interests in extensive upland pastures where large scale, long-term livestock exclosure is not an option. Such wood pasture may evoke previous upland landscapes, characterised by dynamic, open mosaics of trees, heath and grassland vegetation, shown to be present across many western European areas in prehistory (Vera 2000; Fyfe et al 2013; Woodbridge et al 2018).

Tree planting schemes should favour long-term livestock exclusion where practical, due to diminished soil recovery outcomes and lower oak associated biodiversity in wood pasture (Sharrow 2007; Chandler et al. 2018; Mitchell et al. 2019). Exclosure of animals is particularly important on the most compacted slopes within headwater catchments, where the greatest run off is generated. Livestock excluded oak woodland in such areas would provide sites of enhanced natural flood management, nature conservation and foci for further natural colonisation. These areas would be limited as widespread animal exclosure in the uplands is unrealistic. Elsewhere, dynamic wood pasture systems, adjacent to these fenced areas could provide suitable niches for oak sapling development, and facilitate oak woodland expansion along river valley corridors. Suitable livestock numbers in these areas will be difficult to assess as impacts will depend on herbivore preferences (Luoto et al. 2003; Pakeman et al 2019). In this context, the grazing/browsing preferences of different livestock species will prove crucial in determining climate mitigation, nature conservation and ecosystem functioning in the uplands (Evans et al. 2015, Mitchell et al. 2017; Pakeman et al. 2019). Further research on livestock fodder preferences could help identify management policies and refine agricultural payments for natural oak establishment and ESS provision in the UK uplands.

Social and logistical barriers however are the main obstacles stopping woodland expansion in the uplands, particularly in England and Wales, where multiple, fragmented land ownership and complications around 'common grazing rights' prevent agreement (Good et al. 2002; Bonn et al. 2009; Sandom et al. 2018). These constraints highlight the importance of socio-ecological research in future restoration ecology (Burton et al. 2018; Wells et al. 2019). The social acceptability of new woodlands for both farming and recreational interests will be a key factor for future progress.

Chapter five clarifies and refines the grazing and land management impacts and constraints on native oak tree establishment in UK upland pasture. This chapter may help land managers and policy makers to plan and implement effective and timely native woodland schemes in upland pastures where this study shows they have positive impact on soil systems and hydrology with likely NFM benefits. This study recommends livestock grazing (particularly cattle) or disturbance as a potentially useful pre-treatment to open up very dense stands of unpalatable vegetation (such as bracken) and encourage the natural establishment of oak adjacent to woodland edges. Once oak saplings are present saplings will need temporary protection from livestock by fencing areas for a period of 12 years. In areas greater than 20m from the woodland edge oak saplings may require planting. Planted saplings should be protected by fenced exclosure where possible, but where not possible results indicate taller and older oak saplings (4 – 7 years) in particular are likely to benefit from strategic planting in areas of tall bracken or similar unpalatable vegetation to protect from livestock.

Negotiating a compromise between NFM and agricultural interests will be critical for effective catchment management in the UK uplands. Consequently, in showing that the land management requirements for native oak establishment vary through early life stages this chapter may help minimise the expected conflict and trade-off between potential woodland NFM schemes and existing agricultural interests such as livestock grazing.

6.1.5. Research Implications

The thesis has made a significant contribution to advancing important elements and linkages within catchment management highlighted in Figure 1.2 (duplicate below). The study in presenting recorded precipitation from upland and lowland locations alongside seasonal climate uncertainty helps refine likely seasonal flood risk patterns, confirms UK upland catchments as key areas of mitigation, and identifies aspects of climate science where greater clarity would improve NFM and wider catchment management. In examining the impact of native oak woodland establishment on soil systems and hydrological change across multiple upland catchments, this study helps elucidate the viability, variability, and temporal scope of this potential NFM land management option. Additionally, climate pressures act both directly and indirectly on flood risk, and in clarifying the threshold effects of soil moisture on native oak woodland establishment through examination of plant ecology and physiology, results from this study have the capacity to improve the success, define the character, and refine the potential spatial extent of this NFM option. Furthermore, in refining the livestock management and ecological requirements for the establishment of native oak through early life stages, the recommendations of this study may be used to facilitate the implementation, sensitive application and potentially reduce the trade-offs associated with native oak woodland establishment in UK upland catchments.

