Climate change effects on UK woodlands: can species' interactions mitigate the impacts of increased drought?

Gregory James Harrison-Carey

Thesis submitted in partial fulfillment of the requirements of the Degree of Doctor of Philosophy.

School of Biological and Chemical Sciences,
Queen Mary University of London.

September 2015

Statement of originality

I, Gregory James Harrison-Carey, confirm that the research included within this thesis is my own work or that where it has been carried out in collaboration with, or supported by others, that this is duly acknowledged below and my contribution indicated. Previously published material is also acknowledged below.

I attest that I have exercised reasonable care to ensure that the work is original, and does not to the best of my knowledge break any UK law, infringe any third party's copyright or other Intellectual Property Right, or contain any confidential material.

I accept that the College has the right to use plagiarism detection software to check the electronic version of the thesis.

I confirm that this thesis has not been previously submitted for the award of a degree by this or any other university.

Signature:

Date:

Abstract

Anthropogenic climate change threatens the structure and function of forest ecosystems which will in turn affect the provision of goods and services. It is crucial that we are able to predict the effects that climate change will have on species so that management strategies can be put in place to alleviate these impacts. As well as the direct effects on plants of climate variables, such as increased temperatures and changes to the precipitation regime, it is thought that biotic interactions between species can modify the direct impacts. For my PhD I used a spatially-explicit individual based forest stand model, SORTIE, to consider both the direct effect of climate change, and the indirect effects of competition for light between species. I predicted that the lengthening of growing seasons caused by temperature-mediated phenological changes will: (i) give early leafing species a competitive advantage by increasing its own growth whilst reducing resources for neighbouring individuals and (ii) be a means to mediate the negative effects of drought on drought-intolerant species. My results show that plant-plant competition can be a stronger driver of species composition, with the only species to benefit from prolonged growth seasons in woodlands both in the northeastern US (Great Mountain Forest) and Southern England (Wytham Woods) being canopy species. These outcompete sub-canopy species for light, inhibiting their expansion. I provide evidence that current co-dominant drought-intolerant sycamore is significantly impacted even under the current precipitation regime, with ash becoming the dominant species at Wytham after 1000 years. Lengthened growing seasons did not mitigate the effect of drought for drought-intolerant species. Future predictions for the population at Wytham will however need to consider the impact of dieback events such as ash dieback or oak sudden death.

Acknowledgements

First and foremost I must thank my supervisor Prof. Matthew Evans, who was always available if I needed and whose patience has been second to none. Thank you to Aris Moustakas for the help with all things code or stats or anything else I needed over the years. Many thanks to Oxford University for allowing us to research at Wytham, and similarly to Forest Research for the keys to Alice Holt, especially to Sue Benham for showing me the sites and answering every question I had!

Thank you to the School of Biological and Chemical Sciences for their funding.

A special mention to all the friends I've made in SBCS who have all helped me in their own way: Joanne, Lucia, Gareth, Phil, Vicky, Louise, Clare, Eoin, Aurora, Michaela, Nana, Franzi....and no doubt more that I have missed. Thanks to Nick for all of your help with the coding in the early days and beyond, you were invaluable.

And finally none of this would have been possible without the constant support and encouragement from my amazing husband Lee. Thanks for everything.

Contents

List of Tables

List of Figures

List of Abbreviations

A1B	Medium emissions scenario
A1fi	High emissions scenario
AIC	Akaike's Information Criteria
B1	Low emissions scenario
BEF	Biodiversity and ecosystem functioning
CDF	Cumulative Distribution Function
CJS	Cormack-Jolly-Seber model
D10	Diameter at 10cm above ground
DBH	Diameter at breast height
ECN	Environmental Change Network
ECN-AH	Alice Holt dataset
ECN-W	ECN Wytham dataset
GLA	Global Light Analyzer
GLI	Global Light Index
GMF	Great mountain forest
HadCET	Met Office Hadley Centre Central England temperature eries
HadEWP	Met Office Hadley Centre England & Wales Precipitation
HSD	Honest significant differences (Tukey's test)
IPCC	Intergovernmental Panel on Climate Change
LAI	Leaf area index
NVC	National Vegetation Classification
OXF	Oxford University dataset
PFT	Plant functional type
QAIC	Quasi-Akaike's Information Criteria
SDM	Species distribution model
SPI	Standardised Precipitation Index
UKPN	UK Phenology Network

Chapter 1

General Introduction

1.1 Background

1.1.1 Climate change

Increases in anthropogenic emissions of greenhouse gases carbon dioxide, nitrous oxide and methane are changing the climate, with temperature and precipitation being the best studied affected climate attributes (IPCC, 2014). Global land temperatures are expected to rise between 0.3 and 4.8°C by 2100 with warming being highly spatially heterogeneous (IPCC, 2014) . As well as an increase in mean temperatures, the variability of temperatures will also rise leading to an increase in the frequency of extreme events such as heat waves, winter warm spells with more frost-free periods and freeze-thaw-cycles (Rahmstorf and Coumou, 2012, Barriopedro et al., 2011, Henry, 2007). Heat waves are expected to rise by a factor of 5-10 globally (Barriopedro et al., 2011) and a factor of 2 in Europe (Schar et al., 2004). Future changes in precipitation are more uncertain and less predictable (IPCC, 2014). No change of total global precipitation is predicted but temporal and spatial changes are expected with increases in higher latitudes and decreases in the mid-latitudes (IPCC, 2013). This will likely cause an increase in the number of drought events alongside the number of flood events (IPCC, 2014). The frequency and severity of droughts are expected to rise with land surface area experiencing severe droughts increasing from 10% in 2006 to 40% in 2090 and extreme droughts from 3% to 30% (Burke et al., 2006).

The latest projections for the UK climate suggests that mean daily temperatures will increase between 1.3 and 4.4°C, with summer daily maximum temperatures potentially increasing by up to 9.5°C in Southern England (Murphy et al., 2009). Precipitation is predicted to increase in the winter, from a few percent in Scotland up to a 70% increase on the west coast, however summer precipitation is expected to decrease by up to 65% in Southern England (Murphy et

al., 2009). Changes to the climate of the UK have already been recorded, with temperature increases and reductions in summer precipitation compared to previous averages (Jenkins et al., 2009). The severity and rate of these changes will have severe consequences for ecosystems globally and in the UK and predicting these effects needs to be a priority for ecologists.

1.1.2 Ecological implications of climate change

The main direct abiotic impacts of climate change that will affect plant community distributions and structures are the increase in temperature and the increase in the variability of precipitation (Boisvenue and Running, 2006, Walther et al., 2002, Thomas et al., 2004, Parmesan, 2006). The consequences of these impacts on plant communities has been investigated using three different methodologies: documenting trends which link species distributions with environmental conditions often over large, continental or global scales; observing species responses to gradual changes or extreme weather events; and finally by climate manipulation experiments which change the local environment conditions in their habitats.

1.1.3 Evidence from trends

There have been many changes to demographic characteristics that have been linked to changes in the environment, including changes to both species ranges (Walther et al., 2002, Parmesan and Yohe, 2003, Kullman, 2002, Walther et al., 2005) and community structures (Parmesan, 2006, Yang et al., 2011, Dieleman et al., 2015, Munson et al., 2012). These demographic changes have been attributed to the geographical shift of the optimal conditions for species, driving them to higher latitudes and altitudes (Walther et al., 2002, Kearney and

Porter, 2004) due to species-specific tolerances to temperature and precipitation (Mueller et al., 2005, Engelbrecht et al., 2007), with species favouring their optimum ranges (Norby et al., 2001). Many species have been shown to track the temperature increases (Kullman, 2002, Walther et al., 2005) with species colonising higher latitudes at rates estimated between 6.1 and 16.9km per decade (Chen et al., 2011, Parmesan and Yohe, 2003). Species show differential responses in the rate and sensitivity to climatic changes which drives community shifts (Kullman, 2002).

As well as distributions, changes in the physiology and functioning of species, functional types and ecosystems have also been observed. For example, a commonly recorded 'fingerprint' of climate change has been the changes in phenological events - the timing of seasonal activities in organisms - which are recorded getting earlier in many organisms (Menzel and Fabian, 1999, Walther et al., 2002, Parmesan, 2006, Parmesan and Yohe, 2003, Root et al., 2003, Menzel et al., 2006) with spring events across taxa increasing every decade by between 2.3 and 5.1 days (Parmesan and Yohe, 2003, Root et al., 2003, Ma and Zhou, 2012). This trend has been attributed to changes in mean climatic conditions, being especially correlated to rising temperatures (Vitasse et al., 2009, Polgar and Primack, 2011, Reyer et al., 2013b table 1).

1.1.4 Evidence from extreme events

The changes in community structure and functioning described above are a result of shifts in the mean values of environmental conditions, however the increase in variability may have more of an impact on ecosystem structure and functioning, species distributions and survival (Jentsch et al., 2007, Crawford, 2008, Parmesan et al., 2000). The extremes of temperature and precipitation will manifest themselves as extreme events including droughts, floods, heat

waves or early frosts. These events are detrimental to species, and dieback events attributed to extreme droughts (Allen et al., 2010, Allen, 2009, Matsuik et al., 2012, Fensham and Fairfax, 2007, Rolim et al., 2005, Suarez et al., 2004, Kurz et al., 2008), minimum temperatures in spring (Gu et al., 2008, Hogg et al., 2002) or winter (Kreyling et al., 2012, Bokhorst et al., 2010) have been observed in various global regions. As well as dieback events, events such as heat waves can alter community compositions by increasing plant transpiration and drought stress in individuals (Walter et al., 2013).

Of all extreme events, the one that will have the largest impact on temperate terrestrial plant communities will be the increase in droughts, where they occur (Rosenzweig et al., 2001, Kelly and Goulden, 2008, Allen et al., 2010), with species-specific tolerances to droughts driving community shifts (Suarez and Kitzberger, 2008). There is some suggestion that the intensity of precipitation changes could lead to a change of evolutionary force from that of competition for light and carbon to that of water (Hartmann, 2011). In the UK the predicted reduction in summer rainfall, alongside the higher temperatures, will lead to a increase in the number and intensity of droughts (Barriopedro et al., 2011), which may have serious influence on the composition of our woodlands (Broadmeadow et al., 2005, Penuelas et al., 2004).

1.1.5 Evidence from climate manipulation experiments

Climate manipulation experiments investigate the effects of the direct abiotic impacts of climate change on a much smaller scale, changing the environmental conditions that plants experience in their natural habitats. These experiments consider the impacts of climate change either in isolation or in combinations, including increased temperatures (Rustad et al.,

2001, Lin et al., 2010, Dieleman et al., 2012) and changes in precipitation (see Beier et al., 2012).

1.1.5.1 Temperature

Climate manipulation experiments have been shown that temperature regulates many biogeochemical processes including plant productivity (Rustad et al., 2001, Wan et al., 2005, Sullivan et al., 2008, Bai et al., 2013), growth (Melillo et al., 2002, Biasi et al., 2008), plant nutrient uptake (Bai et al., 2013, Qiao et al., 2015) and fine root dynamics (Rustad et al., 2001, Tierney et al., 2003). Plant biomass has been shown to increase with increased temperatures with averages between 12.3 and 19% in terrestrial plants (Kreyling et al., 2012, Lin et al., 2010), although this is dependent on the plant functional type (PFT) and latitude (Rustad et al., 2001, Lin et al., 2010) with some species or PFTs showing no change or a decrease in biomass (Saleska et al., 2002, Klein et al., 2007). Warming, however, also reduces soil moisture (Wan et al., 2005) which alongside reduced precipitation could increase the frequency and severity of droughts.

1.1.5.2 Precipitation

Experimental decreases in annual precipitation events cause a decrease in the annual net primary productivity of plants (Wu et al., 2011) and slower growth (Broadmeadow and Jackson, 2000). There is also evidence that changes in the frequency of precipitation reduces carbon turnover whilst increasing species diversity, even if the total volume remains the same (Knapp et al., 2002). Changes in precipitation are predicted to be spatially and temporally heterogeneous, for example it is projected that the UK will see drier summers (Murphy et al., 2009). Alongside the expected temperature increases, this reduction in summer precipitation

will cause an increase in the frequency of droughts, of which the consequences on plant water relations are well documented (e.g. Bréda et al., 2006, Leuzinger et al., 2005, Granier et al., 2007) with the sensitivities being species-specific based on two competing responses to drought. Anisohydric plants keep their stomata open which can lead to hydraulic failure whereas isohydric plants avoid this by closing their stomata to reduce water loss, however they can eventually face carbon starvation (McDowell et al., 2008, Sala et al., 2010). These competing drought tolerances may be drivers for community shifts in some ecosystems.

1.1.6 Biotic Interactions

Plants do not exist in isolation and so their physiological responses to climate change will not only depend on the direct abiotic effects but also indirectly through community dynamics and biotic interactions (Lortie et al., 2004, Hartmann, 2011, Thorpe et al., 2011). As shown above, changes to species composition can be driven by species-specific trade-offs to environmental conditions such as drought sensitivities or shade tolerances, however these impacts can be altered through biotic interactions (Gilman et al., 2010, Montoya and Raffaelli, 2010). These can be either advantageous or detrimental and include those with other organisms, such as pollinators, fungal mutualists or herbivores, as well as plant-plant interactions in the form of competition or facilitation (Lortie et al., 2004, Tylianakis et al., 2008).

Competition between plants is most significant during stand development when young individuals are competing for resources (Yoda et al., 1963, Luyssaert et al., 2008). The most important resource for plants in temperate areas is thought to be light, when water and nutrients are not limiting factors. This competition is asymmetric with larger trees having an

advantage over smaller ones in light acquisition through shading (Weiner, 1990, Casper and Jackson, 1997) and is the primary factor underlying forest succession theory. This theory suggests that succession is promoted through trade-offs between low light survival and high light growth, with shade-intolerant species exhibiting faster high light growth than shade-tolerant species (Kobe et al., 1995). Interactions between individuals, including competition, are expected to change as a consequence of climate change, either by the introduction to novel species into ecosystems (Alexander et al., 2015, Urban et al., 2012a) or through species-specific responses to the new environmental conditions (Northfield and Ives, 2013).

There have been many studies relating phenological events to temperature and showing that they track climate change-related temperature increases (Sparks and Menzel, 2002, Walther et al., 2002, Menzel et al., 2006, Parmesan, 2006, Schwartz et al., 2006, Jeong et al., 2011). Species will respond differently to the temperature increases and so mismatches between species will have implications for ecosystems (Visser and Both, 2005, Parmesan, 2006, Thackeray et al., 2010, Kerby et al., 2012, Tylianakis et al., 2008). Studies have considered mismatches between a diverse range of trophic levels including between plants and herbivores (Post and Forchhammer, 2008, Post et al., 2008, Visser and Holleman, 2001), plants and their pollinators (Kudo and Ida, 2013, Hegland et al., 2009) as well as animal trophic groups such as birds and their prey (Visser et al., 2012, Both et al., 2009, Burthe et al., 2012, Hipfner, 2008) and fish and their prey (Edwards and Richardson, 2004, Winder and Schindler, 2004). Studies have also considered the impact that climate change will have on plant-plant competition (van Loon et al., 2014, Sutherst et al., 2007, Miller-Rushing and Primack, 2008, Lortie et al., 2004, Brooker, 2006, Gilman et al., 2010, Adler et al., 2012), although this has not been investigated for tree populations within a forest.

One potential way that the intra-specific competition regime for light will be altered under climate change is through species-specific responses of phenology to climate change. Species that increase their growing season as temperatures rise, due to earlier budbursts and later leaf senescence, may not only get an advantage through increased productivity but also increase gain a competitive advantage to their neighbours through shading.

1.1.7 Predicting Ecological Change

Given the implications of the direct abiotic factors, such as altered temperature and precipitation patterns, on plants, it is imperative that we are able to produce accurate predictions for future population changes. These predictions will also need to consider intra-specific interactions to enable us to consider the mediation of the direct impacts as well as the effect that changes to these interactions will have. Individual-based modelling allows us to make community-level predictions from responses of individuals to environmental change (Johnston et al., 2014), whilst also allowing for the inclusion of interactions between individuals, such as competition. For this PhD I have used this methodology to investigate the role of climate change impacts on species compositions of forests. I utilise an existing forest growth model, SORTIE-ND (Pacala et al., 1996) which consists of four submodels: recruitment, growth, allometry, mortality. The model considers one source of competition between individuals - that for light - making it ideal for the prediction of the direct effects of climate change on the community structure, as well as the moderation of these impacts through competition.

1.2 Objectives

There were four objectives for this thesis. The first objective was to modify the growth function of SORTIE-ND to simulate species-specific spring phenological events (budburst) to temperature, allowing the investigation of the role of alterations to species interactions on community dynamics. The second objective was to then parameterise the forest growth model using data collected from the UK to produce a model that represents a broadleaf semi-natural ancient woodland. The third then uses this model to investigate the role of changes to competition regime for light on the UK species, whilst the fourth investigates the direct abiotic effect of drought on the species compositions by altering the mortality function of the model with species-specific drought tolerances, alongside predictions of rainfall. The final objective considers both of these climate change effects together, to investigate the modulation of drought impacts on the species structure through competition intensity.

1.2.1 Structure of the Thesis

For my thesis I used a forest growth model to investigate the two effects of climate change - increasing temperatures and reduced rainfall. This chapter outlines the background to why it is important that we investigate the impact of climate change on woodlands. In order to achieve this in chapter 2 I introduce variable budburst dates into SORTIE-ND, an existing forest growth model that was developed in the US by (Pacala et al., 1993). I combine existing predictions of future temperatures with data from budburst models to give predictions for the effect of species-specific budburst change on the community at the Great Mountain Forest. In chapter 3 I describe the parameterisation of SORTIE/UK using both existing datasets and data collected between 2011 and 2014. In chapter 4 this model was combined with species-specific predictions of budburst change for the UK species with projected temperature

changes to investigate demographic changes. Chapter 5 considers the effect of drought on the species in the model using predicted rainfall data alongside drought-induced mortality, estimated from data. In chapter 6 the combined effects of temperature and rainfall are then explored by running model simulations with both effects simultaneously, allowing me to test the hypothesis that interactions between the species (light competition) will modulate the abiotic effect of climate change for some of the modelled species.

Chapter 2

Using SORTIE-ND to investigate the role of climate change induced changes in growing season length

2.1 Abstract

Biodiversity and ecosystem structure play an important role in the provision of goods and services such as productivity, decomposition and carbon sequestration. However, biodiversity is being lost at an unprecedented rate due to forces including climate change and it is vital that we are able to predict the changes in ecosystem structures as this will have implications for their functioning. To consider the effect that a rise in temperature will have on forests, I used the spatially-explicit individual based forest growth model SORTIE-ND. Using predicted future budburst dates under two climate change scenarios I modelled the effect of species-specific changes to growing seasons on the tree species at the Great Mountain Forest, Connecticut. My model showed that the only species to respond to the changes in growth periods were the current co-dominant canopy species beech and hemlock. When compared to model runs under current climate conditions, in 1000 years beech increased its proportional representation by between 0.68% and 0.83%, representing 5480 and 4045 individuals, under climate change conditions, whereas hemlock reduced by 8194 and 7906 individuals. Since all species were modelled to increase their growth, this suggests that inter-specific interactions are a larger driver of demographic change than the direct effect of climate change. This is the first investigation using an individual based model to consider the role of plant-plant competition modifying the impacts of climate change on woodlands and has implications for future predictions of changes to biodiversity.

2.2 Introduction

There has recently been considerable interest in the relationship between biodiversity, ecosystem functioning and the provision of ecosystem services - goods and processes that have direct benefits to humans with a large range of studies, ranging from experiments to

meta-analyses (Balvanera et al., 2006, Naeem and Wright, 2003, Hooper et al., 2005, Diaz et al., 2006, Raffaelli, 2006, Duffy, 2009). This research into biodiversity and ecosystem functioning (BEF) has shown clear links between biodiversity and services such as productivity, decomposition, the regulation of climatic conditions and carbon sequestration (Diaz et al., 2006).

Currently biodiversity is being lost at an unprecedented rate, faster than found in fossil records (MEA 2005, Barnosky et al., 2011). The cause of this mass extinction has been attributed to anthropogenic drivers, one of the most important being climate change (MEA, 2005; Thuiller et al., 2005, Sala, 2000). Global surface temperatures have risen by 0.85°C in the last 100 years, and the rate of warming is increasing (IPCC, 2014). Future increases in mean surface temperature are estimated between 0.3 and 4.8°C in the next century and it is expected that there will be increases in the occurrence and duration of extreme weather events such as heat waves and precipitation events (IPCC, 2014). These changes in climatic conditions have serious implications for the biodiversity and thus the functioning of ecosystems, from local to global scales.

With this in mind it is clearly imperative that we are able to predict changes in current global diversity based on changes in climate. There are limitations to one of the most popular methods that predict species distributions, species distribution models (SDMs) which define species ranges by environmental condition, tracking the movement of species through the loss or gain of suitable (fundamental) niches. These methods focus on abiotic factors alone and do not account for biotic factors such as dispersal and interactions which will also affect the relocation of species, and have an underlying assumption that current distributions are constrained by climate (Ibanez et al., 2006, Neilson et al., 2005, Boulangeat et al., 2012).

Since climate change will cause novel conditions that are outside the range of current data, SDMs must be used with caution as they may not accurately predict new species distributions (Evans, 2012, Evans et al., 2012, Ibanez et al., 2006). An alternative approach is individual-based modelling (IBM) which is process based and in which the population characteristics are an emergent property of processes at the individual or species level (Norris, 2012). These models are generally spatially-explicit models in which neighbours interact by competition for resources.

This modelling approach has been developed over the past 50 years with some of the earlier examples being of forest growth models (Newnham, 1964, Botkin et al., 1972) and have since been applied to boreal temperate and tropical forests (Medvigy et al., 2009, Moorcroft et al., 2001, Seidl et al., 2012, Moravie et al., 1997). For this study I have used the forest dynamics model SORTIE, which was developed by Pacala et al. (1996), using data from Great Mountain Forest in North-western Connecticut, USA. In this model the life history of individuals in the forest is represented by four submodels: growth, recruitment, mortality and resource competition. The resource considered in this model is light, with individuals shading neighbours and species-specific differences in both light attenuation and shade tolerances causing interspecific competition. The amount of light that an individual receives affects both its growth and survival and so changes to the light competition could be a driver for community shifts.

In order to use IBMs as a predictive tool for climate change we must consider how it will affect individuals, which determines the response of the population. For this study I developed SORTIE to consider one of the effects that projected temperature increases will have on the forest. Temperature is one of the largest expected effects of global climate

change with ambient air temperatures expected to rise between around 1.6°C and 5.5°C in the North East of the US (Melillo et al., 2014). In plants one of the largest direct effects that this will have on is changes to phenological events (Sparks and Menzel, 2002, Menzel et al., 2006, Bertin, 2008, Richardson et al., 2013, Schwartz et al., 2006). Phenological events are controlled by complex biochemical mechanisms which are initiated by environmental conditions, and include events such as budburst, bud cessation, flowering and leaf-fall. There is some debate on which environmental conditions are drivers of phenological responses (e.g. photoperiod; Korner and Basler, 2010), but the vast majority of studies indicate that temperature is the major driving force in temperate areas (Jeong et al., 2012, Menzel and Fabian, 1999, Schwartz and Hanes, 2010, Chuine, 2010, Morin et al., 2009, Vitasse et al., 2009).

Advances in spring phenological events have been observed across many taxa, advancing between 0.2 and 5 days per decade over the last 50 years, which has been attributed to warmer temperatures (Migliavacca et al., 2012, Edwards and Richardson, 2004, Parmesan, 2006, Menzel et al., 2006, Sparks and Menzel, 2002, Jeong et al., 2011, Walther et al., 2002, Schwartz et al., 2006). There is also some evidence of autumn phenological dates being influenced by temperatures (Menzel and Fabian, 1999, Ibanez et al., 2010, Peñuelas et al., 2002, Piao et al., 2006, Julien and Sobrino, 2009) however, data are lacking for North American autumn phenology (Schwartz & Reiter 2000; Richardson 2006) and the effects of temperature are less defined than spring phenological events (Lee et al., 2003) therefore this was not considered in the scope of this study.

Changes in phenology are already considered one of the "fingerprints" of climate change, being one of the most easiest recorded and most common indicators of climate change

(Parmesan and Yohe, 2003, Morisette et al., 2009). It is thought that mismatches in phenology are causing changes in species interactions such as predator-prey or insect-plant asynchrony (Koh et al., 2004, Kiers et al., 2010, Rafferty and Ives, 2011, Bellard et al., 2012, Both et al., 2009, Post and Forchhammer, 2008, Both et al., 2006, Thomson, 2010) as well changes in interactions with their abiotic environments (Inouye, 2008). Importantly species-specific responses to temperature also alter the outcome of plant-plant competition, as the increased length of the growing season increases productivity and growth (Leith, 1974, Cannell et al., 1998, Semchenko et al., 2012, Aber et al., 1995, Goulden et al., 1996, Churkina et al., 2005), as well as potentially affecting the . Changes to interactions between species will have implications for the functioning of ecosystems (Winder and Schindler, 2004, Willis et al., 2008) as well as the distribution of species (Chuine et al., 2010).

In order to consider the effects of climate change in this chapter, and throughout the thesis, I used emission scenarios from the Intergovernmental Panel on Climate Change (IPCC, Nakicenovic and Swart, 2000). These are qualitative descriptions ("storylines") of four global and local social, economic and technological changes. The scenarios I use represent low (B1), medium (A1B) and high (A1fi) emission scenarios, with the B1 representing a global society with clean-low emission technology and the A1B and A1fi representing rapid economic growth in the next century with A1fi being predominately fossil fuel intensive and A1B using more sustainable fuel sources. The scenarios are provided with equal weight in terms of their probability of occurrence and so should all be considered as equally likely.

In this chapter I used temperature-induced budburst changes that were predicted for Harvard Forest by (Migliavacca et al., 2012) to modify the growth submodel of SORTIE in order to predict effects on biodiversity. My first hypothesis was that the predicted phenological

changes will be a driving force behind changes in forest biodiversity. I further hypothesise that those species in the forest that have the greatest advancement of budburst date will increase their abundance more than species in which phenology is relatively insensitive to temperatures changes.

2.3 Methods

2.3.1 Model Description

SORTIE is a forest gap model that was parameterised using data from Great Mountain Forest, Norfolk, Connecticut (Pacala et al., 1996). There are nine species included in the model, which represent the dominant and major subdominant species found in mid- and late-successional stands: American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carriére), sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britt.), white pine (*Pinus strobus* L.), red oak *(Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus americana* L.).

The model comprises of four submodels: resource, growth, recruitment and mortality.
A brief description of the model follows, full parameterisation can be found in Pacala *et al.* (1996).

2.3.1.1 Resource

This submodel is concerned with the light available to an individual and is made up of three parts. The size of an individual's crown is calculated using allometric equations relating tree crown diameter and depth to the diameter at breast height (DBH). The second part is the attenuation of light passing through the crown, calculated using species-specific light

extinction coefficients. Finally, the total light available to an individual is a function of the potential light available, taking into account the spatial and temporal movements of the sun, and the shading from other trees, given their size of crown and attenuation of light.

2.3.1.2 Growth

The annual radial growth rate of an individual are predicted using their DBH and the global light index (GLI). Trees under 750cm in height, increase their annual radial growth proportionally with radius where the larger an individual becomes the progressively slower as it increase in size. The annual radial increase for smaller trees is calculated as followed, following Pacala et al., (1995):

$$annual\ radial\ increment\ =\ radius\ \frac{G_1 GLI}{\frac{G_1}{G_2}+GLI} \qquad (2.1)$$

where:

G_1 is asymptotic growth rate at high light (cm yr^{-1})

G_2 is slope at 1% light (cm yr^{-1} GLI^{-1})

For trees larger than 750cm in height, there is a maximum growth annual radial increment, as per the Constant Area Increment Law (Phipps 1967), which is an annual increment of 1.5mm for a 100cm diameter tree.

2.3.1.3 Mortality

There is a stochastic mortality rate of 1% which affects adults. Senescence is also applied to adults with a DBH above one meter, in which the probability an individual dying (m_s) increases with size, at a rate that depends on the species:

$$m_s = \frac{e^{(\alpha + \beta\,(DBH - DBH_S)}}{1 + e^{(\alpha + \beta\,(DBH - DBH_S)}} \qquad (2.2)$$

where:

α and β are mortality parameters estimated from the data.

DBH_s is the height that senescence begins to affect, 1m.

Mortality for all other individuals is calculated as a function of growth of the previous five years and shading from neighbouring trees.

$$p = z^{-y * growth}$$

where:

z is the rate of mortality in shade

y is a parameter estimated from data

growth is the growth over the previous five years

2.3.1.4 Recruitment

This submodel estimates the number and spatial locations of seedlings produced by adult trees. It is a function of the tree's diameter and uses a log-normal function to calculate the density (numbers $m^{-2)}$ of seedlings at given point, i (R_i).

$$R_i = STR \sum_{j=1}^{n} \frac{DBH_j^{\beta}}{30} * e^{-0.5(\frac{\ln(d_{ij} / X_0}{X_b})^2} \quad (2.3)$$

where:

STR is the fecundity of the tree, defined as the standardised total number of recruits produced by a 30cm tree

DBH_j is the DBH (cm) of the *j*th tree, where j = 1 to n adult trees within 20m

d_{ij} is the distance between point i and the *j*th tree

X_0 is the mean of the function

X_b is the variance of the function

β is a dispersal parameter

2.3.2 Phenological Data

In SORTIE-ND all species are modelled to have the same growing season of 120 days. For this study I modified the model to include variable budburst dates for each species, in order to simulate both variability between species and to allow the simulation of climate change conditions. Baseline budburst dates, defined as 50% leaf emergence, were taken from freely available phenological data that has been recorded since 1990 at Harvard forest, a research forest that is managed by Harvard University and located approximately 65 miles north of the Great Mountain Forest, in Massachusetts (O'Keefe, 2012). Recordings take place every 3-7

days between April and June for 33 woody species. Data are available for between 10 and 30 individuals for all of the species in SORTIE, covering 21 years (1990-2011), apart from Pinus strobus and Tsuga canadensis for which there is 11 years (1990-2001). Budburst dates were converted into julian dates and averaged to provide a baseline budburst date for each species; an example of the variation is shown for oak (*Quercus rubra*) in figure 2.1.

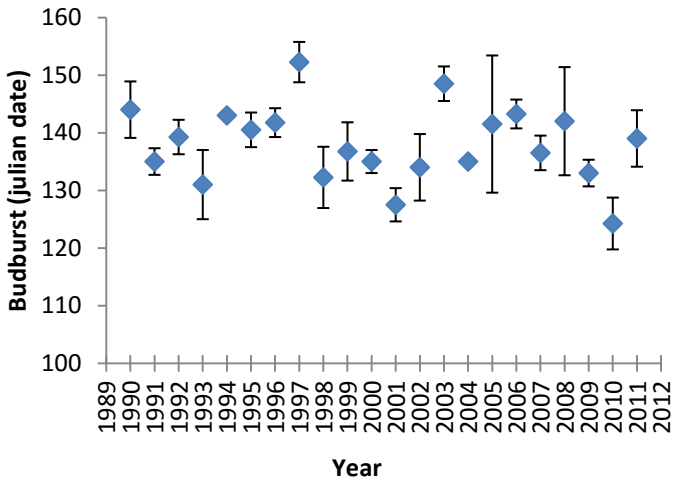


Figure 2-1: Chart showing the mean (lines representing SD) of budburst date for Quercus rubra at Harvard Forest, 1990-2012.

Predictions of changes to budburst date under climate change scenarios were taken from (Migliavacca et al., 2012). To estimate future changes in budburst, they used Akaike's Information Criteria (AIC) to assess the fit of 12 leaf budburst models on 11 North American woody species. They produced predictions under two IPCC emission scenarios, representing low (B1) and high (A1fi) CO_2 emissions (Nakicenovic and Swart, 2000). Data was not

available for the two evergreen species *P. strobus* and *T. canadensis* and so the mean budburst date of the other seven species was used.

The species-specific budbursts were included into the model by altering the annual growth for individuals, which was normalised using the original growing season length in SORTIE, 150 days. To simulate climate change conditions the growing season was increased every 5 year time step for 100 years, after which it was kept constant. The code introduced was as follows:

```
if (iterationCount > 0 && iterationCount < 20) julstart -= julstart5yrRedFactor;
growthlength = julend - julstart;
speciesGrowth = growthlength / 150;
```

where:

iterationCount counts the 5yr time step

julstart5yrRedFactor is a factor for reducing the budburst in the 5 year time steps

julstart is the budburst julian date

julend is the leaf senescence julian date, defaulted to 270

2.3.3 Baseline Conditions

Baseline conditions was considered to be the model in its current iteration, with the growth rate of each species being 150 days.

2.3.4 Model Runs

The model was run eight times for each emission scenario and the baseline conditions, for 1000 years in 5-year time steps. The model was initialised with 16475 individuals of each species, which were distributed at random.

2.3.5 Statistical Analyses

Statistical analyses were performed using statistical program R 2.15.0 (R Development Team, 2013). Differences in the species richness and abundance between emission scenario and baseline conditions were tested for using a one-way ANOVA. This method was also used to investigate differences in the total number of individuals, age and DBH. Homogeneity of variance was tested for using diagnostic plots with normality tested for using a the Shapiro-Wilk test. Where significant differences of the ANOVA were found, Tukey's honest significant differences (HSD) post hoc tests were performed. Differences in the proportions of adults and saplings were tested using Pearson's chi-squared test.

2.4 Results

2.4.1 Budburst

Changes in budburst range from an advance of 5.6 and 12.6 days century^{-1} (mean 8.8 days) in emissions scenario A1, and 2.3 to 5.6 days century^{-1} (mean 4.1 days) in scenario B1. The smallest change is expected in *Fraxinus americana*, with the largest increase seen in Quercus rubra, in both scenarios (Table 2.1).

2.4.2 Richness

There is no change of evenness of the population in the budburst conditions or either the low (B1) or high (A1fi) emission scenarios compared to baseline conditions.

	Baseline budburst (average 1990-2011)	Budburst change (Julian day century$^{-1)}$	
		B1	A1fi
Fraxinus americana	130.2	-2.3	-5.6
Acer saccharum	121.5	-3.5	-7.1
Fagus grandifolia	128.3	-3.5	-7.3
Acer rubrum	126.2	-3.9	-8.7
Betula alleghaniensis	126.2	-3.9	-8.8
Tsuga canadensis	146	-4.3	-9.4
Pinus strobus	154	-4.3	-9.4
Prunus serotina	111.2	-5.4	-9.3
Quercus rubra	127.1	-5.6	-12.6

Table 2-1: Baseline budburst dates as taken from O'Keefe (2012) and predicted changes in budburst date taken from Migliavacca et al. (2012).

2.4.3 Total number of individuals

After 1000 years there are significant differences in the total absolute numbers of individuals in the forest in the emission scenarios ($F_{(2,21)}$=6.53,p =0.006; figure 2.2), with a decrease in numbers in scenario A1fi from 874754 in baseline conditions to 870452 ($p<0.01$). There is also a decrease in the average number total numbers in scenario B1 to 870934, but this is not

significant ($p<0.2$). It is worth noting here that the p-values of the ANOVA here and to most of the other ANOVAs in the thesis would decrease with an increase in replications.

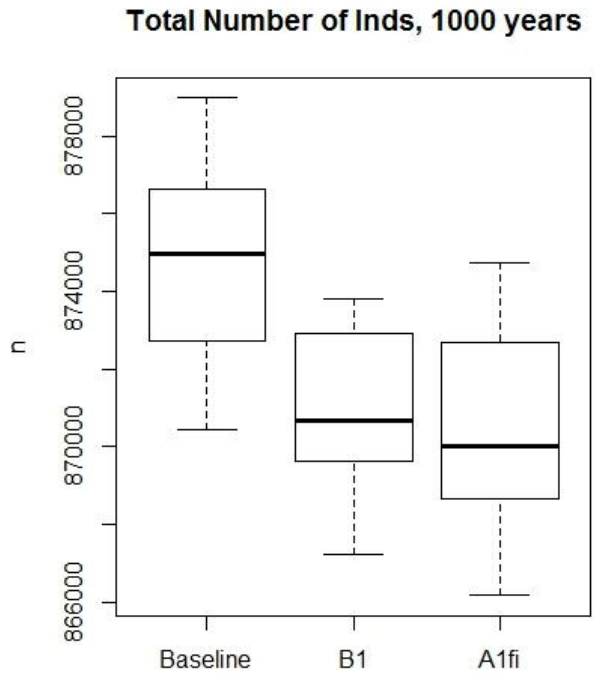


Figure 2-2: Changes to the total absolute number of individuals after 1000 years, for scenarios B1 and A1fi and the baseline temperature conditions. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range.

2.4.4 Absolute numbers and proportional representation of species

There are differences between scenarios in the absolute numbers of beech ($F_{(2,21)}=7.2, p<0.005$) and hemlock ($F_{(2,21)}=8.9, p=0.001$; figure 2.3), as well as the proportions of both (beech: ($F_{(2,21)}=7.2, p<0.005$; hemlock: ($F_{(2,21)}=8.89, p=0.001$; figure 2.4). Post-hoc analyses shows that beech significantly increases from baseline absolute numbers of 343480 (±3322) to 348960 (±2476; p=0.003) in scenario B1 and 347525 (±3112; p=0.03) in A1fi. This is reflected in an increase in proportional representation from 39.2% in baseline conditions to

40% in B1 (p=0.001) and 39.9% (p=0.006) in A1fi. Conversely, there is a reduction in hemlock in both scenarios, from 465334 (±3984) in baseline conditions to 457140 (±3743; p=0.001) and 457428 (±5342; p=0.004) in B1 and A1fi respectively.

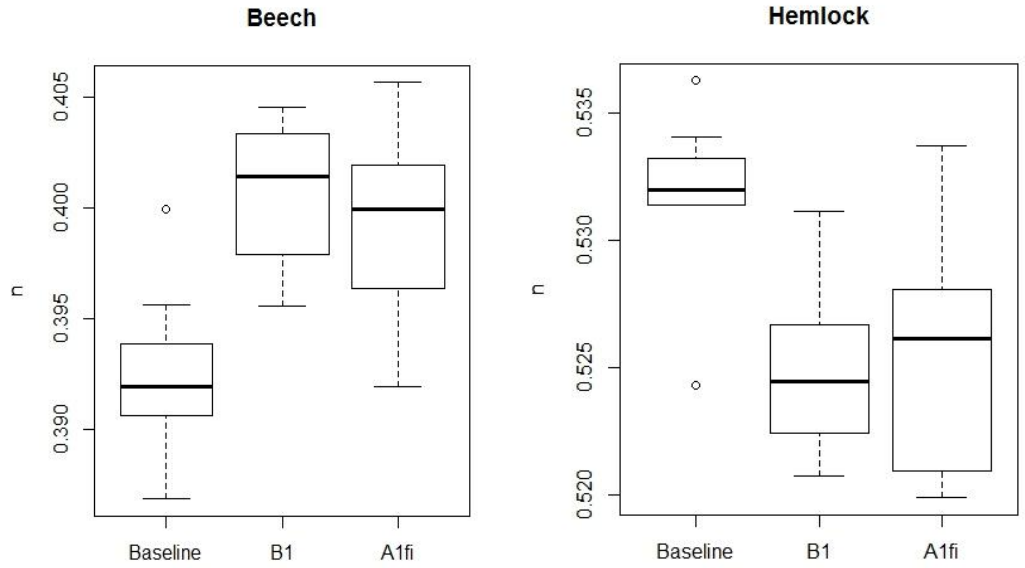


Figure 2-3: Proportional representation of beech and hemlock under B1 and A1fi scenarios and baseline temperature conditions.

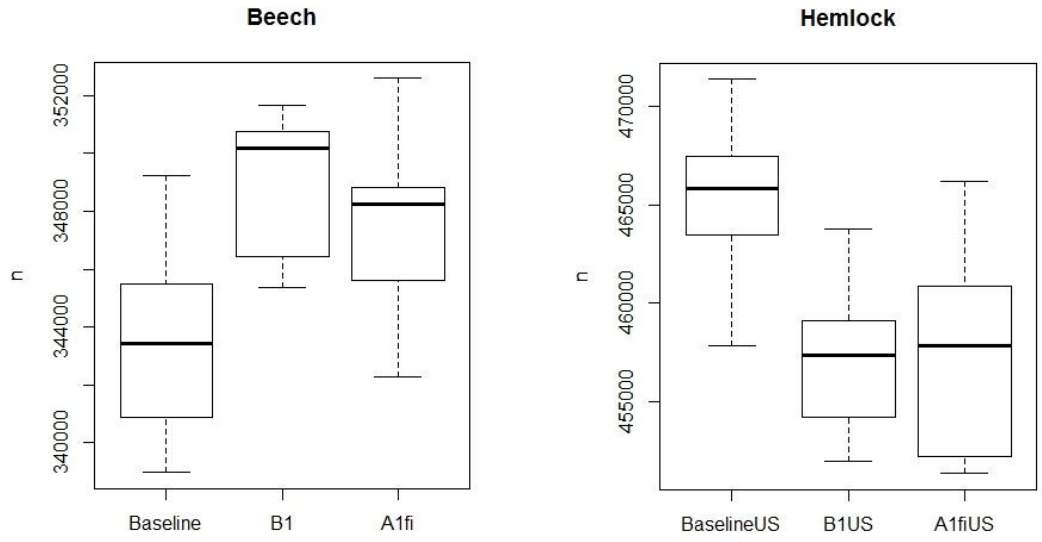


Figure 2-4: Absolute numbers of beech and hemlock in B1 and A1fi emission scenarios and under baseline temperature conditions.