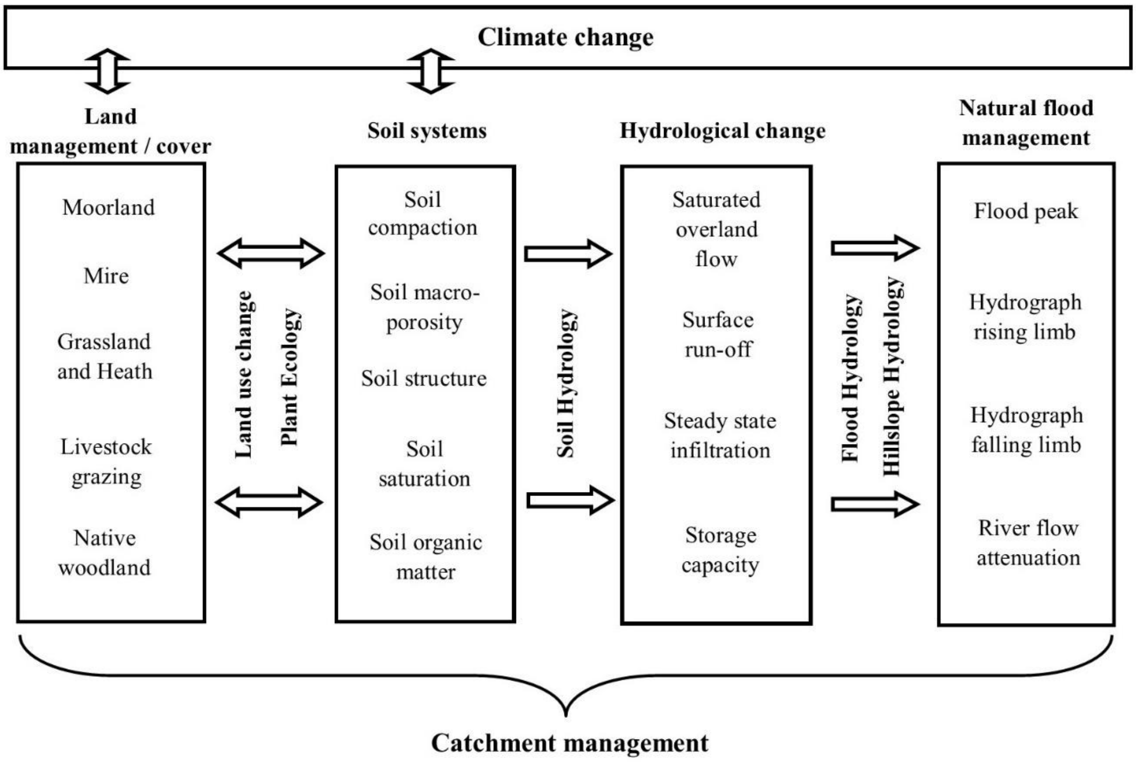

Figure 1. 2 – Importance of climate change – land management – soil systems – hydrological change – natural flood management (NFM) interactions in catchment management, providing the reasoning behind, and linkages between components of the thesis. Arrows indicate the direction of the hypothetical causal relationship. Double headed arrows indicate potential two way association.

6.1.6. UK upland afforestation

As previous upland afforestation during the 20th century has shown, unless incentives which consider multiple benefits are introduced, woodland expansion has the potential to cause substantial environmental damage in the uplands (Bunce et al 2014; Sloan et al. 2018). The design, management and implementation of woodland establishment will strongly influence their future resilience to climate changes and the ecosystem services they provide (Thomas et al. 2014; Burton et al. 2018; Brockerhoff 2017; Broadmeadow et al. 2019; Mitchell et al. 2019). Consequently, the form and function of upland afforestation could not be more important. Yet there is comparatively little evidence for the effect of native woodland expansion on ESS provision in the uplands (Burton et al. 2018; Burgess-Gamble et al. 2017). The dearth of understanding is particularly concerning considering the imminent cessation of the common agricultural policy (CAP) subsidies with the UK's exit from the European Union (Bateman & Balmford 2018; Downing & Coe 2018), the growing policy impetus for afforestation (Climate Change Committee 2019; Defra 2018a, 2019ab), and projected climate changes (Murphy et al. 2018). There is considerable political will for UK woodland expansion, with recommendations that 30,000 hectares of woodland (1.5 billion extra trees) are planted annually (Committee on Climate Change 2019). As economically marginal areas, most dependent on public subsidy (Hanley et al. 2007), upland areas represent optimal locations for their establishment. However, the growing interest in payment for ESS and the rise in agricultural diversification across Europe's traditionally pastoral upland catchments (Hanley et al. 2007; Bateman & Balmford 2018; Pettorelli et al. 2018; Sandom et al. 2018; Baldock 2019) suggests a new research framework is needed.

6.1.7. A new research framework

This study supports calls for a systematic long-term research framework to understand the interacting role of soils and NFM solutions in addressing climate risk (Rogger et al. 2017). Considering the importance of soil moisture-climate interactions (Seneviratne et al. 2010; Green et al. 2019), detailed soil surveys linking hydrological integrity and water infiltration characteristics with vegetation types in upland catchments should be undertaken. Surveys would ideally encompass sub-surface layers (>50cm depth) and be conducted across seasons, factors which are considered large drivers of soil hydrological variability (Marshall et al. 2014; Burgess-Gamble et al. 2017). Information could aid in NFM planning by identifying priority areas, remediation requirements and help tailor responses to minimise inevitable trade-offs (Iacob et al. 2014; Burgess-Gamble et al. 2017; Burton et al. 2018). Future research also needs to link changes in woodland cover with 'in-channel' monitoring of river flows at the catchment or sub-catchment scale. Results could help define the character and scale of woodland required to reduce flood risk during precipitation events of varying intensity (Burgess-Gamble et al. 2017).