These decreases are reflected in the abundances, dropping from 53.2% in baseline conditions by 0.68% to 52.49% in B1 (p=0.006) and by 0.62% to 52.55% in A1fi (p=0.01). There were no significant differences in any of the other species in terms of absolute numbers, or proportional representation (table 2.2)

	Average Absolute Number After 1000 Years		
	Baseline	B1	A1fi
Fraxinus americana	11 (±9)	13 (±12)	10 (±7)
Fagus grandifolia	343480 (±3322)	348960 (±2476)	347525 (±3112)
Betula alleghaniensis	30559 (±1016)	30133 (±810)	30461 (±1213)
Prunus serotina	34712 (±931)	33998 (±804)	34320 (±832)
Tsuga canadensis	465334 (±3922)	457140 (±3743)	457428 (±5342)
Quercus rubra	210 (±70)	261 (±42)	247 (±81)
Pinus strobus	60 (±42)	38 (±31)	48 (±25)
Acer rubrum	19 (±11)	18 (±12)	25 (±15)
Acer saccharum	369 (±64)	373 (±67)	388 (±40)

Table 2-2: Absolute numbers for the 9 species after 1000 years of simulations

Age, DBH, adult-sapling proportions

No differences in DBH, height, or the proportions of adult to saplings were found between scenarios.

2.5 Discussion

My results suggest that the changes in growth season length alone will not cause major community shifts at the Great Mountain Forest, however it does provide evidence for biotic

interactions influencing the response of species to climate change. All species are predicted to increase their growth season length, however only one species increased their proportional representation. I predicted that species with the largest change in growth period would gain a competitive advantage over coexisting species by increasing their productivity as well as decreasing the light to neighbouring individuals. This hypothesis was rejected however as my model showed there was no relationship between the increase of annual growth of a species and its increase in absolute numbers or proportional representations.

Oak is predicted to be the most sensitive species to temperature change, increasing its growing season a full week longer than white ash in scenario A1fi. It is however only beech, with a moderate increase of 3.5 days in B1 and 7.1 in A1fi, that increases its numbers and proportional representation after 1000 years, when compared to baseline conditions. Hemlock, the other co-dominant canopy species, was modelled to have the joint-third longest increase of growing season, however it is seen to decrease in proportion within the forest after 1000 years, when compared to current budburst conditions. These differences between scenarios and the baseline conditions show that changes in the growth caused by advancing budburst dates does affect the population, however the non-linearity with growth season length shows that biotic interactions are a larger impact on most species within the forest.

American beech, alongside eastern hemlock, are current the co-dominant species at the Great Mountain Forest and were shown to remain co-dominant after 1000 years when current budburst data were included, which is similar to predictions by (Pacala et al., 1996). The increase of beech may be attributed to the life history traits that have been used to define late-successional species. Species-specific responses to light are often used to explain the differences between early- and late-successional plants, with a trade-off between high growth

rates at full light with low shade tolerances in the former, and the opposite in the latter (Kobe et al., 1995).

Both canopy species at the GMF have the highest survivorship under low light conditions (beech: 92%; hemlock: 91%) which is a 22% larger survival rate than the next species, sugar maple. Low light survival was confirmed by (Pacala et al., 1996) to best explain dominance of the late-successional trees at the GMF. My results show that the increase in growing season length increased the number of beech, constraining any extra growth of hemlock. This may be caused by the alteration of the light regime due to the increase in the number of beech. This species intercepts the most amount of light of any species, at 78.5% when 30cm in diameter, with the next most dense canopy (hemlock) casting only 46% when 30cm in diameter. Of both the canopy species, beech grows the quickest in low light conditions - taking 55 years to 3m in 1% sun compared to 75.3 years for hemlock - and it is this combination of traits that could mean explain the dominant response to the increase in growing season.

These results are suggestive of the importance of biotic interactions in the response of species to climate change. The role of interactions in the response to climate change has been extensively studied (Visser and Both, 2005, Parmesan, 2006, Tylianakis et al., 2008), however these studies often focus on the interactions between trophic levels. Some studies have considered the role of competition between species (Lortie et al., 2004, van Loon et al., 2014, Brooker, 2006) however there have been no previous studies, of this sort, into the effect of climate change on competition between tree species. This study provides evidence that competition between species plays a significant role in the response of communities to climate change and provides further weight to suggestions that it is vital that biotic

interactions are considered when predicting the structure and distribution of populations (Pearson and Dawson, 2003, Guisan and Thuiller, 2005, Brooker, 2006). The differences between species in the increase of days per century under climate change are modest at the GMF, with a range of 7 days in scenario A1fi (5.6 days century^{-1} in white ash to 12.7 days in red oak). I hypothesise that populations where the mismatches between phenological dates are larger the effects will be more pronounced.

It is known that different tree cohorts - for example, canopy and sub-canopy species - are affected by different stresses. My results supports the work of (Butt et al., 2014) that showed that when the spring phenological dates of trees were delayed that the growth rates were reduced most in under-story species. This was considered to be because of light competition, and the reduction of growing period before the canopy closed. Whilst I did not include the time of budburst in my model, the increase of annual growth would also increase light competition between species by increasing the size of the canopy. Tall trees in the canopy would not be affected by changes in light competition so would only benefit from increased growth. However they would experience greater wind exposure and solar radiation which would increase hydraulic stress and limit growth, especially in drought intolerant species (Niinemets, 2010, Fulton et al., 2014). The level of resource available or disturbance may also affect which cohort individuals become, with trade-offs depending on stress levels (Smith and Sibly, 2008).

These results provide compelling evidence of the plant-plant competition altering the response of a forest communities to climate change. Given the large contribution to climate sequestration, amongst other biogeochemical cycles (Bonan, 2008a), it is vital that we are able to accurately predict changes to population structures. There are some limitations of the

data that preclude them from being used for accurate predictions of the responses at the GMF, for example the start of growth for eastern hemlock was unavailable and so was taken from the average of the other species. However it does provide the first study into the mitigating effects of plant-plant competition on the responses to climate change of a forest.

Chapter 3

Parameterisation of SORTIE/UK

3.1 Introduction

We are already experiencing anthropogenic climate change with higher ambient temperatures and changes to global precipitation regimes (Jenkins et al., 2009, IPCC, 2013, Peterson and Baringer, 2009) compared to the period before the 1970s. These trends are predicted to accelerate in the coming century (IPCC, 2014) and so it is important that we able to predict the impacts they will have on ecosystems. It has been suggested that in order to predict in novel conditions, such as those caused by climate change, a systems approach is the most suited to provide accurate predictions (Evans et al., 2012, Evans et al., Grimm et al., 2005, Norris, 2012). As well as having the potential to provide reliable and realistic outputs (Grimm and Railsback, 2005, Bart, 1995), individual-based models provide the opportunity to model interactions between individuals. This is especially important when predicting the impacts of climate change, as interactions can mediate the direct impacts of climate change (Parmesan, 2006, Yang and Rudolf, 2010, Tylianakis et al., 2008, Suttle et al., 2007, Brooker, 2006, Gilman et al., 2010). In order to predict population changes, we first need a robust model which is able to simulate current conditions.

The Environmental Change Network (ECN) is a monitoring programme that monitors both physical and biological factors which has eight terrestrial sites, including two woodlands that have been monitored since 1992 with a further four sites included in the succeeding six years (Morecroft et al., 2009). All sites are monitored following standard protocols (Sykes and Lane, 1996) and so provide a reliable source of data, especially when comparing or combining plots and are a good source of data for parameterising forest growth models. For our study we chose the forest growth model SORTIE which has been used extensively where it was originally parameterised in Northeastern US as well at other locations (Pacala et al., 1996, Purves and Pacala, 2008, Purves et al., 2008, Kunstler et al., 2011, Kunstler et al.,

2009, Ameztegui et al., 2015, Bose et al., 2015, Juez et al., 2014, Hawkins et al., 2012, Beaudet et al., 2011). It was chosen for its simple concept with only one source of competition between trees as well as the ability to couple it to other trophic levels (Evans et al., 2015). In the model the only competition between individuals is for light, which is intercepted by individuals' crowns, which affects the light environment underneath. The growth of saplings is related to the amount of light that it receives, where as adults grow according to their size. In the original SORTIE survival was dependent on an individual's growth, but (Moustakas and Evans, 2015) showed that at the ECN sites mortality was better explained by size.

The aim of this study was to collect demographic data about tree species in two semi-natural ancient woodlands in order to parameterise SORTIE/UK, using existing datasets from the ECN where possible. These datasets were supplemented by data collected specifically for this project, between 2011 and 2014. In this chapter I describe the data collection and the existing datasets, outline the model that was implemented and discuss the calculation of the parameters.

3.2 Methods

3.2.1 Study Site and Species

The majority of the data are from Wytham Woods, a large woodland 5km north west of Oxford, Oxfordshire (51°46′ N, 1°20′ W), that has been owned and managed by Oxford University since 1942. The semi-natural ancient mixed woodland is an area of about 400ha in an area of mixed-use land with agricultural land and grassland. The woodland has been defined into five areas based on management histories: undisturbed ancient semi-natural

woodland; disturbed ancient semi-natural woodland; secondary woodland; 19th century plantation and 20th century plantation (Morecroft et al., 2008).

For some parameters if was necessary to supplement the data with data from Alice Holt (around 70km SE of Wytham; 51°10' N, 0°50' W) which is around 850Ha and managed by the Forestry Commission. Parts of the woods have similar vegetation to Wytham Woods, consisting of around 140Ha of old-growth oak (*Quercus robur*) with the remaining forest consisting primarily of conifer plantation. Both sites are part of the Environment Change Network (ECN) monitoring programme, which has measured and recorded biological and environmental data since 1992.

For my PhD I focus on eight deciduous tree species representing over 95% of the individuals at Wytham, of both canopy and sub-canopy. These are: sycamore (*Acer pseudoplatanus* L.), European ash (*Fraxinus excelsior* L.), penduculate oak (*Q. robur* L.), European beech (*Fagus sylvatica* L.), birch (*Betula spp.*), field maple (*Acer campestre* L.), common hazel (*Corylus avellana* L.) and common hawthorn (*Crataegus monogyna* Jacq.).

3.2.2 Existing Datasets

There are three available datasets from the two ECN sites:

- ECN Wytham (*ECN-W*): 250 individual trees in 41 plots, measuring DBH on seven occasions (1993, 1996, 1999, 2002, 2005, 2008, 2012) and height three times (1993, 2002, 2012; Morecroft et al., 2008).

- Oxford University plot at Wytham Woods (*OXF*): one plot containing ~20,000 individual trees measuring DBH on two occasions (2008, 2010; Butt et al., 2014).

- ECN Alice Holt (*ECN-AH*): 216 individual trees in 51 plots, measuring DBH on seven occasions (1994, 1997, 2000, 2002, 2005, 2007, 2011) and height on three (1994, 2002, 2011). A further 56 trees in nine plots measuring DBH on five occasions (2004, 2005, 2007, 2012 and 2013) and height on two (2004 and 2012).

These datasets were supplemented over three summers between 2011 and 2014 by Gregory Carey, Matthew Evans and Aristides Moustakas as described below.

3.2.3 Data Collection

3.2.3.1 Tree measurements

The data sets include data on the diameter at breast height (DBH) which was measured for all trees as per the standardised methods - the circumference of the tree was measured at 1.3m above ground level using a diameter tape. The height of individuals was also measured using a Laser Range Meter (Hilti PD40, Hilti, Schaan, Liechtenstein) to the nearest 0.5m. During fieldwork we re-measured the DBH of trees with DBH larger than 10cm at the sites, with an additional measurement of the diameter at 10cm above ground (D_{10}) for individuals with a DBH under 10cm. This was done by measuring two perpendicular diameters (to the closest 0.1cm) which were averaged to give a mean D_{10} for each sapling.

Measurements of the crown were taken for adults, comprising both height and radius. For the crown height the distance between the ground and the lowest point where there was at least

three quarters of foliage was measured using a Laser Ranger Meter (Hilti PD40), to the nearest 0.1m. This was measured only on trees where height data was available, which was used alongside the measurements to estimate the crown height. The radius of the crown was measured using by projecting the two longest perpendicular diameters on to the ground and measuring to the nearest cm using a tape measure. These were halved and averaged to produce a single radius for each individual

3.2.3.2 Light environment

Light meter readings were taken at three positions underneath individual trees, 1m away from the trunk at a height of 1.3m. To calculate the percentage of light reaching each tree light recordings were also taken in a nearby large open gap. These recordings were taken using two PAR Quantum sensors (SKP215, Skye Instruments Ltd., Llandrindod Wells, UK) that had been calibrated to the same reference lamp. Under the canopy this was used with a meter (SKP200, Sky Instruments Ltd., Llandrindod Wells, UK) and measured to the closest decimal place. In the open gap a data logger (SDL5050 DataHog 2, Skye Instruments Ltd., Llandrindod Well, UK) was used which measured the mean light condition every ten minutes, from ten second readings. The light intensity (L_{ci}; where i = 1-3) for each tree was calculated as below:

$$L_{ci} = \frac{L_{cait}}{L_{oat}} \qquad (3.1)$$

Where:

L_{cait} is the ith measurement of absolute light levels below the canopy taken at time t

L_{oat} is the absolute light levels in the open gap at time *t*.

L_{c1}, L_{c2} and L_{c3} for each tree were averaged to produce a single value (*Lc*) for each individual tree.

In order to estimate the canopy openness photographs were taken at 1.35m above ground level using a fish-eye lens of single-species stands, using a compass to ensure that the top of the photograph was due North (0°). The images were then analysed for light transmission using the program gap light analyser (GLA; *http://www.eocstudies.org/gla/*).

Figure 3-1: Example fish-eye lens photograph of single canopy

3.2.3.3 Growth

The mean growth rates of individual trees were estimated using a time-series of DBH measurements taken from the datasets. The DBH measurement at time point *t* was subtracted from the measurement at *t*+1 to give the growth for the period of time between datasets. This was divided by the number of years between datasets to give an estimate of the growth rate.

Multiple measurements from an individual were averaged to give a single growth rate per individual.

3.2.3.4 Recruitment

There was not enough information about seedlings in the datasets for our investigation. Fieldwork was carried out by Evans and myself at Wytham Woods during the winter of 2013 which used $1m^2$ quadrats along transects. However, not enough data was collected to estimate the parameters. These were therefore taken from data collected in Quebec (Swift, 2005). These were different species but species of the same Genus (where possible) were assumed to be similar, with understory species hazel and hawthorn replaced with understory species *Prunus serontina* (table 3.1).

UK Species	Species in Swift (2005)
Sycamore (*Acer pseudoplatanus*) Field maple (*Acer campestre*)	Sugar maple (*Acer saccharum* Marshall)
European ash (*Fraxinus excelsior*)	White ash (*Fraxinus americana* L.)
European beech (*Fagus sylvatica*) Pedunculate oak (*Quercus robur*)	American beech (*Fagus grandifolia* Ehrh.)
Birch spp. (*Betula* spp.)	Yellow birch (*Betula alleghaniensis* Britt.)
Common hazel (*Corylus avellana*) Common hawthorn *(Crataegus monogyna*)	Black cherry (*Prunus serotina* Ehrh.)

Table 3-1: Species replacements from Swift (2005) to SORTIE/UK for recruitment parameters

3.2.3.5 Data Collection

The data were collected as following:

G Carey collected:

- Diameter at 10cm above ground level on saplings at ECN-AH.
- Light environment around saplings in ECN-AH.
- Crown radius and crown height for adults in ECN-AH.
- Canopy openness for a sample of 165 trees in Wytham Woods

M Evans and A Moustakas collected:

- Diameter at 10cm above ground level on all saplings in ECN-W, a sample of 88 from OXF and some from ECN-AN.
- Light environment around all saplings in ECN-W, a sample of 88 from OXF and some from ECN-AH.
- The height of a sample of 88 saplings from OXF.
- Crown radius and crown height for all adults in ECN-W and some from ECH-AH.

3.2.4 Model Description

The model used is a derivative of SORTIE-ND, a descendent from the original program developed by Pacala et al. (1993). For the purposes of my PhD I have used a version that was developed by Bithell and Brasington (2009) in C++. Sortie-ND is an individual-based forest simulator that was developed to study neighbourhood dynamics (ND) between individual

trees. The original program was developed with data from the Great Mountain Forest, Norfolk, Connecticut, US but has since been used for forests globally (e.g. Coates et al., 2009, Kunstler et al., 2009, Ameztegui et al., 2015, Bose et al., 2015). The fate of the individual trees in the model is regulated by five submodels: allometry, resource, growth, recruitment and mortality which are defined below (see figure 3.2).

For SORTIE/UK, trees of all species were defined according to their size into two life history stages: adults and saplings. Adults are individuals which have a diameter at breast height (DBH) of larger than, with saplings being individuals with a DBH of less than 10cm and a height larger than 1.35m. In SORTIE-ND seedlings were defined as individuals that were smaller than 1.35m, however a lack of data in the datasets meant that this life stage had to be excluded from SORTIE/UK. Therefore new individuals were initialised having a height of 1.35m (minimum sapling height), with their DBH calculated using species-specific allometric equations.

The model is written in C++, approximately 2.5MB and is 2500 lines spread over 8 files. It is composed of a grid of 250 x 150 cells each comprised of 20m, totalling $15km^{2,}$ the approximate size of Wytham. Each model run begins with 16987 individual, in proportions that are seen at Wytham (see table 3.2). The model has a burn-in time of 350 years.

3.2.5 Allometry

This defines the size and shape of trees based on species-specific allometric functions. There are different functions based on the life history stage of the individual.

Species	*Initial number*
Ash	4830
Beech	1092
Birch	80
Field maple	112
Hawthorn	185
Hazel	202
Oak	1577
Sycamore	8908

Table 3-2: Initial numbers of species in SORTIE/UK

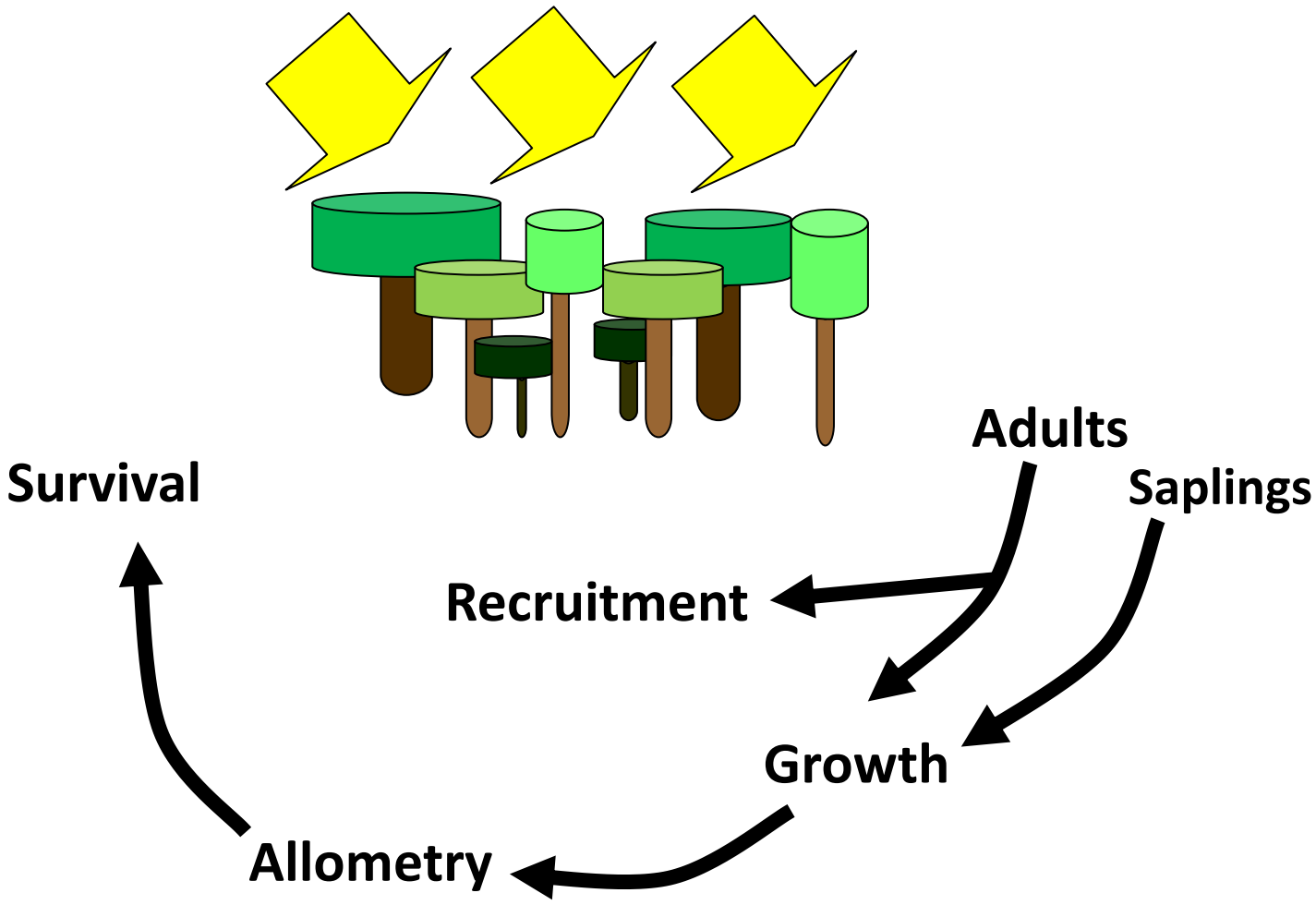


Figure 3-2: Representation of the model structure of SORTIE.