Greater mechanistic detail of woodland impacts on soil recovery is required, possible mechanisms include increased water infiltration via preferential flow down coarse roots to deeper soil layers (Archer et al. 2013). Other potential mechanisms include increased aggregate stability and SOC from leaf litter inputs and root decay (Devine et al. 2014) and increased porosity (particularly macro-pores) of soils associated with altered soil biota, including deep burrowing (anecic) earthworms (Fischer et al. 2010). There are large gaps in the current functional knowledge of the hydrological impacts of many woodland tree species (Aranda et al. 2012; Chandler et al. 2018). This knowledge gap highlights the need for improved understanding on the relative balance of woodlands NFM mechanisms across seasons, how they interact, and how woodland design and placement determine effectiveness (Nisbet & Thomas 2006; Nisbet et al. 2011; Burgess-Gamble et al. 2017).

Considering the importance of soils in determining tree abundance, distribution and functioning response to ACC (Walthert & Meier 2016; Lévesque et al. 2016; Rogger et al. 2017), a long-term research framework, which examines the interacting role of climate-soils-trees in determining a range of woodland NFM mechanisms and other ESS is required. Future research should consider the interacting role of a range of mechanisms determining the behaviour and character of woodland establishment in the uplands.

The early onset of spring temperatures and extension of the growing season in Europe (Menzel et al. 2006; Schwartz et al. 2006), potentially favour increased oak growth and acorn production (Scharnweber et al. 2013; Caignard et al. 2017), and represents likely expansion in the elevation extent of the bioclimatic envelope for upland oak woodland. However, the response of trees to temperature increases in the uplands will depend on multiple factors including, soil moisture characteristics (Rozas & García-González 2012a;

Brzostek et al. 2014; Rieger et al. 2017), interactions with the soil microbial community (Brockett et al. 2012; Mitchell et al. 2012; Lau et al. 2017), micro-environment/climate (Gričar et al. 2013; Hafner et al. 2015; Suggit et al. 2018), and through interaction with a range of biotic stressors (Marçais et al. 2006, 2014; Capretti & Battisti, 2007; Bradshaw & Holzapfel 2010). Of particular importance is the uncertainty in growing season climate in the uplands (Murphy et al. 2018; Murphy et al. 2019). Research is needed that addresses a range of climate scenarios (Suggit et al. 2017), microclimate/aspect (Suggit et al. 2018), and considers multiple ACC factors (soil moisture, air temperature, CO_2) (Parmesan & Hanley 2015).

In view of the significance of soil moisture in determining root apparatus, the terrestrial carbon uptake, and mechanisms of NFM (Seneviratne et al. 2010; Rogger et al. 2017; Green et al. 2019); future research should seek to assess the character of tree development (above and below ground) in relation to soil moisture across different soil types, compaction levels, and in response to varying grazing pressures and plant competitors. Work should examine the response of a range of native tree genotypes and consider multiple ACC and management scenarios (Thomas et al. 2014; Whittet et al. 2017; Burton et al. 2018). Outcomes would allow land managers and woodland creation practitioners to effectively design planting schemes to maximise NFM and other ESS service benefits, and help government to successfully incentivise sensitive planting. Multidisciplinary research combining climate science, plant science, soil science, hydrology and social science will be essential for addressing severe climate risks associated with ACC.

A network of recently created and naturally colonising upland woodlands could be established for long term testing of ESS provision. Such a network could work with woodland creation practitioners, landowners, public bodies and NGOs. Research goals would use newly established and establishing woodlands to assess the role of character (tree species mix, density, provenance etc.), establishment method (tree guards, natural regen vs planted etc.) and placement (soils, position on hillslope/within catchment) on a range of ecosystem services and public benefits (including NFM). Additionally, the network could work directly with tree planting organisations and landowners to facilitate bespoke experimental set ups through modification of planting schemes (tree species, density, planting methods) and management (livestock grazing etc.). Such a network would help satisfy the increasing need to link woodland restoration research with practice (Thomas et al. 2014; Wiens & Hobbs 2015; Miller et al. 2017), return potentially sizable research outcomes, and help facilitate climate mitigation and enhanced ESSs in the UK uplands.

Appendix 1 – Chapter 2 supplementary information

Table A2.1 – Changes in the location and instrumentation of weather stations used in trend analysis. Details of weather stations was obtained from the National Meteorological Archive (Met Office, 2018).

Climate record	Change	Date
PLY	Location and instrumentation	1940
COW	Instrumentation	1991
DCF	Instrumentation	1961
PRT	Location and instrumentation	2009
HRR	No change	-
WHR	No change	-
DBW	No change	-

Table A2.2 – Deviation between 'observed' and median 'projected' (UKCP18 - 25km resolution) changes (%) in average annual and seasonal precipitation totals by 2040 - 2069 for lowland and upland locations (observed change (%) - projected change (%)). Details as for Table 5, but refers to 2070 – 2099 and RCP 6.0 and RCP 8.5 climate change scenarios.

	Lowland		Upland			
	PLY		COW		DCF	
Season	RCP 6.0	RCP 8.5	RCP 6.0	RCP 8.5	RCP 6.0	RCP 8.5
Spring	▲17	▲17	▲24	▲24	▲23	▲23
Summer	▲21	▲26	▲24	▲29	▲21	▲27
Autumn	▼1	▼1	▲11	▲11	▲7	▲6
Winter	▼7	▼11	▲8	▲5	▼4	▼7
Annual	▲3	▲3	▲13	▲13	▲8	▲8

Table A2.3 – Deviation between 'observed' and median 'projected' (UKCP18 - 25km resolution) changes (%) in average annual and seasonal precipitation totals by 2070 - 2099 for lowland and upland locations (observed change (%) - projected change (%)). Details as for Table 7, but refers to RCP 6.0 and RCP 8.5 climate change scenarios. DCF is outside the time-period of analysis.

	Lowland		Upland	
	PLY		COW	
Season	RCP 6.0	RCP 8.5	RCP 6.0	RCP 8.5
Spring	▲15	▲15	▲30	▲30
Summer	▲22	▲32	▲37	▲46
Autumn	▲8	▲8	▲31	▲31
Winter	▼20	▼27	▲9	▲3
Annual	▲1	▲1	▲24	▲23

Appendix 2 – Chapter 3 supplementary information

Table A3.1 – Details of current (2018/2019) and previous grazing intensity for summer (May – October) and winter (Dec – March) seasons in upland catchments. Details include current (2018/2019) and previous grazing intensity in summer (May – October) and winter (December – March) seasons along four study catchments (Colly Brook, Dean Burn, Erme, Holy Brook) in Dartmoor, SW England. Grazing intensities are presented in livestock units per hectare (LSU ha^{-1}) and were calculated after discussions with respective landowners. EW = Establishing woodland, GP = Grazed pasture.

	Catchment							
	Colly Brook		**Dean Burn**		**Erme**		**Holy Brook**	
	Current grazing intensity (LSU ha^{-1})							
Land use	Woodland	Pasture	Woodland	Pasture	Woodland	Pasture	Woodland	Pasture
Summer	0	0.719	0	0.177	0	0.201	0	0.659
Winter	0	0	0	0.177	0	0.012	0	0.659
	Previous grazing intensity (LSU ha^{-1})							
Time period covered	2002 - 2016	Pre 2002	N/a		2004 - 2015		1991 - 2013	
Summer	0.287	3.932	-		0.210**		1.466	
Winter	0 (3.146*)	3.932	-		0.080**		1.466	

**March – April, ** Averaged from 2009 and 2015 audits.*

Table A3.2 - Relationship between surface sheer vane (19mm blade) compaction measurements (Kpa) and visual assessment of soil structure conducted along four study catchments (Colly Brook, Dean Burn, Erme, Holy Brook) in Dartmoor, SW England. The scale made by pairing surface sheer vane readings with field visual assessments of soil structure during field visits conducted at each catchment location in early summer 2019.

Surface soil compaction (Kpa)	Visual assessment of soil structure
0 – 30	Excellent
30 – 45	Good
45 – 60	Moderate
60 – 90	Moderate to Poor
90 – 130	Poor
130+	Very poor

Table A3.3 – Correlation between the slope angle of catchment sites and saturated hydraulic conductivity (Ksat) in upland catchments. Reported are the correlation (r) and significance (P) of mean values of slope angle and Ksat in establishing woodland (EW) and grazed pasture (GP) areas along four catchments (Colly Brook, Dean Burn, Erme, Holy Brook) in Dartmoor, SW England (n = 4). Statistically significant ($P \leq 0.05$) correlation was assessed by Pearsons product-moment correlation and denoted in bold. degrees of freedom = 2.

Slope angle vs Ksat			
Woodland		Pasture	
r	P	r	P
-0.167	0.832	**0.978**	**0.021**

Table A3.4 – Difference in the physical properties of surface soils between upland catchments. Details show the mean (±SE) values of surface soil organic matter (%) (SOM), bulk density with stones (g cm^{-3})(BD), percentage of 'small stones' (%) and macro-porosity (%)(M porosity) recorded along four study catchments (Colly Brook, Dean Burn, Erme, Holy Brook) in Dartmoor, SW England (n = 12).

	Catchment							
	Colly Brook		**Dean Burn**		**Erme**		**Holy Brook**	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
SOM (%)	16.6	0.9	18.5	0.6	11.9	1.2	12.3	0.3
BD (g cm^{-3})	0.694	0.029	0.633	0.024	0.794	0.057	0.813	0.018
Small stones (%)	12.9	1.6	48.8	1.5	14.4	1.6	55.6	1.4
M porosity (%)	11.8	0.3	9.5	0.3	9.3	0.6	7.6	0.2