3.2.5.1 Saplings

Saplings require two functions: a linear equation relating DBH to their diameter at 10cm (D_{10}) and a power function relating the height (H) to the D_{10}:

$$DBH = a + b\ D_{10} \quad (3.2)$$

$$H = a\ D_{10}^{\ b} \quad (3.3)$$

where:

a and *b* are estimated parameters.

3.2.6 Adults

Allometry for adults is calculated by three allometric equations: an exponential relationship between height (*H*) and DBH and power functions between crown radius (*CRad*) and DBH and between crown height (*CH*; distance between the base and the top of the crown of the tree) and tree height

:

$$H = 1.35 + (maxht - 1.35)(1 - e^{-b*DBH}) \quad (3.4)$$

$$CRad = a\ DBH^{b}\ \textbf{or}\ \log CRad = \log a + b \log DBH \quad (3.5)$$

$$CH = a\ H^{b}\ \textbf{or}\ \log CH = \log a + b \log H \quad (3.6)$$

where:

maxht (*m*) = maximum height for each tree species in the ECN-W and ECN-AH datasets.

a and *b* are estimated parameters.

3.2.7 Resource

The only resource considered in SORTIE/UK is light, following SORTIE-ND (Pacala et al., 1996). This is a pre-emptable resource with individuals intercepting light depending on their canopy size and their position. Canopies of individual trees intercept a proportion of the light that they receive based on species-specific light transmission parameters, with the remaining light reaching any smaller neighbouring individuals. Incoming light is set by the global light index (GLI) with SORTIE explicitly considering the latitude and topography of the site as this affects the light that an individual receives due to the angle of the sun to the tree's canopy. Light is available to the individuals for 150 days of the year, between the 120th (April 29/30) and 270th (Sept 26/27) Julian days. This is the same as the resource submodel in SORTIE/ND, section 2.3.1.1.

3.2.8 Growth

There are different functions controlling the growth for saplings and adults. The growth of saplings is dependent on the amount of light it receives, as well as their size, whereas adult growth is solely a function of size. Note that this is different from the growth in section 2.3.1.2.

3.2.8.1 Saplings

The radial growth of saplings (G_{sap}; in cm yr^{-1}) was calculated using both a Michaelis-Menten function and a power function as follows:

$$G\ sap\ = \frac{\alpha\ L}{(L + \alpha/\beta)}\ D_{10}{}^{\Phi} \qquad (3.7)$$

where:

α is the growth rate in 100% light

β is the growth rate with 1% light conditions

L is the amount of light that of light that an individual receives

Φ is an estimated exponent which determines the size effect of the function

3.2.8.2 Adults

The radial growth of adults (G_{adu}) is defined by two equations, which is simplified version of the Neighbourhood Competition Index (NCI) growth equation taken from (Canham et al., 1994):

$$G_{adu} = MaxG \times SE \quad (3.8)$$

where:

MaxG (cm yr^{-1}) is the maximum growth rate recorded in the datasets. The 99th percentile of the recorded was taken to account for some extreme values.

SE is a size effect which is calculated by:

$$SE = e^{-0.5\left(\frac{ln(DBH/X_0)}{X_b}\right)^2} \quad (3.9)$$

where:

X_0 and X_b parameters are estimated from the datasets.

3.2.9 Mortality

(Moustakas and Evans, 2015) showed that that mortality (*m*) at Wytham is better explained by tree size than by light and growth rate; SORTIE-ND uses light related mortality functions (2.3.1.3). In order to account for relocation errors in the datasets Moustakas and Evans (2015) used capture-recapture program MARK which uses a Cormack-Jolly-Seber (CJS) model to estimate mortality:

$$m = \frac{1-(e^{\Phi_1+(\Phi_2*(\frac{DBH-meanDBH}{sdDBH})}))}{e^{\Phi_1+(\Phi_2*(\frac{DBH-meanDBH}{sdDBH})}} \quad (3.10)$$

where:

Φ_1 and Φ_2 are parameters estimated from the CJS model fitted to the datasets

meanDBH (cm) is the species-specific mean DBH from the datasets

sdDBH (cm) is the species-specific standard deviation from the datasets.

3.2.10 Recruitment

Recruitment is estimated using two functions, one to describe dispersal and the other to fecundity. As in section 2.3.1.4, dispersal in SORTIE/UK is estimated using a lognormal function which describes the density (numbers $m^{-2)}$ of seedlings at a given point, i (R_i):

$$R_i = STR \sum_{j=1}^{n} \frac{DBH_j{}^{\beta}}{30} * e^{-0.5(\frac{\ln(d_{ij}/X_0}{X_b})^2} \quad (3.11)$$

where:

STR is the fecundity of the tree, defined as the standardised total number of recruits produced by a 30cm tree

DBH_j is the DBH (cm) of the *j*th tree, where j = 1 to n adult trees within 20m

d_{ij} is the distance between point i and the *j*th tree

X_0 is the mean of the function

X_b is the variance of the function

β is a dispersal parameter

Since new individuals in the model are introduced as saplings, the survival rate of seedlings was calculated using the mortality function. This was used as the initial density for seedlings which were distributed from the parent tree, using a lognormal distribution.

3.2.11 Data analysis

Images taken with the fish-eye lens of canopies were imported into Global Light Analyzer software (GLA; *http://www.eocstudies.org/gla/*). GLA compares the contrast between the pixels to calculate the percentage canopy openness for each photograph. The mean values calculated from photographs of canopies from the same species were taken to provide an average canopy openness for each species.

Full methodology for the estimation for the allometric and growth and parameters can be found in Evans et al., (2015; see appendix i). Mortality at Wytham was found to be best explained by a model based on size for both size classes of species; the methodology and parameters for this can be found in (Moustakas and Evans, 2015).

3.3 Results

3.3.1 Parameter estimation

Estimations for all parameters can be found in table 3.4.

3.3.2 Openness

The fish-eye photographs taken under species canopies gave figures for the light transmission coefficient parameter. The species from the most to least shady are as such: field maple > beech > hazel > sycamore > hawthorn > oak > birch > ash (table 3.3).

Species	Number of Individuals	Light Transmission Coefficient
Field maple	2	0.0852
Beech	15	0.1208
Hazel	2	0.1392
Sycamore	12	0.1871
Hawthorn	5	0.2002
Oak	4	0.2062
Birch spp.	7	0.2327
Ash	2	0.3013

Table 3-3: Light transmission coefficients for the eight species

	Equation no. & parameter	Field Maple	Sycamore	Birch	Hazel	Hawthorn	Beech	Ash	Oak
Allometry Parameters (as found in Evans *et al.*, 2015)									
DBH to Diameter at 10 cm slope of regression	(3.2 *a*)	0.56	0.56	0.4	0.33	0.48	0.75	0.27	0.58
DBH to Diameter at 10 cm Relationship regression intercept	(3.2 *b*)	2	2	2.86	4.25	2.51	0	4.74	1.43
Height-Diameter at 10 cm Relationship slope	(3.3 a)	0.12	0.12	0.82	2.36	1.37	0.11	0.1	0.11
Height-Diameter at 10cm exponent	(3.3 *b*)	1.88	1.88	0.93	0.54	0.61	1.95	2.03	1.95
Maximum Height (m)	(3.4 *maxht*)	19	30.5	22.5	19.5	15	39	37.5	35.5
Adult height slope	(3.4 *b*)	0.046	0.041	0.049	0.069	0.051	0.007	0.007	0.016
Crown radius slope of regression	(3.5 *a*)	0.19	0.36	0.04	0.01	0.16	0.29	0.11	0.22
Crown radius exponent	(3.5 *b*)	0.83	0.72	1.37	2.15	0.99	0.77	1.06	0.78
Crown height slope	(3.6 *a*)	0.13	0.24	0.21	0.21	0.31	0.13	0.01	0.02
Crown Height parameter *b*	(3.6 *b*)	1.53	1.28	1.28	1.44	1.3	1.47	2.48	2.01
Growth Parameters (as found in Evans *et al.*, 2015)									
Growth D_{10} exponent	(3.7 Φ)	0.845	0.845	0.845	0.845	0.845	0.845	0.845	0.845
High light growth	(3.7 α)	0.1250	0.0118	0.1690	-0.0160	0.0264	0.1520	0.0082	0.0546
Low light growth	(3.7 β)	0.1590	0.0215	0.1370	0.0680	0.0055	0.0750	0.0001	0.0348
Max Growth rate (cm yr-1)[1]	(3.8 *MaxG*)	0.59	0.48	0.77	0.54	0.62	0.97	1.47	1.81
Size effect parameter x0	(3.9 x_0)	20.13	20.56	15.68	9.62	12.93	31.87	19.9	26.45
Size effect parameter xb	(3.9 x_b)	93.12	135.25	66.26	12.74	55.06	1013.79	58.52	495.06

	Equation no. & parameter	Field Maple	Sycamore	Birch	Hazel	Hawthorn	Beech	Ash	Oak
Mortality Parameters (as in Moustakas & Evans, 2014)									
Annual mortality rate parameter phi1[2]	(3.10 *phi1*)	5.5700	5.6200	3.4000	5.6500	4.8300	4.6800	5.3600	4.2300
Annual mortality rate parameter phi2[2]	(3.10 *phi2*)	-0.2070	5.2300	0.1430	-0.1900	-0.0900	-0.2270	0.4400	1.8300
Mean DBH	(3.10 *meanDBH*)	18.7000	19.9300	27.5800	10.8300	14.7300	27.5100	20.8300	37.3900
SD of DBH	(3.10 *sdDBH*)	6.5800	16.3900	13.0200	3.7400	7.1000	30.2200	11.6800	39.4500
Recruitment Parameters (taken from Swift, 2005[3])									
Recruitment parameter *STR*	(3.11 *STR*)	725	725	10249	1976	1976	224	946	224
Recruitment parameter *β*	(3.11 *β*)	2.95	2.95	1.3	0.72	0.72	3.55	5.65	3.55
Recruitment parameter	(3.11 *x0*)	4.67	4.67	38.29	7.84	7.84	4.01	29.71	4.01
Recruitment parameter	(3.11 *xb*)	0.6	0.6	0.1	2.84	2.84	0.69	0.26	0.69

Table 3-4: Full parameters from field measurements for the eight species in the model for the allometry, growth, mortality and recruitment parameters. Notes: 1: The 99th percentile value was taken of field measurements due to extreme values. 2: These parameters are estimated from analysis in MARK. 3. As not enough data was available, species are replaced for species in the same genus from Swift, 2005, see table 3-1.

3.4 Discussion

Data was collected for model parameterisation as laid out in 3.2.3.5, and methodology for the parameterisation can be found in Moustakas & Evans (2015) and Evans *et al.* (2015). As with any parameterisation, the resulting parameters will only represent the variation with the data that was collected. For some parameters there was limited data available, for example data for the light transmission coefficient was available for between two and fifteen individuals. However, for the allometry and growth parameters, data from 88 individuals was available (Evans et al., 2015) and a large dataset of 281 individuals was available to estimate mortality parameters (Moustakas & Evans, 2015). Data collection for light transmission proved difficult, as it was necessary to find single-species stands for each species. This data collection was conducted only at Wytham Woods, and so it would be necessary to expand this to other woodlands to ensure a greater data set. The available datasets did not provide enough data for our recruitment submodel, and so the species were replaced with species from Swift (2005). Improving the data for this submodel was outside of the scope of this thesis, however this will be necessary for future research implementing Sortie/UK in order to produce reliable estimates.

As well as increasing the amount of data that is collected, a sensitivity analysis of the parameters would increase confidence in the accuracy of the outputs of the model. This would involve changing parameter values and assessing the impact that this has on the model's output. This would need to be done alongside a validation of the model, to ensure that the assumptions of the parameter values are reasonable to represent the real forest system. This could be done qualitatively, using expert assessments on the potential natural vegetation (PNV) of an area (e.g Ellenberg 1986), or quantitatively using existing data. This could be done either by using pollen data records (e.g. Heiri et al., 2006), however this only

offers a low temporal resolution, or by estimating the age of the stand and using recent surveys of the community structure and compositions. This method however relies on assumptions of the age of the stand, presumes no management and ignores extreme weather events.

This thesis considers the fate of the woodland under projected climate change conditions, however the above validation should be done as a steady state system, with current climate conditions. Wytham woods is a semi-natural ancient woodland that has had a mixed management regime, ranging from largely unmanaged ancient woodlands to nineteeth and twentieth century plantations, with some timber extraction taking place across the site (Morecroft et al, 2008). The current dominant species are sycamore and ash but research has suggested that sycamore, which has increased at the site since the nineteenth century, has lower regeneration and growth than its current co-dominant ash (Morecroft et al, 1997). This has been attributed to its general poor growth under dense canopies, which is consistent with other sites (Savill 1997). This would suggest that if unmanaged the forest could become dominated by ash solely, or other present canopy species such as beech and oak could increase their proportion within the forest.

Chapter 4

The role of biotic plant-plant competition in response to climate change induced changes in growing season duration

4.1 Abstract

One of the major effects of climate change is increasing global air temperature. Temperature regulates many processes within plants, and one of the major biological signals of climate change has been an advance in spring phenology. This response is species-specific, and so has the potential to change plant-plant interactions by differentially increasing productivity and altering light competition regimes. These interactions are thought to have the potential to mitigate the effects of climate change, and so these indirect effects may have significant impacts on populations. In order to test the effects of changes of growth periods on species I used an individual-based model with light interactions as the sole source of competition, using the semi-natural woodland Wytham Woods as a model. I predicted that the species with budburst dates that are most sensitive to temperature will increase their representation in the forest by gaining competitive advantage over other species. For some species this was true, with ash and sycamore maintaining their dominance of the forest whilst increasing their densities in the forest. However, with other species that are predicted to have longer growing seasons under increased temperatures, no differences were seen. This suggests that the life histories of the tree species must also be considered, with earlier canopy closure potentially affecting those species with low shade tolerance.

4.2 Introduction

Anthropogenic drivers such as increased greenhouse gas emissions and land-use changes are predicted to cause global surface temperatures to rise in the next century between 0.3°C and 4.8°C (IPCC, 2013), with the UK expected to have hotter, drier summers and milder, wetter winters as well as an increase in extreme weather events (Murphy et al., 2009). There is growing evidence of the direct effect that global climate change is having on plants (Walther

et al., 2002, Parmesan and Yohe, 2003, Parmesan, 2006, Choat et al., 2012, Root et al., 2003, Guisan and Thuiller, 2005, Cramer et al., 2001). However indirect effects are thought to have to have the potential to modify these direct effects for some species (Parmesan, 2006, Yang and Rudolf, 2010)

One of the largest indirect impact of climate change on plants may come from changes to interactions between different trophic levels and amongst plant species (Parmesan, 2006). Interactions with other trophic levels can either be mutualistic (e.g. pollination, seed dispersal and plant-fungus mutualisms) or antagonistic (e.g. herbivory or parasites) (Tylianakis et al., 2008). Climate change is expected to have negative effects on some of these interactions with mismatches in the responses to environmental change (Suttle et al., 2007, Inouye, 2008, Winder and Schindler, 2004, Visser and Both, 2005). These mismatches may also be exacerbated by environmental change occuring at rates that are too fast for adaptation (Jump and Penuelas, 2005). Plant-plant interactions, which comprise facilitation and competition, have long been acknowledged as a key driver of community composition and dynamics (Tansley, 1917, Went, 1942, Bruno et al., 2003, Maestre et al., 2005). These types of interactions may mediate the direct impact of climate change on individuals and species.

There is evidence of facilitation benefiting plants experiencing climate change conditions, for example the increased growth and reproduction under enhanced CO_2 conditions of two subarctic species was amplified when in the presence of each other (Shevtsova et al., 1995). A review of 727 papers showed that there is generally a shift from competition to facilitation, or at least a reduction in competition, under environmental stresses (He et al., 2013). However there is also some evidence of a shift from facilitation between species to strong competition (Klanderud, 2005, Klanderud and Totland, 2005). The impact that competition

has on the response of some plant species to climate change has been investigated (van Loon et al., 2014, Klein et al., 2004, Wang et al., 2006, Klanderud, 2005, Klanderud et al., 2015, Tomiolo et al., 2015), however there are few studies on the effect that competition will have on the response of woodland trees to climate change, and how this might change long term ecological phenomena such as succession. Results from (Laurance et al., 2004) suggest that successional changes in the Amazonian rainforest could be explained by fast-growing species gaining a competitive advantage with increased growth caused by higher CO_2 levels.

One of the largest sources of competition between plant species is light (Pacala et al., 1994, Casper and Jackson, 1997, Lamb, 2008). One potential change to this competition regime is through changes to species-specific growth periods. The growth period of plants is governed by phenological events, which are recurring biological events as budburst, leaf unfolding, leaf colouring and fall, bud set, bud dormancy and release from dormancy, all of which are controlled by environmental conditions (Leith, 1974). For deciduous trees, budburst and leaf senescence regulate the amount of time that a plant is in leaf, and therefore photosynthetically active (Cannell et al., 1998). As with many phenological events in temperate plants, budburst is thought to be most regulated by temperature (Fu et al., 2012), with recent changes in budburst date being regarded as a signal of global climate change (Parmesan and Yohe, 2003). Earlier spring phenological events have been attributed to higher global temperatures (Bertin, 2008, Dijkstra et al., 2011, Fu et al., 2012, Menzel et al., 2006, Pellerin et al., 2012, Richardson et al., 2013, Schwartz et al., 2006) however the relationship with bud senescence is less clear (Menzel et al., 2006).

With temperatures forecasted to rise over the next century it is expected that spring events will continue their trend of getting earlier. However, species are known to respond at

different rates to temperature and such inter-specific differences are of interest because they could change the outcome of competition between individuals and so change patterns of succession (Suttle et al., 2007, Urban et al., 2012a, Mason et al., 2014, Benito-Garzon et al., 2013). As well as being a potential source of competitive advantage for those species that have the largest response of growth period, and thus productivity, to the increase in temperature, the increase of time that a species is in leaf could also provide an advantage in the competition regime for light by increasing the shade to neighbouring individuals. Light competition is asymmetric, with larger trees having an advantage over smaller ones in light acquisition, through shading (Casper and Jackson, 1997, Weiner, 1990) and the earlier a species is in leaf, the greater the shade that coexisting species experience. Little has been done to quantify these changes of competition in forests, though it could have major implications for changes in leaf area index (LAI), defined as the one-sided leaf area per unit ground surface area (Watson, 1947) and thus climate change through vegetation-climate feedbacks (Claussen et al., 1998, Bonan et al., 2003, Dekker et al., 2010). Van Loon *et al.* (2014) modelled the change of LAI due to competition between neighbouring individuals in a monoculture of soybean (*Glycine max*), however natural forests are rarely monocultures and shading from interspecific neighbours are also an important source of competition.

In order to look at the effect that interspecific differences to climate change will have on a coexisting species I have used the spatially explicit individual-based forest dynamics model SORTIE/UK , which was developed from SORTIE-ND (described in chapter 3). This model has a simple competition regime only involving light, and so is suitable to investigate the effect that climate change induced temperature changes will have on light competition between the species. In the original model by (Pacala et al., 1996), the model had a growth period of 150 days for all species, however I modified SORTIE/UK so that each species has

its own growth period. Predicted budburst changes under increased temperatures were also used, which allowed for population-level changes to emerge from changes of budburst date, at the species level.

My hypothesis was that changes in budburst alone can be a driver of population change, by differentially altering the competitive ability of trees. Species that show a greater response to temperature, and prolong their annual growth periods when ambient temperature is higher, would be expected gain a competitive advantage over species that have lower sensitivity to temperature rises by increasing their productivity as well as by altering light conditions underneath their canopy.