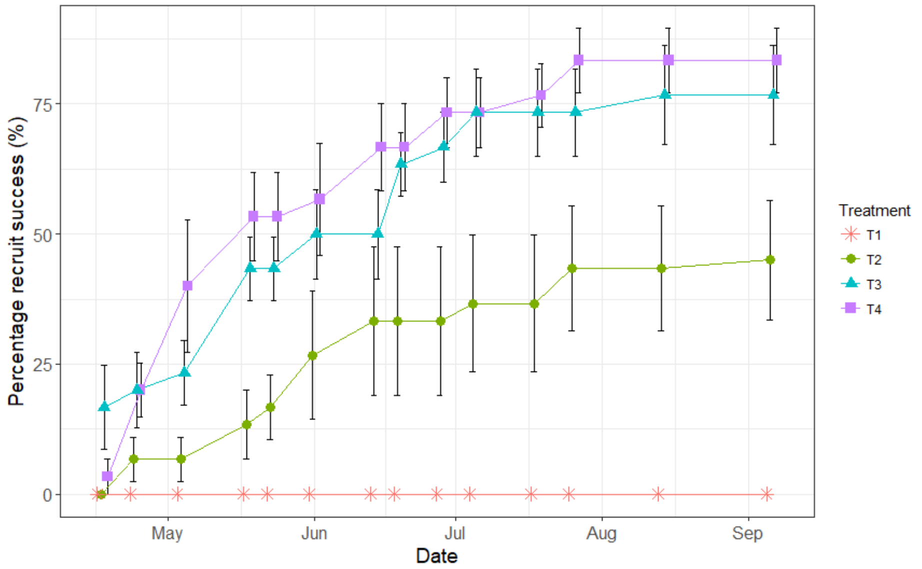

Figure A4.1 – Percentage (of total acorns planted) of native oak (*Quercus robur*) successfully emerged from acorn during summer 2017 recorded in a Plymouth University based pot experiment and subject to 'Flooded' (T1), 'High' (T2), 'Medium' (T3), and 'Low' (T4) water table (WT) treatments. T1 = WT +35mm below soil surface, T2 = WT -69mm below soil surface, T3 = WT -153mm below soil surface, T4 = WT -223mm below soil surface.

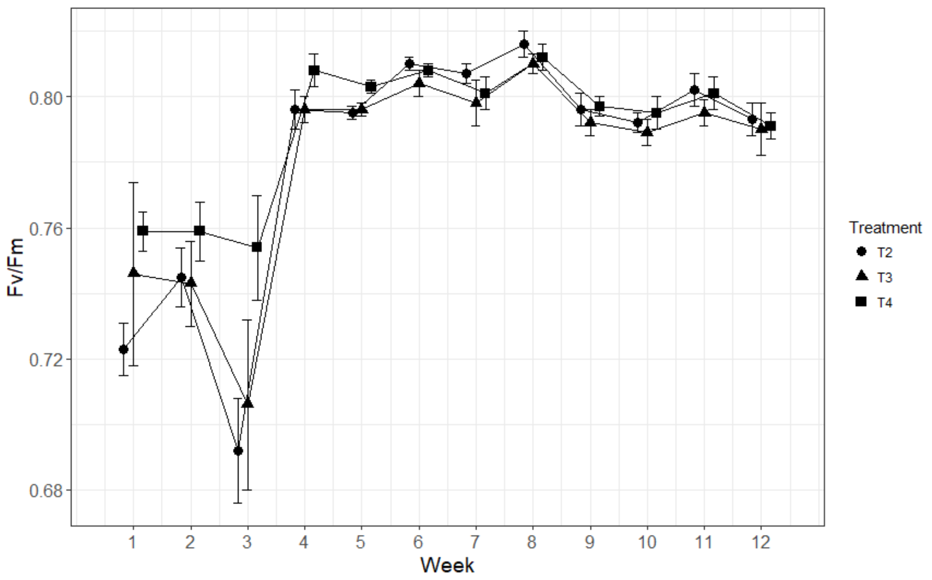

Figure A4.2 – Fv/Fm (using chlorophyll fluorescence) from the leaves of *Quercus robur* seedlings growing in high (T2 = -69mm WT), medium (T3 = -153mm WT) and low (T4 = -223mm WT) water table (WT) treatments in pots at Plymouth research facility (Scardon Garden). Fv/Fm and soil moisture were recorded alongside each other recorded over a twelve-week period between 30 May (week 1) – 15 August 2017 (week 12).

Table A4.1 – Mean vegetation cover in experimental pots planted with *Quercus robur* acorns in organic soils and subject to 'Flooded' (T1), 'High' (T2), 'Medium' (T3), and 'Low' (T4) water table (WT) treatments maintained in a Plymouth University based pot based experiment (n = 6). T1 = WT +35mm below soil surface, T2 = WT -69mm below soil surface, T3 = WT -153mm below soil surface, T4 = WT -223mm below soil surface. Floral surveys were conducted in October 2017.