4.3 Methods

4.3.1 Study Site & Data

Wytham Woods is a semi-natural ancient woodland located around 5km north west of Oxford (1°20′W 51°46′N). There is about 400ha of mixed woodland, of which this study concerns eight species which represent 98% of the tree species: sycamore (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*), European beech (*Fagus Sylvatica*), penduculate oak (*Quercus robur*), common hazel, (*Corylus avellana*), common hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), and birch (*Betula* spp.).

4.3.2 Budburst data

Current budburst data were taken from the UK Phenology Network (UKPN; www.naturescalendar.org.uk) which are volunteer-run surveys of seasonal events for animal, insect, plant and fungi species. Budburst is defined as the emergence of new leaves, and the

date for each species between the years 1999-2013 was converted into Julian date and averaged to provide a baseline budburst date for each species. The only available data for Hazel was the first flowering date, and so two months was added to this date to approximate the budburst date.

Budburst data taken from the UKPN was used in model runs of baseline conditions to simulate if current conditions were to continue with no climate change affecting budburst date.

4.3.3 Allowing climate change to change budburst date

I investigated the effect of climate change on the population by using the predicted species-specific budburst responses to temperature alongside climate projections for Southern England. For sycamore, ash and oak budburst correlations between budburst and temperature were taken from (Morecroft et al., 2008), who used 13 years of data to correlate budburst to temperature for these species at Wytham Woods. For the other species, I performed a regression analysis of the budburst dates taken from the UKPN alongside average monthly temperatures, which were calculated from daily averages from the Met Office Hadley Centre Central England Temperature series (HadCET; Met Office), for the years 1999-2013. Regressions were performed with temperature data from months February, March and April, to investigate the change of budburst date per °C.

Climate projections were obtained from the Met Office's UK Climate Projections (UKCP09; Murphy et al., 2009), which provides projections of monthly average air temperature between 2020 and 2080 for a 25km^2 grid, which included Wytham Woods. The UKCP09 model uses a cumulative distribution function (CDF) to provide probabilistic projections, which provides a

cumulative probability of the climate projections. For this study I used the 50% probability, the central estimate, where half of the simulations were below this figure, and half above. Projections of future March temperatures were used for three IPCC scenarios - low (B1), medium (A1B) and high (A1fi). These were combined with the predicted species responses of budburst to temperature to produce estimates of the change in budburst date, up to 2080, after which they remain at the 2080 date.

4.3.4 Model Runs

The model SORTIE/UK (for parameterisation see chapter 3) was adapted to allow species-specific budbursts. Budburst change was modelled as a function of growth change, which was normalised to 150 days, the original growth period in SORTIE/ND (Pacala et al., 1996) and introduced as such:

```
grow(int iterationCount) {

double julreductioncount = iterationCount;
if (iterationCount > 20) julreductioncount = 20;
double daylength = params[kind].julend - (params[kind].julstart
- (julreductioncount
* params[kind].julstartReductionFactor ) );

double speciesGrowth = daylength / 150;
```

where:

iterationCount is the current time-step in the model

julend is the Julian date of the end of the growth period (270)

julstart is the Julian date of the start of the growing period

julstartReductionFactor is a factor to reduce the budburst date per time-step

For the three emission scenarios, as well as under baseline conditions, models were run for 1250 years, at five year time steps. Each simulation was initialised with the same forest structure, with the species, size and spatial structure as recorded at Wytham Woods.

4.3.5 Statistical Analysis

Statistical analyses were performed in R 1.3.0 (R Core Team, 2013). Differences in the absolute number of individuals and the proportional representation of species between emission scenarios and baseline conditions were analysed using one-way ANOVA, with the scenario as the fixed factor. Normality was tested for using the Shapiro-Wilk test, with homogeneity of variances being confirmed using diagnostic plots. Where significant differences between scenarios were found, and assumptions of the analyses met, a Tukey's honest significant difference (HSD) post hoc test was performed.

Correlations between four life history variables (canopy openness, time to 3m in 1% light, time to 3m in full light and survival rate at 1% light; table 4.1) was investigated for using Pearson's correlation coefficient, or Spearman's rank correlation where variables were not normally distributed.

	Mean Canopy Openness	Time to 3m in Full Sun (Years)	3m in 1% light	5-Yr survivorship of 1cm diameter sapling 1% sun
Oak	20.62	6	135	93.13
Hazel	13.92	4	248	99.77
Hawthorn	20.02	5	266	99.32
Birch	23.27	240	528	95.77
Field Maple	8.52	323	571	99.77
Sycamore	18.71	19	609	97.55
Ash	30.13	8	768	99.05
Beech	12.08	269	796	99.24

Table 4-1: Life history traits of the eight species.

4.4 Results

4.4.1 Budburst changes

The budburst response of the species at Wytham was shown to be most significantly related to March temperatures for four of the eight species for the years 1999-2013, (table 4.2). March was also found as the most significant temperature period for budburst by Morecroft et al., (2008). In hazel no significant correlation to temperature was found, and so it was presumed that it will not change budburst date. The change of budburst per °C of March temperatures was used alongside predictions for oak, sycamore and ash from Morecroft et al. (2008) to predict budburst dates under climate change (table 4.3).

	February Average	March Average	April Average	February-March Average	March-April Average	February-April Average
Ash		*			*	.
Beech		.			*	.
Hawthorn	**	**		***	*	**
Hazel						
Oak	*	***	*	***	***	***
Birch	.	*		*		.
Sycamore	.			.		
Field Maple		*	*		**	*

Table 4-2: Significance of regression analyses between budburst date of species and the average daily temperature of months February, March and April, as well as combined average temperatures for February and March; March and April and all three months.

	Change in budburst date (days $°C^{-1}$)
Field maple	3.035
Sycamore	6.2
Birch	4.165
Hazel	0
Hawthorn	3.944
Beech	2.545
Ash	5.1
Oak	4.1

Table 4-3: Change in budburst with mean temperature in March, days per degree.

4.4.2 Model outputs

In all model simulations, after 1250 years the structure of the forest changes considerably when compared to present day (see table 4.4). A similar pattern of succession is seen in all of the scenarios, as well as baseline conditions, with a continuous rise of sycamore over the 1250 years and modest increases in the understory species hazel and hawthorn (figure 4.1). Ash also increases from initial numbers, displaying an oscillating pattern until around 650 years when the numbers remain approximately constant. All other species remain relatively stable throughout the simulation, although oak declines slowly throughout the simulation and birch declines to extinction (Figure 4.1).

	Proportional Representation (%)				
	Current	After 1250 Years			
		Baseline	B1	A1B	A1fi
Ash	26.9	30.2	34.407	35.163	35.473
Beech	1	0.325	0.303	0.301	0.283
Birch	0.4	0	0	0	0
Field Maple	0.7	0.07	0.041	0.049	0.054
Hawthorn	6.9	1.562	1.644	1.523	1.5
Hazel	8.9	4.502	4.252	4.143	4.075
Oak	1.9	0.024	0.021	0.023	0.022
Sycamore	51.9	63.317	59.329	58.797	58.593

Table 4-4: Proportional representation of current population at Wytham Woods and after simulation of 4 years of baseline temperatures and three emissions scenarios, B1, A1B and A1fi.

The total number of individuals after 1250 years increases under all emission scenarios compared to the baseline conditions (ANOVA: $F_{3,24} = 327$, $p < 0.0001$; Table 4.4). Tukey's HSD post hoc test shows that there are significant differences between all scenarios ($p < 0.05$) and the baseline conditions. There are also significant differences between the three scenarios ($p<0.05$), except between medium (A1B) and high (A1fi) scenarios ($p = 0.296$; figure 4.3).

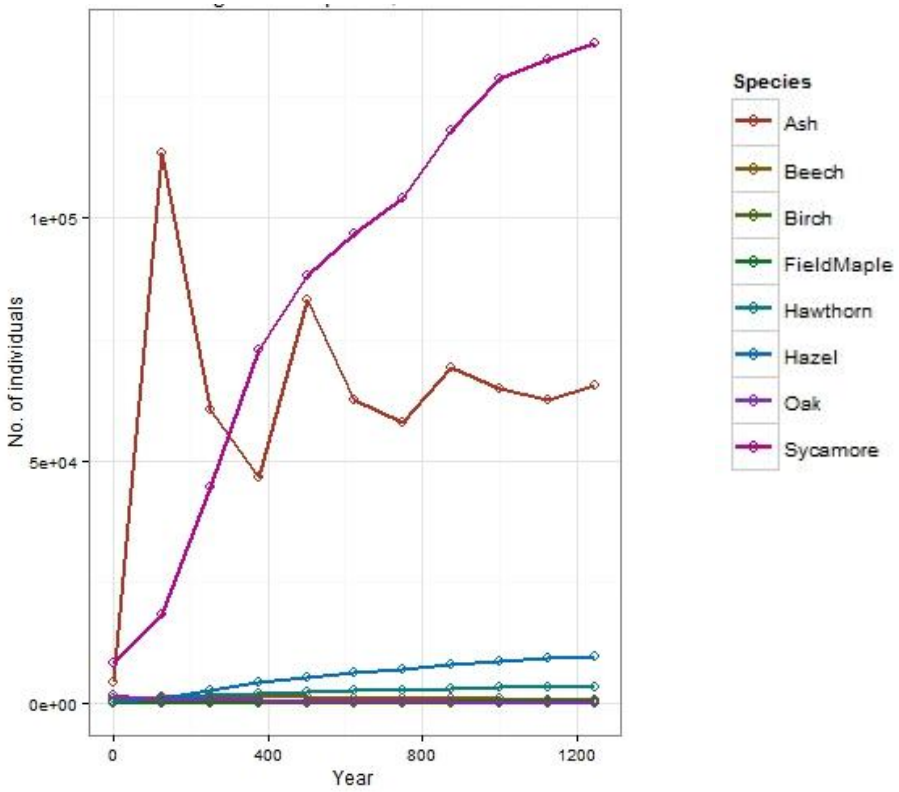


Figure 4-1: Time-series showing 1250 years growth of the eight species in baseline conditions. All other scenarios show a similar succession pattern.

There are significant differences in the total number of individuals of three of the eight species, ash, sycamore and field maple, between the three scenarios and the baseline (figure 4.3). There is a large increase in the number of ash individuals, of between 23% and 30% (15304 to 19447), in all the three emission scenarios, in comparison to the baseline conditions (Tukey's: $p<0.05$). There are fewer individuals in the B1 emissions scenario in comparison to the other two ($p<0.05$), however no significant difference is seen between the mid and high emission scenarios ($p=0.454$).

Sycamore also sees an increase in the total number of individual numbers in all scenarios compared to baseline, however this is much lower than ash, at between 1.6 % and 2.3% (2204

to 3222; $p<0.05$). There are no significant differences between the number of individual sycamores between emission scenarios. Numbers of field maple significantly decrease between the lowest emissions scenario (B1) and the baseline conditions ($p<0.002$).

	Number of individuals (±SD)			
	Baseline	B1	A1B	A1fi
Ash	64972 (±861)	80276 (±2102)	83159 (±1747)	84419 (±1297)
Beech	700 (±88)	714 (±102)	712 (±43)	674 (±79)
Field Maple	151 (±20)	96 (±16)	117 (±23)	128 (±37)
Hawthorn	3361 (±218)	3835 (±327)	3603 (±341)	3570 (±340)
Hazel	9686 (±631)	9920 (±317)	9798 (±777)	9698 (±323)
Oak	51 (±22)	50 (±14)	55 (±12)	52 (±15)
Sycamore	136221 (±1122)	138425 (±885)	139051 (±504)	139443 (±1152)
Total	215142 (±2961)	233316 (±3763)	236495 (±3447)	237984 (±3243)

Table 4-5: Absolute numbers (± SD) of the eight species at Wytham after simulations for 1250 years of baseline temperatures and three emission scenarios: B1, A1B and A1fi.

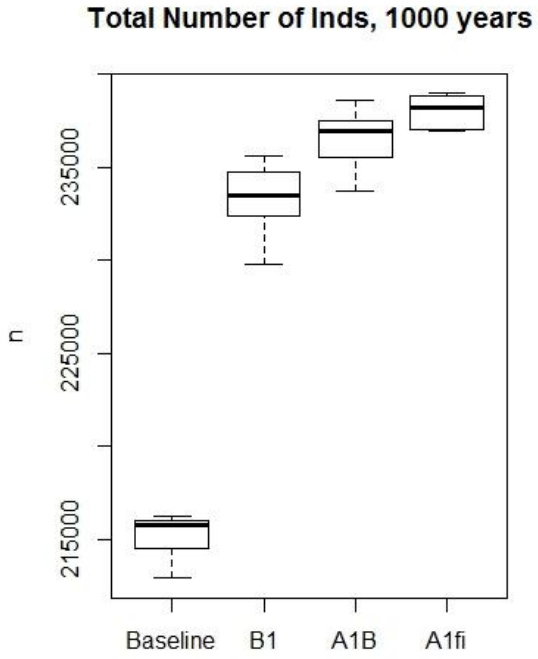


Figure 4-2: Changes in the absolute number of individual trees in the woodland after 1000 years with baseline temperature conditions and under three scenarios. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range.

Changes in individual numbers are seen equally at both adult and sapling life stages, with the proportions remaining the same for all scenarios (figure 4.4). The average DBH, height and age remains the same between scenarios.

There were no significant correlations between the any of the four life history variables: canopy openness, time to 3m in 1% light, time to 3m in 100% and survivorship in 1% light.

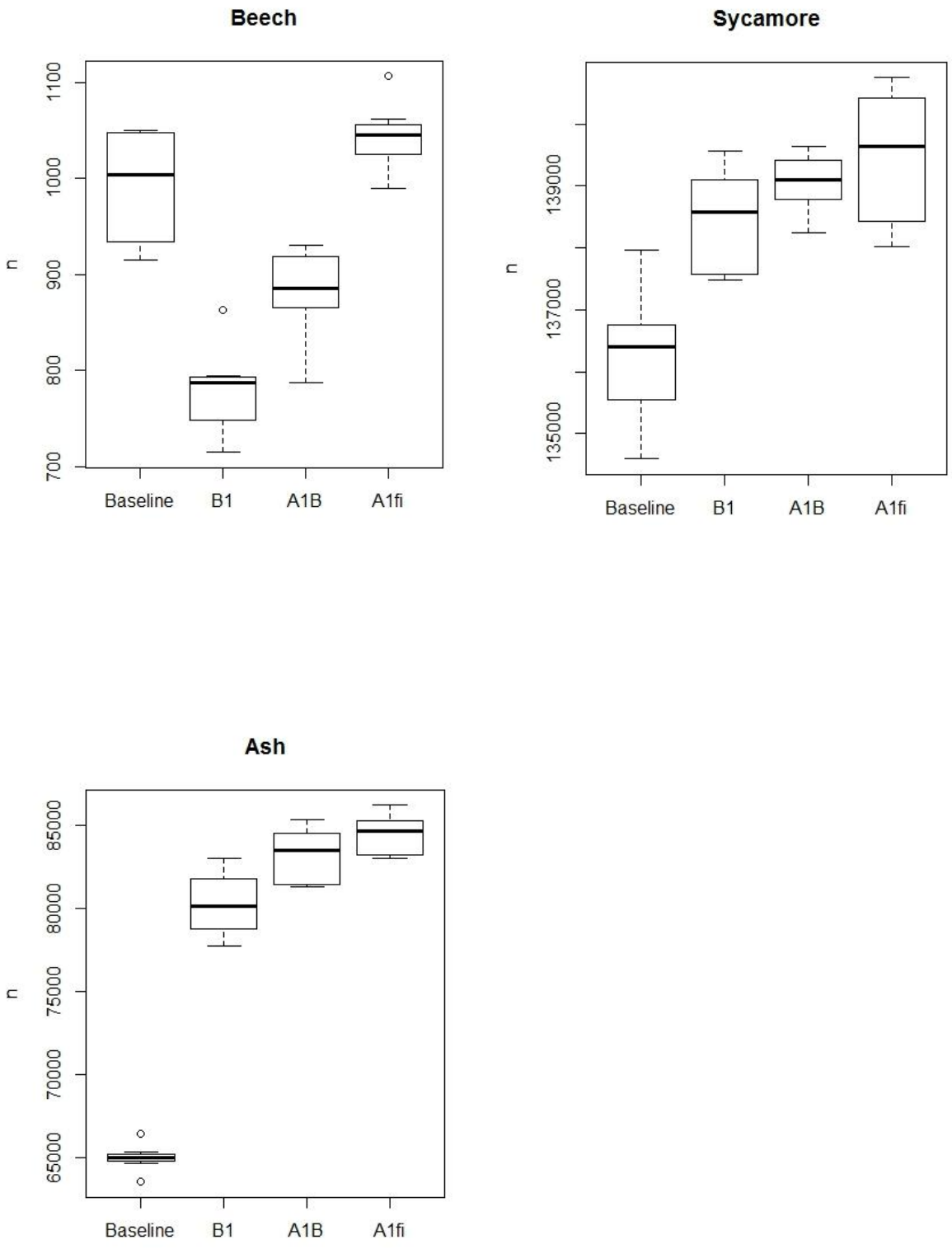


Figure 4-3: Changes in the number of individuals for the three species with significant differences between baseline conditions and three emission scenarios: beech, sycamore and ash. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range, or 1.5 times the interquartile range with individual outliers represented by circles.

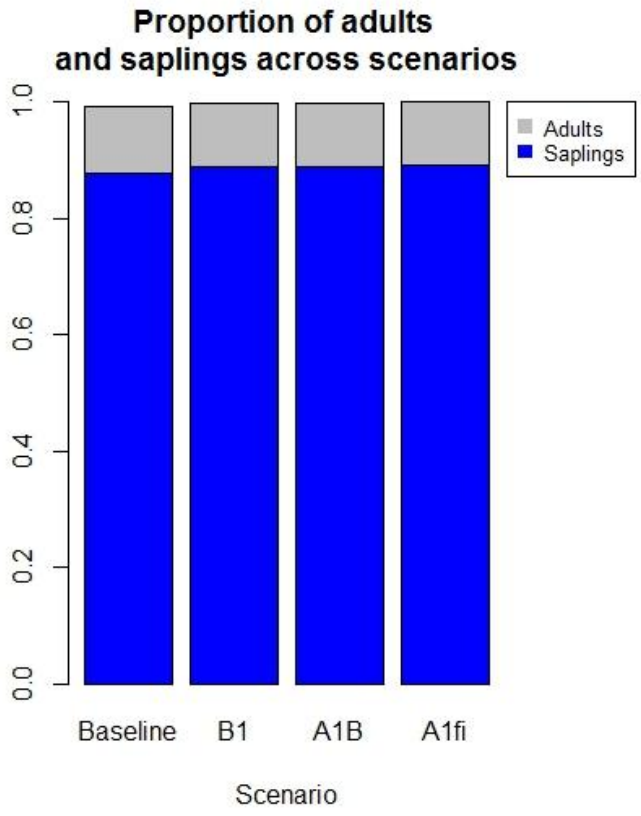


Figure 4-4: Proportions of adult and sapling across scenarios.

4.5 Discussion

Under all scenarios, with no management practices, it can be expected that the forest will have reached climax after 1250 years from the present day, with the absolute numbers of each species remaining roughly constant after 650 years. The co-dominant species remain ash and sycamore, however both of these increase their proportional representation with every other species reducing in proportion.

It was predicted that temperature-mediated increases of growth through budburst events occurring earlier would lead to competitive advantages of species over coexisting species. The results do not support this hypothesis with no clear relationship between the relative density of a species with its increase in growth period. Sycamore is the most sensitive to temperature, with budburst becoming earlier by 6.2 days for every degree Celsius rise, however the increase in the numbers of Sycamore after 1250 years under climate change conditions are modest when compared to ash, whose budburst is expected to move by 5.1 days per degree. The budburst of field maple is expected to be 3 days earlier per increase in degree Celsius, however the number of individuals of this species decreases after 1250 years in the lowest emission scenario B1.

There are no other significant differences in the forest in terms of individual number of species after 1250 years of model simulation. Birch becomes extinct in all conditions including baseline, which is not an unexpected result as both birch species present at Wytham Woods, *Betula pendula* and *Betula pubescens* are early successional pioneer species (Hynynen et al., 2010). Understory species hazel and hawthorn show increases in numbers over the 1250 years, even with temperature increases, as budburst date for hazel was shown to not be correlate with temperature, this was not expected. One explanation for this may be the current-day suppression of these species by deer. As disturbance was not included in the model, this reduction in herbivory could explain the increase in numbers with time.