	Vegetation in pot based water table experiment			
Vegetation	**Flooded WT (T1)**	**High WT (T2)**	**Med WT (T3)**	**Low WT (T4)**
Sphagnum papilosum	98	86	97	93
Sphagnum Fallax	48	57	53	30
Eriophorum angustifolium	42	28	4	1
Carex ecinata	4	5	2	0
Molinia caerulea	10	15	15	16
Agrostis canina	37	20	27	18
Potentilla erecta	1	5	6	4
Narthecium ossifragum	1	2	3	1
Juncus bulbosus	15	9	0	12
Viola palustris	1	4	5	24
Dosera rotundifolia	0	1	0	0
Pilosella officianarum	0	1	0	0

Table A4.2 - Presence of vegetation (as % occurance) recorded in 15cm^2 areas immediately surrounding juvenile (two-year-old) native oak (*Quercus robur, Quercus petraea*) planted in freely draining (FD), seasonally waterlogged (SW) and waterlogged (W) soils of upland pasture (Dendles Waste) in Dartmoor, southwest England.

Vegetation	Vegetation cover in upland pasture soils		
	Freely draining (FD)	Sesonally waterlogged (SW)	Waterlogged (W)
Molinia caerulea	38	0	81
Carex bi nervis	56	38	8
Potentilla erecta	13	42	50
Viola palustrus	0	0	79
Juncus bulbosa	0	0	44
Carex Echinata	0	0	46
Sphagnum Palustre	0	0	90
Agrostis capillaris	96	100	2
Carex flacca	0	0	0
Holcus lanatus	0	2	4
Festuca ovina	10	0	56
Sphagnum capifolium	0	0	8
Erica tetralix	0	0	2
Luzula spp	4	6	8
Polytrichium commune	0	0	44
Juncus effusus	13	29	29
Calluna vulgaris	8	0	2
Eriophorum angustifolium	0	0	8
Agrostis stolonifera	0	0	8
Galium saxatile	67	38	0
Anthoxanthum odoratum	54	100	0
Rhytidelpus squarousus	52	54	0
Vaccinium myrtillus	23	0	0
Caliaergon moss	40	23	0
Deschampsia flexuosa	4	0	0
Carex flava	0	4	13
Bare ground	23	10	0

Appendix 4 – Chapter 5 supplementary information

Table A5.1 – Tree condition score criteria used to assess 'grazing damage' on naturally colonising young (<12 years) native oak recruits.

Tree condition score	Damage to leaves and leading shoots (% of plant)
1	>75%, Signs of severe damage to stems and shoots.
2	50%, and/or signs of moderate historic damage to stems and shoots
3	25%, and/or signs of minor historic damage to stems and shoots.
4	10 %, and/or no other signs of historic damage to stems and shoots.
5	No damage

Table A5.2 – Grazing intensity in Piles copse exclosure and open plots. Reported are livestock units (LSU ha^{-1}) and the type of animal stock present.

	Exclosure		Open	
	Summer	Winter	Summer	Winter
LSU (ha^{-1})	0		0.201	0.012
Animal type	none		Cattle	sheep

Table A5.3 – Details of the intensity (livestock units per hectare – LSU ha^{-1}) and character (animal type) of grazing within Dendles Waste exclosure and open plots established in spring 2018.