Significant different of the proportions of species are seen between the three emissions and baseline after 1250 years. Since the only difference between models is the growth period, the non-linearity between this and proportional representation suggests that there are other

drivers influencing the species at Wytham. One potential driver is the differences in life histories traits between species. In the model, the only source of competition is that of shading neighbours from light, which is the major-above ground competition in forests (Kobe et al., 1995, Pacala et al., 1994, Casper and Jackson, 1997, Lin et al., 2004). Succession in forests is driven by interspecific differences in sensitivity to shade - a trade off between survival and low light conditions and growth in high light conditions (Pacala et al., 1996, Rees et al., 2001, Nakashizuka, 2001, Kunstler et al., 2009). Succession is driven by two contrasting strategies, with early-successional plants having high growth and survival in high light conditions, with low rates of growth and survival in resource-poor conditions. Late-successional plants display the opposite, having traits adapted to surviving well in low light conditions (Rees et al., 2001, Grime, 1979).

Sycamore is the most sensitive species to temperature, and has the second densest canopy, after beech, with co-dominant species ash being the second most sensitive. With the canopy closure occurring earlier in the year, this could potentially be a driver of succession. It could be expected that shade tolerant species will out-compete shade intolerant species as shade increases in intensity and duration. Sycamore and ash are the sixth and seventh slowest growing species in low light conditions with relatively high low-light survival, indicative of late-successional species, which may be the driver of increases in these species under climate change conditions. However, it cannot explain all of the results, with no change seen in beech the slowest growing species in low light conditions, but which also has higher survivorship in low light than sycamore and ash. Field maple is seen to decrease from baseline conditions in the low emissions scenario, but this has the highest survivorship in all species (joint with Hazel; 99.77% in 1% light) and is the fifth slowest growing. Low survivorship may be a predictor for the survival of some species however, with oak and birch having high mortality

in low light conditions of under 96% with the latter becoming extinct and oak decreasing over the 1250 years. Hazel was shown not to be sensitive to March temperatures, however my analyses only considered temperatures beginning in February. As Hazel has a relatively early budburst, future research should include winter temperatures as it is possible that the species will be correlated to earlier temperatures.

Pacala et al., (1996) suggested the different succession strategies can be inferred from trade-offs between the high light survival and low light survivorship, shade cast by a canopy and dispersal distance. These represent differences in allocation of energy in an individual, with lower survival in species that devote much of their energy to growth (Kobe et al., 1995). At Wytham no relationships between these life history traits are seen (table 4.1), and so at least in this study these trade-offs are unclear. There are however traits which are suggestive of succession dynamics. Succession theory suggests that early-successional species would grow quickly in high light, giving it a temporary advantage over taller, dense canopy late-successional species (Pacala and Rees, 1998). There is some evidence for this in our data, with hazel and hawthorn having the highest growth in low light, and beech showing a much slower growth rate. However, late successional ash and sycamore also have high growth in high light, with early-successional birch displaying slow growth in low light. This could be due to the small sample size of birch, and the age of Wytham Woods. If most of the individuals that were recorded were already in ancient woodland with dense canopies, then these individuals may grow slower than those in newly disturbed areas.

This study has implications for both forest management strategies and climate modelling. There is concern that the invasive species sycamore is of conservation threat to native species, especially ash (Binggeli, 1993, Peterken, 2001, Morecroft et al., 2008). This study

shows that even in baseline conditions, sycamore is not outcompeting ash, and that the latter is in fact expected to gain the most from temperature rises (Morecroft et al., 2008). The results also show that subdominant canopy species oak and beech persist in the forest, at similar population densities as seen today. This not only maintains the species diversity of the forest but is important for species that form symbioses with these species. Individual-based models can be used to provide accurate predictions of management strategies (Liu and Ashton, 1995, Phillips et al., 2004, Porté and Bartelink, 2002), and using them in parallel, forest managers will be able to moderate effects of climate change.

The results in this chapter consider increased growth period to proportionally increase the growth of a species, however this does not take into the considering the change in CO_2 availability. Gas exchange has been shown to be strongly seasonal with maximum photosynthetic rate occurring even up to 70 days later than the budburst date (Morecroft et al., 2003), with evidence of interspecific differences (Morecroft and Roberts, 1999). Future research on the growth periods, it would be desirable to take this into consideration that the changes in CO_2 uptake would have on productivity and thus growth.

The results from this model show also that species responses to climate change are not linear, and non-direct effects such as a competition and species life history traits can be equally important factors in determining species composition, and so should be included when predicting changes to populations. Currently most vegetation-climate models are estimating feedbacks using phenomenological models of tree succession which do not take into account competition and thus might be misestimating carbon balances within forests, which could have impacts on the climate predictions themselves (Samuelsson et al., 2011, Wang et al., 2015). Although some regional climate models do consider feedbacks with individual plant

functional types (PFTs), individual characteristics are averaged across cohorts, which does not allow for interactions between species to be considered (Smith et al., 2011).

Chapter 5

The direct effect of climate change induced changes in drought frequency on tree species at Wytham Woods

5.1 Abstract

The frequency and severity of summer droughts is likely to increase in the UK, due to reduced summer precipitation alongside increased temperatures, which is expected to be most pronounced in Southern England. This will have profound consequences on ecosystems, with it predicted to lead to reductions in growth and increases in mortality in plant species. In this study I use an individual-based model to examine the effects of increased droughts on tree species at a semi-natural ancient woodland, Wytham Woods. Currently the woodland is co-dominated by relatively drought-intolerant sycamore (*Acer pseudoplatanus*) and drought tolerant ash (*Fraxinus excelsior*). The model predicts that after 1000 years there will be a change of dominance from both of these species to a majority canopy of ash, with sycamore reduced to 2.4% of the population. The change in canopy has an indirect effect on other species, changing the light environment due to ash having a much less dense canopy than sycamore. This causes increases in understory species birch and field maple, as well as the canopy species, oak. By using this methodology I was able predict community level changes as an emergent property of species-specific reactions to climate change but to also discover indirect effects, such as these changes in the competition regime.

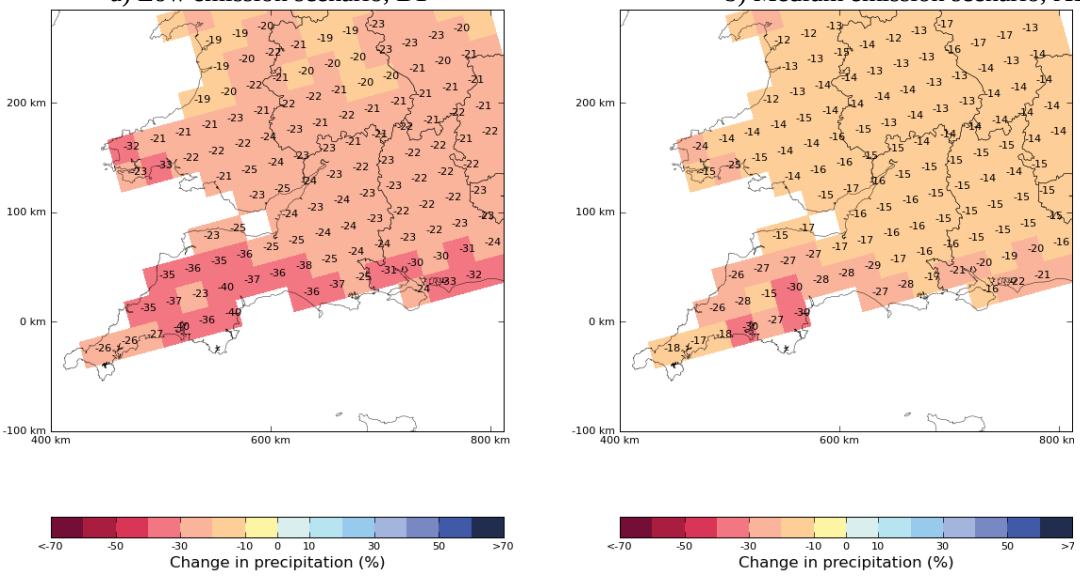
5.2 Introduction

Climate change is expected to cause substantial changes in the climate of the UK over the next century. Current climate projections suggest that during the summer months there will be proportionally less precipitation and an increase in mean air temperature, leading to an increase in the frequency, duration and severity of droughts (Murphy et al., 2009). The largest changes are expected in Southern England, where summer precipitation is expected to

decrease by up to 40% (figure 5.1), with increases to mean summer air temperatures of up to 8°C, by 2080 (Murphy et al., 2009). Previous estimates from the UKCIP02 predict decreases in soil moisture content by up to 46% (Hulme et al., 2002). These changes are predicted to occur at an accelerating rate (Smith et al., 2015) which has serious implications for the responses of ecosystems.

a) Low emission scenario, B1

b) Medium emission scenario, A1B



c) High emission scenario, A1fi

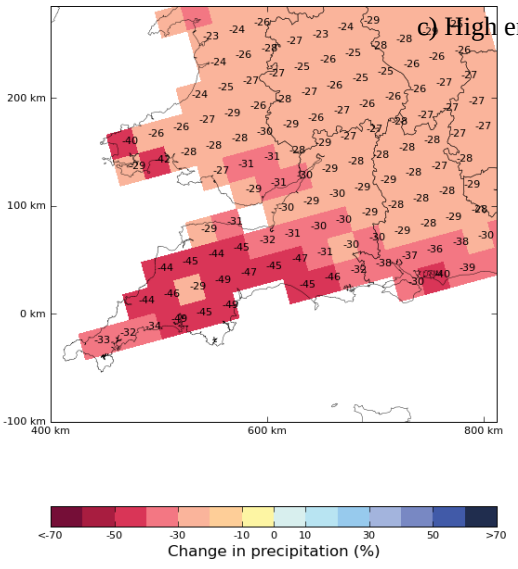


Figure 5-1: Predictions of percentage change in average summer precipitation by 2090-2099 for low (a), medium (b) and high (c) emission scenarios. © UK Climate Projections 2009.

In temperate areas, such as the UK, most aspects of climate change will benefit plants in the short-term, with increased temperature and CO_2 partial pressure expected to increase productivity, growth, leaf area and growing season, until nutrient availability becomes limiting (Broadmeadow and Jackson, 2000, Broadmeadow and Randle, 2002, Sparks and Menzel, 2002, Tylianakis et al., 2008, Lukac et al., 2010, Norby et al., 2005, Wu et al., 2012). There is however increasing evidence that water limitation caused by the increasing drought severity and duration is leading to an overall reduction in growth, and an increase in mortality in plants (Gitlin et al., 2006, Van Mantgem and Stephenson, 2007, Worrall et al., 2008, Rehfeldt et al., 2009, van Mantgem et al., 2009). These responses to drought events are lagged in some species, influencing the long-term productivity of individuals (Peterken and Mountford, 1996, Bigler et al., 2007).

The reduction, or loss, of drought-sensitive species will have detrimental effects on associated organisms, and local ecological processes (Carnicer et al., 2011, Hanewinkel et al., 2013). The resulting shift in population structure may also have severe consequences for broader processes such as nitrogen and hydrological cycles as well as global carbon cycles and vegetation-climate feedbacks (Dixon et al., 1994, Soja et al., 2007, Bonan et al., 2003, Bonan, 2008b). Differences to drought tolerances could be a mechanism by which otherwise less competitive, or historically dominant species, may confer an advantage over, or coexist with, currently dominant species (Terradas et al., 2009, Cavin et al., 2013). Any changes of dominance between competing species will change habitat structures, affecting all trophic levels (Chapin Iii et al., 2000, Ellison et al., 2005, Thibault and Brown, 2008, Cavin et al., 2013).

Changes to dominant species are particularly important in woodland and forests, as dominance reversals would alter light conditions in the understory, affecting the growth of coexisting species. Given that climate change effects may lag for years after drought events, meaning that observing the results on light competition will take generations, we are unable to make predictions using regression functions or by comparing predicted environment conditions to currently similar environments (Mette et al., 2013, Williams and Jackson, 2007).

In this study I look at a mixed-species forest in Southern England, where the current dominant species are sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus excelsior*). The former is a non-native species in the UK and is regarded to some as a threat to native species including ash (Morecroft et al., 2008). Sycamore is a drought-intolerant species, it's native habitat being cool and damp areas in central Europe (Lemoine et al., 2001, Rusanen and Myking, 2003, Scherrer et al., 2011), whereas ash is much more tolerant to drought conditions (Lemoine et al., 2001, Scherrer et al., 2011, Morecroft et al., 2008). Using a climate-matching method (Broadmeadow et al., 2005) suggested that sycamore will decline in most of the UK as a consequence of increased droughts, whilst ash will be less affected. This could lead to a dominance reversal from sycamore to current co-dominant species ash, and potentially allow other drought-tolerant canopy species such as pedunculate oak (*Quercus robur*) or beech (*Fagus sylvatica*) to establish dominance.

In order to predict population-level change I use a spatially-explicit neighbourhood model, which is able to demonstrate population level changes from changes at the individual level. By introducing drought tolerances at the species level any population-level effects will be an emergent property from interactions between individuals and species. My hypothesis was that

at this mixed-species forest, future droughts will reduce the dominance of drought-intolerant sycamore, allowing other canopy species such as ash, oak and beech to thrive and become the dominant species.

5.3 Methods

5.3.1 Study Site

Wytham woods is a mixed land-use area of agricultural land, grassland and around 400ha of semi-natural ancient mixed woodland. It is a well-known site of ecological research located in 5km north-west of Oxford, South East England (1°20′W 51°46′N), owned and managed by Oxford University. It has an altitude between 60 to 165m above sea level with a mean annual precipitation at 730mm y^{-1} and an average annual temperature of $10.1^{O}C$ (Butt et al., 2014). Forty-one $10m^2$ plots have been surveyed since 1993 across the site as part of the Environmental Change Network. We used data from ten species of tree that account for over 98% of the tree biodiversity at the site: sycamore (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*), European beech (*Fagus sylvatica*), penduculate oak (*Quercus robur*), common hazel, (*Corylus avellana*), common hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), and birch (*Betula* spp.).

5.3.2 Data Description

Ten individual trees in each of the 41 plots were measured over 19 years at three year intervals from 1993 to 2008 and again in 2014. If trees within a plot were not relocated in a survey year then they were presumed dead, and replaced with the nearest unmarked individual. The data therefore provides both growth and mortality data; however it is notable that there are relocation errors in the dataset, with trees that are presumed dead appearing in

later surveys. It is therefore necessary to include relocation probability to ensure that mortality probabilities are not inflated (Kéry and Schmid, 2005).

A previous study by (Moustakas and Evans, 2015) showed that the mortality of the population at the study site was explained best by a model of diameter at breast height (DBH) only, with models including light and growth having less explanatory power. DBH is a measurement of the diameter of the tree at 1.35m above ground level, and was measured every time a tree was located. For this study I wanted to look at the effect of drought on mortality rates of the population. In order to do this I defined drought using the Standardised Precipitation Index (SPI; McKee et al., 1993), which is able to define drought events over any time frame and considers only rainfall. It normalises the rainfall data using a probability distribution over the time frame that is considered, allowing for the estimation of both dry and wet years using the following equation:

$$SPI = \frac{(monthly\ precipitation - average\ precipitation)}{s.d.precipitation} \quad (5.1)$$

The average and standard deviation of the full precipitation data that are available, which is recommended to be at least 30 years (WMO 2013). The closer the resulting SPI is to -3, the more severe the drought, whilst +3 is an extremely wet period.

Monthly average precipitation data for the years 1970-2014 were downloaded from the Met Office Hadley Centre England & Wales Precipitation series (HadEWP; Met Office). This provides regional rainfall data for five sub-regions of England and Wales, using stations in 5-km^2 grids (Simpson and Jones, 2012), with the southeastern region including the area of Wytham Woods. This study considers the effect of summer months and so the average

rainfall for the months June, July and August were used to calculate the annual SPI. Years falling between each sampling interval were averaged to provide an SPI for that sampling time.

5.3.3 Estimating survival rates

In order to estimate the survival rate of species, capture-mark-recapture software package MARK was used (White and Burnham, 1999). This applies a modified Cormack-Jolly-Seber model (CJS; White and Burnham, 1999), allowing the estimation of both survival and relocation rates. Individuals that are not located during a survey are presumed to be dead unless they are relocated at a later time point. An example of the input file for three individuals would look like:

1111011;
1111111;
1111000;

where the first line shows an individual that was not located on the fifth survey but consequently relocated; the second is an individual that has been located at every survey; and the third is an individual that was not relocated after the fourth survey and so is likely to have died.

Two covariates, DBH and SPI were included in the analysis to investigate their effect on the probability of survival (ϕ), with the probability of relocation (p) being kept constant between time periods after no *a priori* annual bias for this was found in the data (Moustakas and Evans, 2015). A total of four models were fit to each species which included the covariates

DBH and SPI as well as the additive and interactive interactions of the two (table 5.1). For all models a logit link function was used due to the use of covariates (White and Burnham, 1999). The model that best explained the data for each species was established using the corrected Akaike criterion for finite sample size (QAICc; Hurvich and Tsai, 1989).

Model	Model Description	
	Survival Probability (Φ)	Relocation probability (p)
Φ: DBH; p: c	Constant between years; varies with DBH	Constant between years
Φ: SPI; p: c	Constant between years; varies with SPI	Constant between years
Φ: DBH + SPI; p: c	Constant between years; varies with SPI and DBH independently	Constant between years
Φ: DBH*SPI; p: c	Constant between years; varies with SPI and DBH dependently	Constant between years

Table 5-1: Model descriptions for the four mortality models, run for all species.

The compliance with the assumptions underlying the model was tested by generating a saturated CJS model for each species, where both survival and probability varied with time period on which a 1000-iteration parametric bootstrap for each model was performed within MARK (White and Burnham, 1999). This saturated model simulates data that meets all assumptions of a CJS model: no overdispersion, independence of individuals, same probability of relocation, same probability of survival, no lost marks and instantaneous sampling. This generates a variance inflation factor for each species (^c), which I used to re-run each model correcting for overdispersion in the data.

5.3.4 Future Rainfall Projections

In order to investigate the effect of future drought on the population at Wytham, I used forecasted precipitation data obtained from Met Office Hadley Centre UKCP09 Model

(accessed through http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/; Murphy et al., 2009). Monthly averages were calculated using the absolute precipitation data, which provides daily average precipitation for the years 2020-2080. Data were taken from the 25m^2 grid square 1547, which encompasses Wytham Woods, with the 50% cumulative distribution used for each of the emission scenarios: low (B1), medium (A1B) and high (A1fi). The rainfall for the summer months June, July and August were averaged, and the SPI calculated using the predicted rainfall alongside the HadEWP data from 1970. The data were averaged every ten years to provide decadal average SPI.

5.3.5 Model Runs

The new survival estimates were incorporated into the spatially-explicit model that has been parameterised for the species at Wytham (see chapter 3), with the mortality function of the model updated as following:

```
dam = (exp(
            params[kind].phi1
            + (params[kind].phi2
             * ((trunkDiameter*100) - params[kind].meanDBH)
     / params[kind].sdDBH))
                   + (params[kind].phi3 * avSPI))
            / (1
             + (exp(params[kind].phi1
              + (params[kind].phi2
                   * ((trunkDiameter*100) - params[kind].meanDBH)
       / params[kind].sdDBH)))
                        + (params[kind].phi3 * avSPI));
```

where:

dam is the mortality probability for an individual at a single time step

params[kind].phi1 is the first mortality parameter

params[kind].phi2 is the parameter relating mortality to DBH

params[kind].phi3 is the parameter relating mortality to SPI

The SPI was kept constant after 80 years, in line with current predictions of a plateau of climate change in most scenarios after around this time (IPCC, 2014). A model to simulate current baseline conditions was run using the average SPI for the years 1970-2015. Each of the four models were run eight times simulating 1250 years in 5-year time-steps. Each simulation was initialised with the same forest structure, with the species, size and spatial structure as recorded at Wytham Woods during fieldwork.

5.3.6 Data Analysis

Statistical analyses were performed in R 1.3.0 (R Core Team 2013). Differences between the emission scenarios and baseline were analysed using one-way ANOVA. Normality of the data was tested for using the Shapiro-Wilk test, with homogeneity of variances being confirmed using diagnostic plots. Where there were significant differences between scenarios, and the assumptions of the tests were met, a Tukey's honest significant difference (HSD) post hoc test was performed.

Differences in age, DBH and height between scenarios were also investigated using a one-way ANOVA. Differences in the proportion of adult and sapling s were tested using a Pearson's chi-squared test.

5.4 Results

5.4.1 Survival Estimates

The model which most closely explained the mortality of all of the species at Wytham was an additive one that included both DBH and SPI (table 5.2). This model was only the best fitting model for field maple, but was the second best fitting model for sycamore and birch (after SPI and DBH respectively), where the difference in QAIC from the best fitting model was less than 1, meaning that there is no difference between these models (Bozdogan, 1987). In Oak and Hawthorn the mortality model is the third best fitting model by $QAIC_c$ but these also have very low difference in $QAIC_c$ from the first model (1.8 and 2.1 respectively) and so I considered to be an appropriate choice of model to represent all species.