	Exclosure	Open
LSU (ha^{-1})	0	0.080
Animal type	none	Sheep, ponies, deer

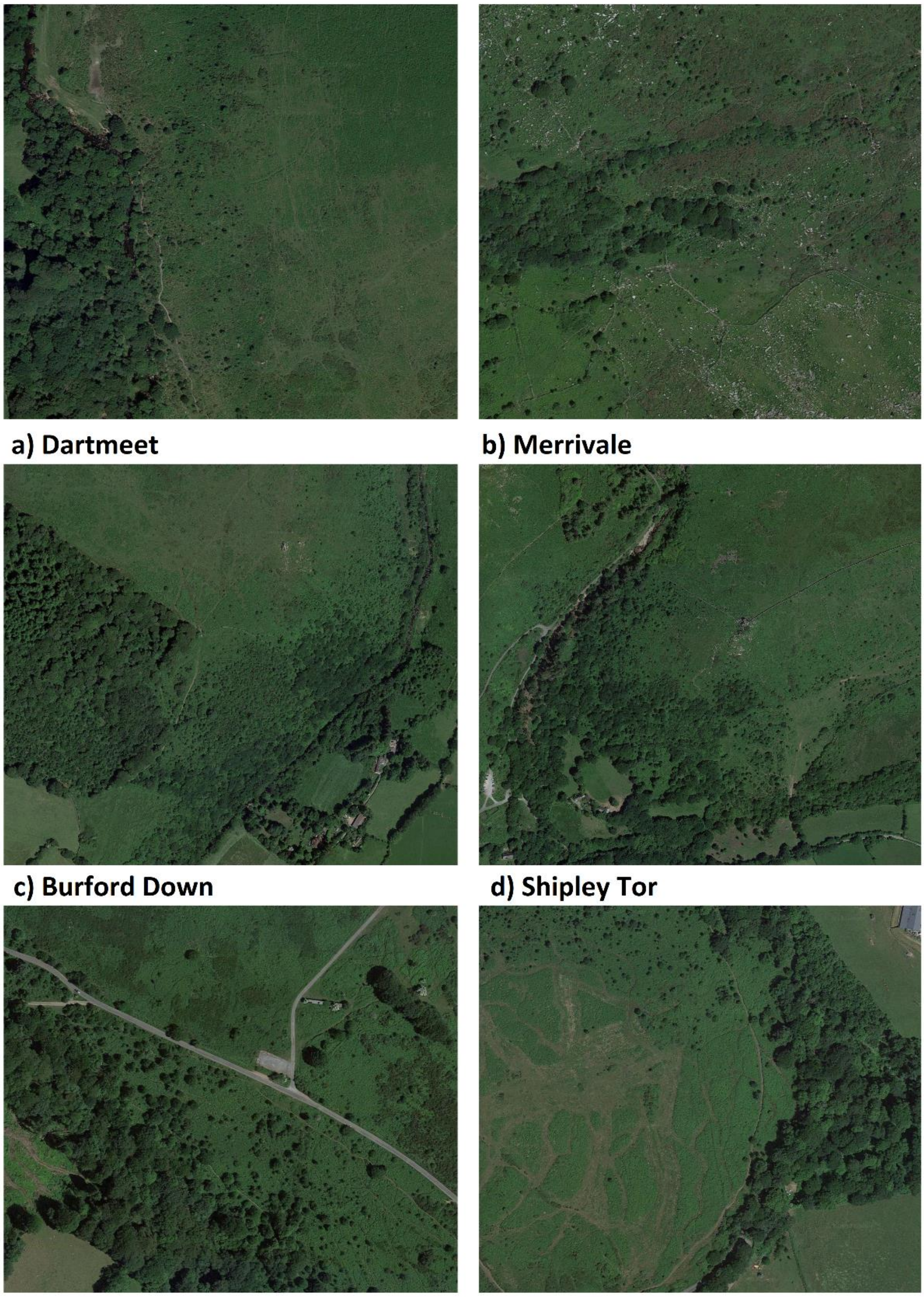

Figure A5.1 – Satellite images of six locations experiencing natural colonisation of native oak (*Quercus robur, Quercus petraea*) in the upland pastures of Dartmoor, southwest England. Sites were identified using both desktop (satellite imagery [Google 2017]) and ground-truthing walking surveys (November – April 2017).

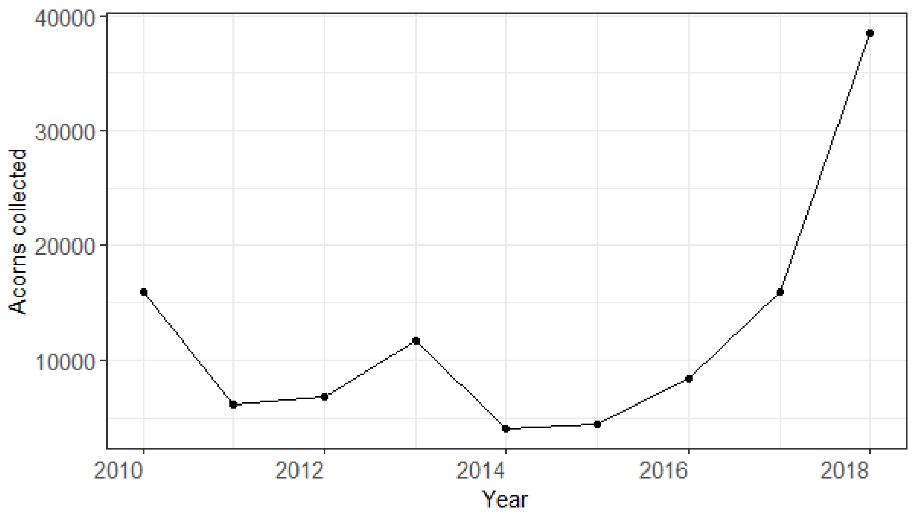

Figure A5.2 – Annual number of acorns collected during autumn in the uplands of Dartmoor, southwest England (2010 – 2018). Data represents the number of acorns collected by Moor Trees (Moortrees.org) volunteers each autumn. Acorns were collected by a small group (10 – 20 people) of volunteers across five principle locations (Shaugh prior - , New Bridge - , Hembury Wood - , Yarner Wood - , Dunsford Wood -) following the same transect walks each October.

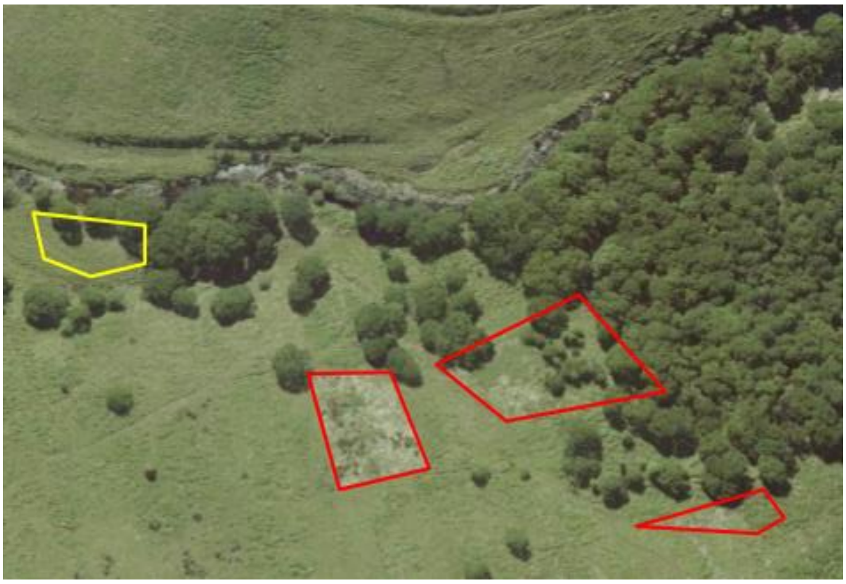

Figure A5.3 – Four livestock exclosures erected in 2006 (red) and 2011 (yellow) in the upland pastures (Piles Copse) of Dartmoor, southwest England (Howell 2013) and used in this study.