	Best Model	2nd Best Model	3rd Best Model	4th Best Model
Field Maple	**DBH + SPI**	DBH*SPI	DBH	SPI
$\Delta QAIC_C$		2.209	2.7354	5.0511
Sycamore	SPI	**DBH + SPI**	DBH	DBH*SPI
$\Delta QAIC_C$		0.5584	0.608	1.7052
Birch	DBH	**DBH + SPI**	SPI	DBH*SPI
$\Delta QAIC_C$		0.2277	0.566	2.3382
Hazel	DBH	SPI	DBH + SPI	DBH*SPI
$\Delta QAIC_C$		0.5607	2.0256	3.9964
Hawthorn	SPI	DBH	**DBH + SPI**	DBH*SPI
$\Delta QAIC_C$		0.2275	2.1111	3.9388
Beech	DBH*SPI	**DBH + SPI**	SPI	DBH
$\Delta QAIC_C$		9.15	11.115	11.4922
Ash	DBH*SPI	SPI	DBH	**DBH + SPI**
$\Delta QAIC_C$		4.6759	5.3489	6.5877
Oak	SPI	DBH	**DBH + SPI**	DBH*SPI
$\Delta QAIC_C$		0.0218	1.8311	3.8845

Table 5-2: Model selection for each species. ΔAICC1 is the difference in QAICc between the model and the best fitting model. The chosen to represent the mortality for all species is in bold.

5.4.2 Drought estimations

The lowest SPI (therefore the highest drought) was during the period 1993-1996 (Table 5.3). During 1997 to 2012 there was a period of summer rainfall that is above average, with there being moderate summer rainfall in the time period 2009-2012, when compared to the average since 1970. The SPI calculated from UKCP09 data predicts that there will summers will be increasingly dry when compared to the average in future decades (table 5.4).

Years	SPI
1993-1996	-1.0728
1997-1999	0.2020
2000-2002	0.0029
2003-2005	0.2830
2006-2008	0.8103
2009-2012	1.0476

Table 5-3: Standardised precipitation index (Seidl et al.) for the years 1993-2012, with 3 year time step when calculated with rainfall from 1970

Years	SPI
2012-2020	-0.0440
2021-2030	-0.1874
2031-2040	-0.2484
2041-2050	-0.4314
2051-2060	-0.5325
2061-2070	-0.6168
2071-2080	-0.6960

Table 5-4: Standardised precipitation index (Seidl et al.) for the years 2012-2080 for decadal averages when calculated with rainfall from 1970

.

5.4.3 Model Runs

In all scenarios, including the baseline, the dominance in the forest changes from a co-dominance of sycamore and ash to a canopy that is comprised primarily of ash. In baseline conditions, with the same drought regime seen in the last 30 years, ash is predicted to

increase in relative abundance from nearly 27% to 84%. This is largely caused by the decrease in current co-dominant sycamore from 60% to only 2.4% of the population. As well as ash another canopy species, oak, is predicted to increase from its current 2% to 7.5%. There are reductions in the relative abundance of all other species. Whilst there are minor differences between scenarios, these changes are reflected in all of the emissions scenarios, with ash representing between 83.7 and 83.8 of the population (table 5.5).

	Proportions (%)				
	Current	After 1250 Years			
		Baseline	B1	A1B	A1fi
Ash	26.9	83.6	83.7	83.8	83.7
Beech	1	0.7	0.7	0.7	0.7
Birch	0.4	0.4	0.4	0.4	0.5
Field Maple	0.7	0.3	0.3	0.3	0.4
Hawthorn	6.9	3.7	3.7	3.6	3.4
Hazel	8.9	1.2	1.1	1.1	1.2
Oak	1.9	7.5	7.6	7.7	7.8
Sycamore	51.9	2.6	2.5	2.4	2.4

Table 5-5: Proportions of the eight species as in 2014 and projected 1250 years in 3 emission scenarios: B1, A1B and A1fi and baseline (1970-2014) rainfall conditions.

Patterns of succession are similar in all scenarios, with the largest changes occurring after 250 years. During the first 250 years the numbers of sycamore individuals remains about the same in the baseline conditions, decreasing slightly in all emission scenarios (figure 5.2). After this, there is a steady decline in number of individuals, whilst there is an exponential increase in ash. A similar pattern of increase is seen in hawthorn and oak, after the 250 years. Beech and hazel increase in number for 300 years, beech numbers then reducing during the next 1000 years whilst hazel numbers remains nearly constant. There are modest increases in birch and field maple during the entire 1250 years.

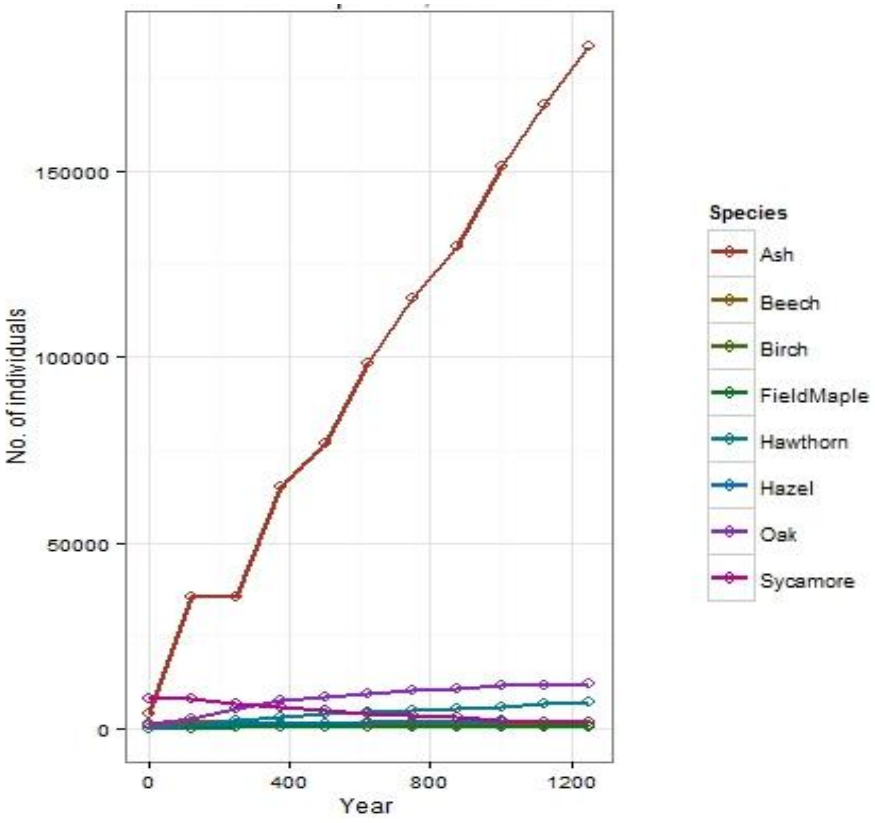


Figure 5-2: Time series showing 1250 years of growth of eight species in baseline conditions. All other scenarios displayed similar trends.

The overall number of individuals in the forest is seen to decrease with increased intensity of drought (ANOVA: $F_{(3,28)}=4.6$, $p<0.001$). In comparison to baseline conditions the total absolute number of individuals, 136305, decreases most in the scenario A1B, on average by 2011 individuals. The number of individuals reduces on average by 1848 in the A1fi and 1155 in the B1 emission scenarios. Post hoc tests suggest no difference between any of the scenarios, although they are seen to decrease along a drought gradient, with very low variance within scenario A1fi (figure 5.3).

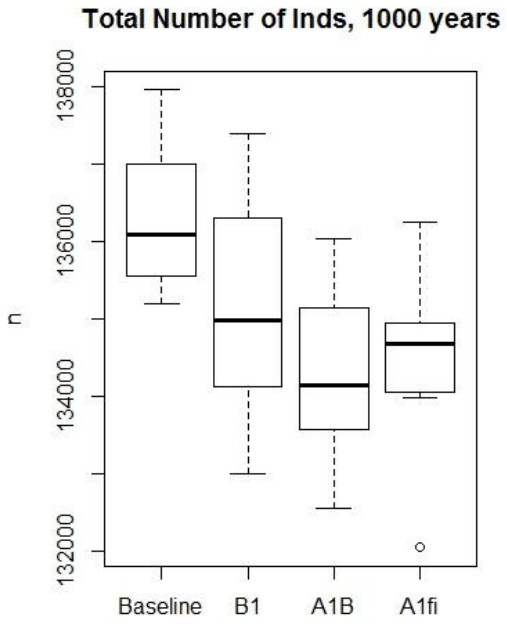


Figure 5-3: Total absolute number of individuals after 1250 years in four model runs: baseline precipitation conditions and three emission scenarios (B1, A1B, A1fi). The dark horizontal line represents the median number of individuals from the eight runs, with top

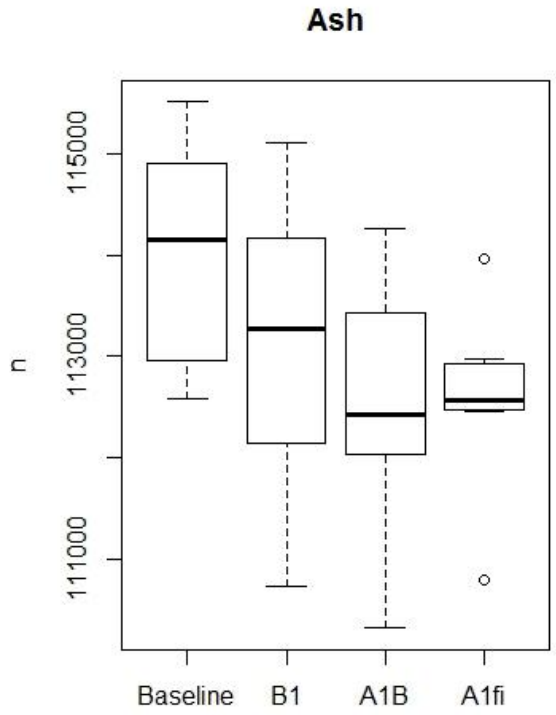
There are significant differences in the number of individuals between scenarios and the baseline in three of the species: beech ($F_{(3,28)}$=3.4, p<=0.03), birch ($F_{(3,28)}$=4.4, p=0.01) and sycamore ($F_{(3,28)}$=0.5, p<0.067; table 5.6). Similar to the overall numbers, beech and ash reduce in numbers with increasing drought intensity. Birch shows the largest differences between scenarios, increasing between 18.41% in the A1B to 28% in A1fi, rising from 478 individuals after 1250 years in baseline conditions, to 556 and 565 respectively. It increases the most in scenario A1fi, by 85 individuals to 887. Both beech and sycamore see declines in comparison to the baseline conditions. Beech reduces from 972 to 804, 885 and 887 in scenarios B1, A1B and A1fi respectively. Sycamore reduces by 190, 301, 289 individuals from 3515 at baseline (figure 5.4).

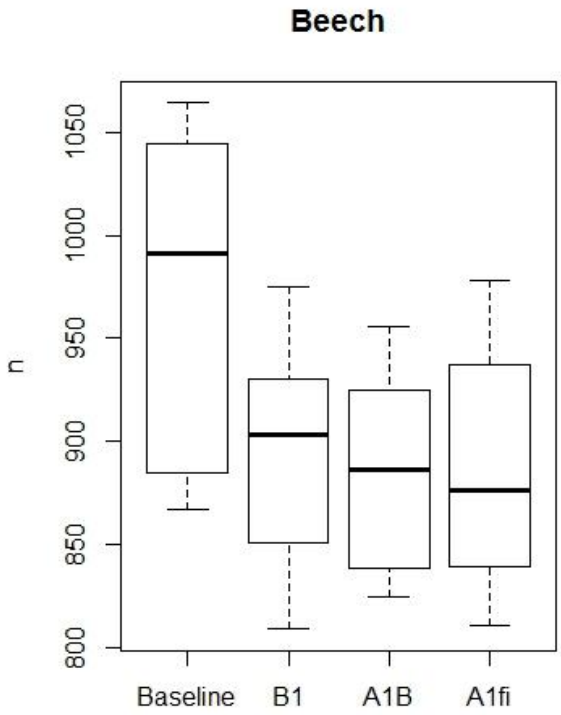
The pattern of changes to relative abundance of each of the species is identical to changes in

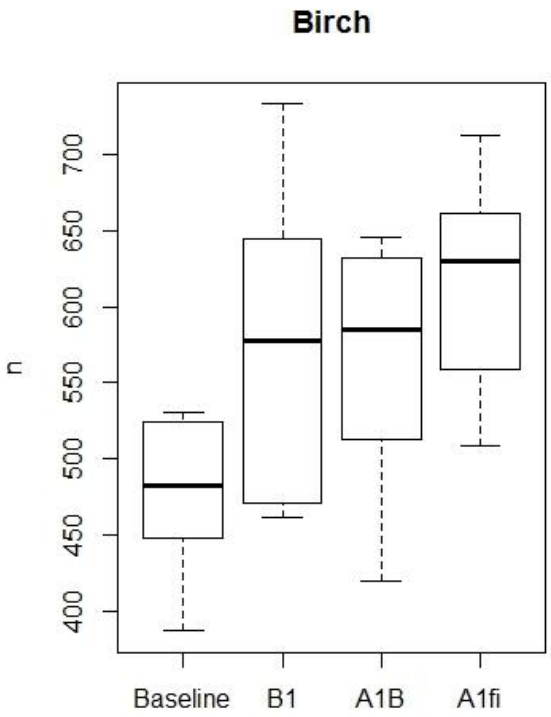
absolute numbers (see table 5.6). Between scenarios, there are no significant differences between the age, DBH or height of the species. There are also no differences between the ratio of adults to saplings (χ^2=0, df=3,p=1).

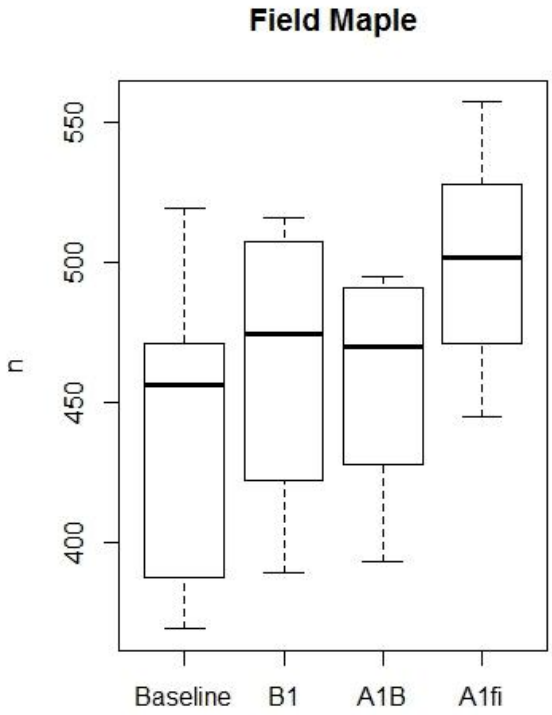
	Emissions Scenario			
	Baseline	B1	A1B	A1fi
Ash	114015 (±1101)	113127 (±1433)	112543 (±1240)	112586 (±878)
Beech	972 (±89)	894 (±57)	885 (±49)	887 (±61)
Birch	478 (±50)	573 (±103)	566 (±79)	615 (±68)
Field Maple	440 (±53)	464 (±49)	458 (±39)	500 (±39)
Hawthorn	5032 (±361)	4933 (±237)	4815 (±203)	4609 (±430)
Hazel	1589 (±113)	1514 (±49)	1502 (±138)	1610 (±143)
Oak	10264 (±251)	10320 (±296)	10311 (±90)	10424 (±344)
Sycamore	3515 (±175)	3325 (±60)	3214 (±97)	3226 (±113)
Total Numbers	136305 (±2187.168)	135150 (±2283.922)	134294 (±1934.792)	134457 (±2076.672)

Table 5-6: Predicted absolute numbers (± SD) of the eight species in the model after 1250 years, in baseline conditions and three emission scenarios: B1, A1B and A1fi.


Ash
n
115000
113000
111000
Baseline
B1
A1B
A1fi


Beech
n
1050
1000
950
900
850
800
Baseline
B1
A1B
A1fi


Birch
n
700
650
600
550
500
450
400
Baseline
B1
A1B
A1fi


Field Maple
n
550
500
450
400
Baseline
B1
A1B
A1fi

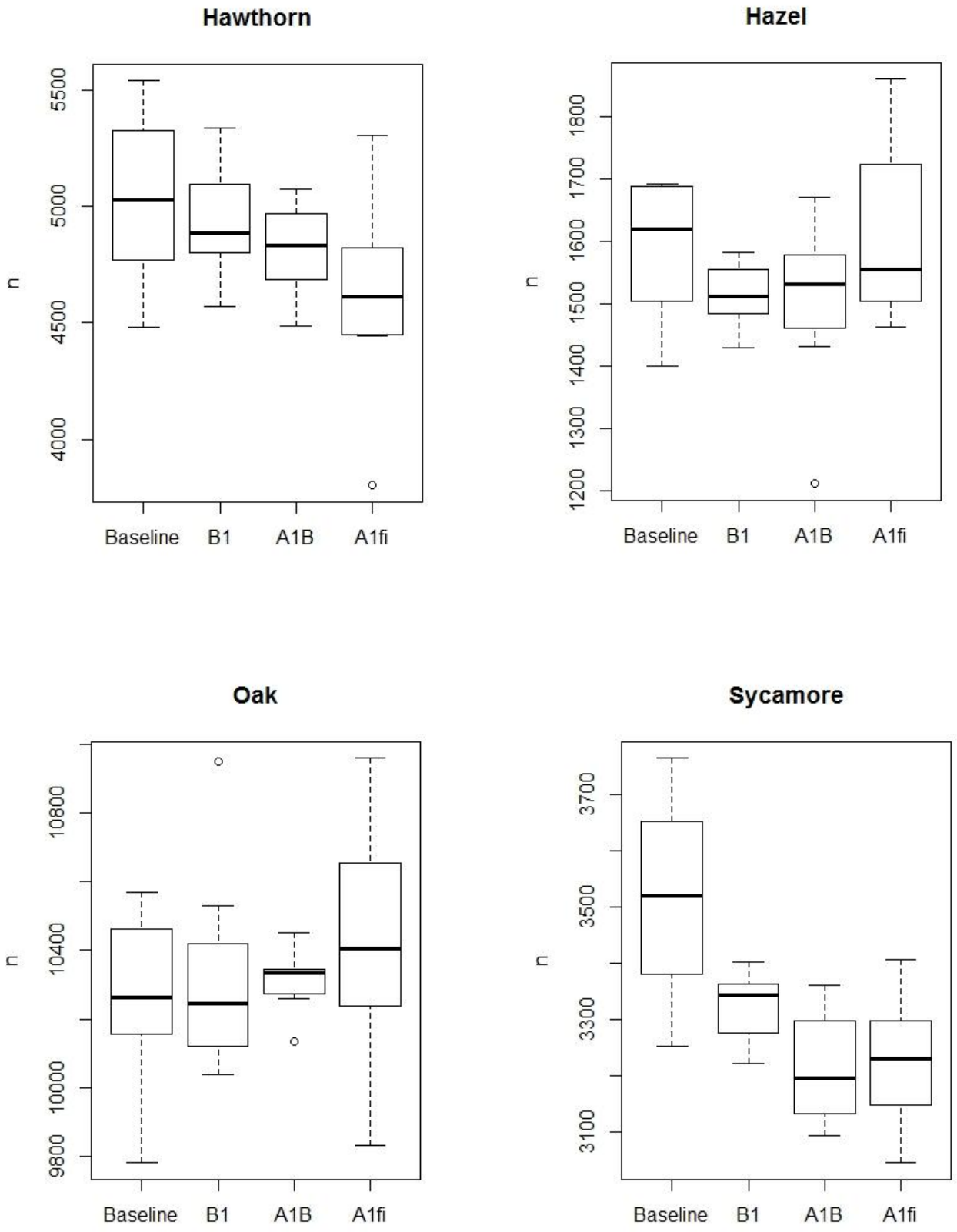


Figure 5-4: Projected absolute numbers for each of the eight species under the three emission scenarios B1, A1B and A1fi and baseline precipitation conditions. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range, or 1.5 times the interquartile range with individual outliers represented by circles.

5.5 Discussion

These results show that even under the current climate conditions a regime shift of the species at Wytham Woods is likely, with a change from the dominance of ash and sycamore to a dominance of ash. This is consistent with previous predictions that sycamore will decline in much of the UK due to increases in drought, especially in the South East of the country (Broadmeadow et al., 2005). Morecroft et al. (2008) also showed that sycamore showed a drought sensitivity between 1993 and 2005 at Wytham, with its slowest growth at the driest period. They also showed that ash consistently grew quicker than sycamore, independent of the rainfall conditions. This intolerance of sycamore to drought, as well as the the higher growth in ash, is a means for the relatively drought intolerant ash to increase in number greater than sycamore.