Table A5.4 – Natural colonisation of native oak in upland pastoral sites in Dartmoor, southwest England. Mean (± SE) ontology (age), dispersal (distance from woodland edge (m)), root collar diameter (RCD - mm), grazing damage (see tree condition scoring – table a.1) of naturally colonising native oak (*Quercus robur*, *Quercus petraea*) and surrounding grass (*Poaceaea spp*), bracken (*pteridium aquilinum*) and bare ground cover (%) recorded in six upland pasture sites on Dartmoor, southwestern England. n = number of oaks surveyed.

	Sites of native oak colonisation											
	Dartmeet *n = 63*		**Merrivale** *n = 35*		**Ashburn valley** *n = 17*		**Shipley Tor** *n = 18*		**Burford Down** *n = 25*		**Hay Tor Down** *n = 22*	
	Mean	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Tree age (Years)	3.0	0.2	3.5	0.4	5.9	0.7	3.6	0.4	2.6	0.2	2.2	0.2
Distance woodland edge (m)	16.1	2.2	11.8	0.9	13.6	2.3	9.8	2.4	11.7	1.4	14.9	1.6
RCD (mm)	5.0	0.6	6.4	1.1	15.1	2.2	9.3	2.1	5.4	0.4	5.8	0.7
Grazing damage (condition score)	2.9	0.1	2.7	0.1	3.0	0.1	2.9	0.1	2.7	0.1	3.0	0.1
Grass cover (%)			35	5	21	6	29	5	56	6	73	6
Bracken cover (%)			9	2	52	7	12	5	1	0	4	1
Bare ground cover (%)			5	2	24	4	14	5	5	2	11	3

Table A5.5 – Presence (✓) of vegetation surrounding (within 50cm^2 square) naturally colonising native oak (*Quercus robur*, *Quercus petraea*) saplings (<12 years old) in six upland pasture sites (Figure 5.1, Table 5.1) in Dartmoor, southwest England. n = number of floral survey replicates.

	Sites of native oak colonisation					
Vegetation	**Dartmeet** ***n = 63***	**Merrivale** ***n = 35***	**Ashburn valley** ***n = 17***	**Shipley Tor** ***n = 18***	**Burford Down** ***n = 25***	**Hay Tor Down** ***n = 22***
Festuca spp	✓	✓		✓	✓	✓
Holcus lanatus	✓	✓	✓	✓	✓	✓
Anthoxanthum odoratum	✓	✓	✓	✓	✓	✓
Phleum pratense	✓	✓		✓		
Potentilla erecta	✓	✓	✓	✓	✓	✓
Ulex europaeaus/gallii	✓					✓
Rubus fruticosus	✓	✓	✓	✓	✓	✓
Pteridium aquilinum	✓	✓	✓	✓	✓	✓
Oxalis acetosella	✓	✓		✓	✓	✓
Polytrichium spp	✓	✓				
Rhytidiadelphus squarrosus	✓	✓	✓	✓	✓	✓
Thuidium tamariscinum	✓	✓		✓		
Rumex acetosa	✓	✓	✓	✓	✓	✓
Calluna vulgaris	✓	✓		✓		
Hyacinthoides non-scripta	✓	✓	✓	✓	✓	
Vaccinium myrtillus	✓	✓		✓		
Galium saxatile	✓	✓	✓	✓	✓	✓
Agrostis spp	✓	✓	✓	✓	✓	✓
Hedera helix	✓	✓	✓	✓	✓	✓
Melampyrum sylvaticum		✓		✓		✓
Lonicera periclymenum		✓	✓	✓		✓
Conopodium majus		✓			✓	✓
Ranunculus ficaria					✓	

Vegetation	**Dartmeet**	**Merrivale**	**Ashburn valley**	**Shipley Tor**	**Burford Down**	**Hay Tor Down**
Dactylis glomerata					✓	
Veronica spp			✓		✓	✓
Viola riviniana	✓				✓	✓
Carex spp	✓	✓				✓
Lazula spp		✓	✓			
Prunella vulgaris					✓	✓
Polygala vulgaris	✓					✓
Digitalis purpurea	✓					✓
Cerastium fontanum		✓	✓		✓	
Lotus corniculatus					✓	
Dominant NVC community	**U4, U20, W23**	**U4, U20**	**U20**	**U4, U20**	**U4,U20**	**U20**

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