As well as ash, the change in dominance allows for other canopy species *Q. robur* to increase their proportional abundance, compared to present day within the forest by up to 6%. As well as the increase in gaps caused by mortality of sycamore allowing opportunities to grow into the canopy (Watt, 1947), another mechanism that can explain the increase in oak is the change in light competition. The new dominant species, ash, has a much higher light transmission through its canopy than sycamore (Evans et al., 2015); this increases the light to understory species which would lead to higher growth and survival rates in species, such as oak.

Further evidence for this change in light regime are in the steady increases of birch and field maple, both of which are understory species. Birch especially is intolerant of low light conditions, with low growth and high mortality (Hynynen et al., 2009), so its survival suggests a direct effect of the change of dominance to ash, with its relatively high light

transmission. Birch also exhibits a tolerance to drought, which is contrary to previous studies that show that birch is relatively drought intolerant. This could be because of the small number of data available for birch in the dataset. There is a reduction in the proportion of the other canopy species at Wytham, beech. One explanation is because of competition between beech and oak, the latter of which has greater drought tolerance due to its deeper rooting and lower susceptibility to cavitation (Aranda et al., 2000, Rose et al., 2009).

The resilience of sycamore in the first 250 years of the simulation is evidence for the lag effects of drought in species. A lagged effect on individuals is not directly modelled in this study, and as time steps are every 5 years, the lag of a few years reported elsewhere was not considered here (Bigler et al., 2007). However, the decline after 250 years suggests could be suggestion of a generational lag. If drought affects the mortality of saplings more than larger trees, then this may not be seen in the forest stand for a generation. Although the model with no interaction between DBH and drought was chosen for all of the species, in sycamore there was a very close concurrence of each of the four models, with a difference of 1.7 between them all. This does not therefore rule out an interaction between DBH and drought, suggesting that adults may be less susceptible to drought than saplings, as has been shown in other species (He et al., 2005, Mediavilla and Escudero, 2004), meaning that any established trees would not be as affected by drought as their offspring. Whilst one drought event could affect a population, the effects would be more pronounced with progressive droughts as predicted under climate change, and shown by the increasingly negative SPI. At Wytham Woods there is a very high survival rate of sycamore trees, between 97.8 and 99.9%, and so almost adults survive until senescence. Once these larger individuals senesce, then the increase of drought and the lower survival of saplings could explain the decline in numbers over the next 1000 years that is seen. Because of this generational lag, any indirect effects of

climate change, such as those occurring through light competition, could also take a generation to be seen.

There are only very minor differences in the response of trees to the future emission scenarios compared to the current rainfall regime, with only three species seeing significant differences, and only very small differences between these. This suggests that for Wytham woods, the decreases of rainfall under climate change that are predicted over the next 80 years will not be a driver of change to community structure compared to current conditions. One explanation is that changes have already been occurring in the local area due to the recent climate change. The data I used to estimate survival rates of the tree species was taken over the last 30 years, and there is evidence from others that the survival rate in some species has reduced in the last 50 years compared to records from 1766 (Jenkins et al., 2009). If the survey data were taken during a period of increased droughts then this will be reflected in the survival rates.

For this study I focussed on the mortality of species in relation to the average rainfall, however it is likely that extreme events will cause dieback events and determine species distributions (Gitlin et al., 2006, Worrall et al., 2008, Rich et al., 2008). For future research it would be necessary to use data on species mortality responses to extreme drought events, which could be performed experimentally if field data is not available. As well as extreme summer drought events, winter rainfall will have an impact on dieback events, with lower rainfall decreasing soil moisture and exacerbating low summer rainfall and increasing mortality in drought intolerant species. When predicting future drought conditions, I averaged the annual SPI every decade, which also failed to capture the full range of drought conditions that would be expected. The averages also are not comparable to the recent drought

conditions which were averaged every three years, in line with the surveying regime. Future research should take this into consideration, ensuring that future projections are comparable to recent events as well as taking into account extreme events.

With ash accounting for around 80% of the woodland after 1000 years in all model simulations, the reduction in diversity has implications for future resilience of the forest (Elmqvist et al., 2003). As forests become dominated by one species, there is danger of regime shifts, or ecosystem collapses (Scheffer and Carpenter, 2003, Petit and Hampe, 2006). This is of particular concern with ash dominated woodlands in the UK because of the dieback events caused by the *Hymenoscyphus fraxineus* fungus that have been occurring in the UK since 2012 (Mitchell et al., 2014). Evidence from Europe suggests that this may be a widespread infection with up to 99% of individuals of the species being susceptible to the disease (Kjaer et al., 2012, Pautasso et al., 2013).

One limitation of this study is the use of widely available rainfall data from HadEWP, which only begins in 1970. If climate change has been having an effect for the last 30-50 years, then this SPI will be skewed upwards, in comparison to that expected under more historical conditions in the woodland. Other methods also use temperature data to predict drought indices, which may produce a better overall picture of soil moisture availability for the plants. These methods will still be marred with skews with digitised data available from the HadEWP only covering the period since 1970, when climate change may have already be having an effect on the local climate. There are data recorded from 1914, and whilst this is less accurate due to there being fewer data, it may provide drought predictions representative to pre-climate change conditions.

Additionally, this study does not consider any evolutionary effects, although these will be important in a species' response to climate change. There is evidence that responses could be mediated by different phenotypes in the short-term (Choler et al., 2001, Bolnick et al., 2011), and changes to phenotypes in the long term (Jump and Penuelas, 2005, Bilela et al., 2012). There is, for example, already evidence for the acclimation of drought tolerance of sycamore, by osmotic adjustment, changes in root distribution and stomatal closure (Khalil and Grace, 1992).

This study provides a good example of population-level properties emerging from changes at the individual- and species-level. By using an individual-based systematic approach, not only are we able to investigate the direct effect of drought on the population, but other, indirect, impacts can come to light and be investigated further. It would be a logical step to investigate the light experienced by individual trees, and the role that neighbouring species has on their own growth and survival.

Chapter 6

The combined effects of drought and growing season length on tree species at Wytham Woods and potential mediation through interactions

6.1 Abstract

Changes to ecosystems are predicted to happen as a consequence of anthropogenic climate change. For temperate plants the potential impacts of increased temperature on growth and productivity will be offset in some species by the increased water deficit caused by increased temperatures and decreased summer rainfall. As well as this direct effect, there will be changes to biotic interactions, benefitting some species at the cost of others. Using Wytham Woods as a model system I provide evidence that biotic interactions - -increased growth period caused by temperature - can increase a species' fitness, but only when not constrained by drought. The current co-dominance of sycamore and ash in Wytham is predicted to change to a sole dominance of ash, which in 1000 years will represent between 88% and 89% of the trees in the forest. This is likely due to the drought intolerance of sycamore, as the predicted increase of its growing season by 6.2 days $°C^{-1}$ did not offset the negative effect of drought in this species. An increase in growth period does however increase the fitness of ash, which increases its proportional representation by 0.6-1.08% than when the effects of drought alone are considered. The change in dominance causes changes in the outcome of plant-plant competition, with the less dense canopy of ash allowing more light to penetrate the canopy, facilitating the growth of shade intolerant species birch, and understory species hazel.

6.2 Introduction

Climate change is one of the largest threats to global biodiversity (MEA 2005, Winn et al., 2011), with the highest observed global carbon dioxide, methane and nitrous oxide atmospheric concentrations all being recorded in the last decade (IPCC, 2014). This is predicted to drive global land surface temperatures to rise between 0.3 and 4.8°C by 2100 with non-uniform changes in precipitation across the globe (IPCC, 2014). Along with land-use change and increased species invasions this is causing unprecedented biodiversity loss and changes in distribution (Gaston, 2005, Thuiller et al., 2005, Thomas et al., 2004). In the UK, over the next century it is predicted that there will be higher than average annual temperatures, with drier summers and increased precipitation in winter (Murphy et al., 2009). Extreme events, such as drought, may consequently increase in frequency and severity (Murphy et al., 2009). There is evidence that in the last 50 years there have been higher temperatures and lower summer precipitation than average, from the preceding period (Jenkins et al., 2009). This will have profound impacts on species composition across the UK.

The increase in anthropogenic CO_2 emissions, and associated rise in temperature, are expected to have a positive effect on plant species in temperate areas, until nutrient availability becomes the limiting factor (Broadmeadow and Jackson, 2000, Broadmeadow and Randle, 2002, Sparks and Menzel, 2002, Tylianakis et al., 2008, Norby et al., 2005, Lukac et al., 2010, Wu et al., 2012). However, other associated climate changes such as an increased water deficit, from lower summer precipitation and higher temperatures, and increased extreme events will have a detrimental effect on plant species and are likely to be a driver for demographic change in temperate areas (Gitlin et al., 2006, Allen et al., 2010, Van Mantgem and Stephenson, 2007, Worrall et al., 2008, Rehfeldt et al., 2009, Rich et al., 2008). Die-back events caused by droughts attributed to anthropogenic climate-change have already

been recorded (Martinez-Vilalta et al., 2012, Bigler et al., 2007, Bréda et al., 2006, Ciais et al., 2005) and like any mortality events will increase forest gap formation, facilitating succession (Botkin et al., 1972). The interspecific differences in the mortality response will cause demographic changes (Breshears et al., 2005, McDowell et al., 2008, Allen et al., 2010), even leading to rapid shifts in dominance if the current dominant species are drought sensitive (Allen and Breshears, 1998).

There are suggestions that these direct abiotic effects of climate change on woodlands, such as increased drought, could be modified by interactions between species, their resources and associated species (Parmesan, 2006, Yang and Rudolf, 2010). In plants these include both positive (plant-fungal mutualisms, seed dispersers and pollinators) and negative (hemiparasites, herbivores, pathogens) interactions from other trophic levels as well as plant-plant competition (Tylianakis et al., 2008). These interactions themselves are however also at risk from climate change, largely due to phenological mismatches in species (Visser and Both, 2005, Miller-Rushing and Primack, 2008, Both et al., 2009). These indirect changes of climate changes on biotic processes will lead to additional, often less predictable, demographic changes on populations (Suttle et al., 2007, Tylianakis et al., 2008, van Loon et al., 2014).

The most important above-ground plant-plant competition is that of shading from neighbouring individuals (Pacala et al., 1994, Casper and Jackson, 1997, Lamb, 2008). Light is a pre-emptable resource causing asymmetric competition, especially in high density communities, with larger trees receiving proportionally more light per leaf than smaller plants (Schwinning and Weiner, 1998, Bauer et al., 2004). This can constrain the growth of smaller neighbouring individuals and facilitate the self-thinning of populations (Weiner, 1990),

although impacts may be positive in some circumstances by reducing evapotranspiration and thermal stress (Semchenko et al., 2012). Like other interactions between species, the competition between plants for light may be affected by mismatches in phenology.

Changes in temperatures are driving spring phenological events earlier in most species (Bertin, 2008, Dijkstra et al., 2011, Fu et al., 2012, Pellerin et al., 2012, Richardson et al., 2013, Schwartz et al., 2006, Root et al., 2003, Menzel et al., 2006), although some species show no change, and there are a few with later phenological dates (Parmesan and Yohe, 2003, Both et al., 2009). These responses in phenology are species-specific, and so with an increase in average mean air temperature the differences in the responses of species will broaden, and drive changes to species interactions. Whilst there is some evidence for changes in autumn phenology in some species, these relationships are less clear and so have not been considered in this study (Menzel et al., 2006).

There are at least two mechanisms of demographic change that result from species-specific phenology change. Firstly, the extension of the growing season will increase the photosynthetically active period as individual trees come into leaf earlier in the spring, increasing productivity and growth for a species (Cannell et al., 1998). Secondly, by increasing the time at which a species is leafing it can confer an advantage in light competition by reducing the light that neighbouring trees receive, affecting their growth (Semchenko et al., 2012). These changes may affect the ability of different species to gain resources early in the season (Dunnett and Grime, 1999), benefiting some species to the disadvantage of others (Miller-Rushing and Primack, 2008). This gives certain species competitive advantages (Tilman and Lehman, 2001, Freckleton and Watkinson, 2001,

Klanderud, 2005, Wang et al., 2006), and could even lead to shifts in dominance (Tylianakis et al., 2008).

In this study I used an individual based model to project the impact of climate change on a mixed-woodland in the UK, Wytham Woods. In this approach the population-level changes emerge from changes to processes at the individual level, and it allows for biotic processes such as competition to be considered alongside direct abiotic effects, such as increased mortality. In the previous two chapters I considered the impact of two aspects of climate change separately – the length of the growing season and drought. This allowed for the investigation of the impact of individual aspects of climate change on the tree populations at Wytham Woods, however as they are both expected to occur it is not realistic to project the effects of climate change without examining their effects together. In this study, I look at these two effects - temperature-mediated budburst change and drought-induced mortality - together. Climate change will affect species in many ways but these are arguably the major effects that predicted temperature and rainfall changes will have on woodland species in South East England.

I predicted that the negative effects of drought on intolerant species are likely to be mitigated by any increased productivity from longer growth periods. The species that will increase their representation in the forest most will be those that are both drought tolerant and the most responsive to temperature.

6.3 Methods

6.3.1 Study Site

Wytham Estate is located 5km north-west of Oxford in South East England (1°20′W 51°46′N), and is owned and managed by Oxford University. It is a mixed land-use area of agricultural land, grassland with about 400ha of semi-natural ancient mixed woodland. (Morecroft et al., 2008) defined five areas of the woodland based on management histories: undisturbed ancient semi-natural woodland; disturbed ancient semi-natural woodland; secondary woodland; 19th century plantation and 20th century plantation. The area is at an altitude between 60 to 165m above sea level, has a mean annual precipitation of 730mm y^{-1} and a mean annual temperature of 10.1°C y^{-1} (Butt et al., 2014). Forty-one $10m^2$ plots have been measured since 1993 across the site. Ten of the species that were monitored represent 98% of the tree biodiversity: sycamore (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*), European beech (*Fagus Sylvatica*), penduculate oak (*Quercus robur*), common hazel, (*Corylus avellana*), common hawthorn (*Crataegus monogyna*), field maple (*Acer campestre*), and birch (*Betula* spp.).

6.3.2 Model Description

SORTIE-ND (www.sortie-nd.org) is a spatially-explicit individual-based model which was originally developed in North America (Pacala et al., 1996), that we have parameterised using data collected from UK woodlands (Evans et al., 2015; see chapter 3). The model comprises of four submodels: recruitment, growth, mortality and allometry. This model was chosen in - part due to its simple concept that trees compete for one resource, light, both by interception of available sunlight and by changing the environment below their canopy. We have considered two life stages in this model, saplings and adults; not enough data was available

for seedlings for us to include this age class. Adults are defined as having a diameter at breast height (DBH) above 10cm, and saplings are initiated in the model at 1.35m tall, their DBH defined by their allometric relationships (Evans et al., 2015).

There are two allometric equations parameterised for saplings, relating both DBH and height to diameter at 10cm (D_{10}). In adults, an individual's traits are related to their DBH - their height and crown radius, with crown height being related to height. In all species sapling growth is dependent on light availability, where as adult growth dependent on size only. Mortality has been shown to be based on size of the individual (Moustakas and Evans, 2015), with a senescence function on large trees to avoid unrealistically large trees. Recruitment of seedlings is based on two functions: the dispersal arrangement of recruitments, and the fecundity of the parent tree (see chapter 3).

6.3.3 Temperature-induced growth changes

As in chapter 4 the effect of temperature on Wytham Woods considered here is the regulation of budburst timings by spring temperatures. The baseline budburst times were calculated from the/ mean date of budburst for each of the eight species, for the period 1999 to 2013, taken from the UK Phenology Network (UKPN; www.naturescalendar.org.uk).

Predictions of the change in budburst date due to temperature increases in sycamore, ash and oak were taken from (Morecroft et al., 2008), who correlated the budburst date of these species to temperature at Wytham Woods using 13 years of data. For the five remaining species, I used regression analysis to correlate the average UK budburst to the average spring temperatures found at Wytham Woods between the years 1999 and 2013. These regressions provided an estimate for the change in budburst per °C.

These predictions were combined with the projections of the average air temperature change up to 2080, providing estimates for the change in budburst date. Predictions of future temperature changes in the South East England were obtained from the Met Office's UK Climate Impact Programme (UKCP09; Murphy et al., 2009), which provides average air temperatures between 2020 and 2090. The 25km^2 grid 1547 was used, which includes Wytham Woods. The predicted air temperature for March under three emission scenarios - Low (B1); Medium (A1B) and High (A1fi) - were used in the analysis. After 2090, the budburst date for each species remains the same in the model.

6.3.4 Drought-induced mortality

Drought was defined using the standardised precipitation index (SPI; McKee et al., 1993), as in section 5.3.2. This normalises rainfall data over any time frame, estimating the extent of both wet and dry years using the equation to calculate monthly precipitation:

$$SPI = \frac{(monthly\ precipitation - average\ precipitation)}{s.d.precipitation} \quad (6.1)$$

In severe drought years the SPI is closer to -3, with extremely wet periods being closer to +3. To calculate the baseline SPI, the monthly average precipitation for the years 1970-2014 were obtained from the Met office Hadley Centre England & Wales Precipitation series (HadEWP; Alexander and Jones, 2001). The summer rainfall, the sum of the averages of June, July and August, were used from the southeastern region, encompassing Wytham Woods.

Predictions for future SPI were obtained using data obtained from the Met Office Hadley centre UKCP09 Model (Murphy et al., 2009), which provided estimates for monthly daily

average precipitation in the 25km^2 grid square 1547, which includes Wytham Woods, for the years 2020-2089. Estimates for three IPCC emissions scenarios were used: low (B1), medium (A1B) and high (A1fi). Future yearly SPI data were calculated using these estimates as well as including the HadWEP data to ensure a comparison to precipitation levels in baseline conditions.

Current survival rates were estimated using capture-recapture software MARK (White and Burnham, 1999), with SPI, as well as diameter at breast height (DBH) and their combination, as covariates (Moustakas and Evans, 2015). Annual location probability (p) was kept constant, and the models with highest AIC for each species were chosen as those that most closely described the data (White and Burnham, 1999). These mortality parameter estimates were then used with future estimates of precipitation to give estimated annual mortality for each of the species. After 80 years, these mortality parameters are kept at the 2080s levels.

6.3.5 Baseline conditions

In the context of this chapter, baseline conditions were considered to be when the budburst for each species is the same as current day (section 4.3.2), and the drought conditions were averaged for the years 1970-2015 (section 5.3.3).

6.3.6 Model Runs

The SORTIE/UK model (as parameterised in chapter 3) was updated with the new growth and mortality estimates to give predictions of effects of climate change on the species at Wytham. For baseline conditions and the three emission scenarios, models were run for 1250 years, in 5-year time-steps. Eight runs were performed for each scenario, each simulation

being initialised with the same starting forest structure that was based on the species, size and spatial structures as recorded at Wytham Woods.

6.3.7 Data analysis

Statistical analyses were performed in R 1.3.0 (R Core Team 2013). Differences between climate change scenarios and baseline conditions were analysed using a one-way ANOVA. Normality was tested for using Shapiro-Wilk test, with homogeneity of variance being confirmed using diagnostic plots. Tukey's honest significant differences (HSD) post hoc tests were performed where significant differences were seen between scenarios. Differences in age, DBH and height were also tested using one-way ANOVAs. Differences in the proportions of adults and saplings were tested using Pearson's chi-squared test.

The relative abundance of each species in each scenario in this chapter were compared to the results from previous chapters, which considered budburst (section 4.4) and drought (section 5.4) separately, using t-tests. The total absolute number individuals in each of the scenarios was also compared against the results from previous chapters using t-tests.

6.4 Results

6.4.1 Climate change predictions

6.4.1.1 Budburst

The species most sensitive to March temperature is sycamore, which is expected to budburst 6.2 days earlier for every 1°C. Hazel was not shown to be sensitive with March temperatures and so the budburst for this species was kept constant. The order of species from most

sensitive to least is sycamore > ash > birch > hawthorn > field maple > beech > hazel (figure 6.1).

6.4.1.2 Drought

The calculation of the SPI showed than when comparing rainfall from 1970 with predictions up to 2080, there is forecasted to be a continuous decrease in precipitation from the 2010s to the 2070s, beginning at an SPI of -0.0440 decreasing until -0.6960 (table 6.1).

Only birch and oak do not have a negative response to drought conditions. The most intolerant to drought is sycamore and beech with ash, field maple, hazel, hawthorn having intermediate tolerances (figure 1).

Years	SPI
2012-2020	-0.0440
2021-2030	-0.1874
2031-2040	-0.2484
2041-2050	-0.4314
2051-2060	-0.5325
2061-2070	-0.6168
2071-2080	-0.6960

Table 6-1: Forecasted standardised precipitation index (SPI) for the years 2012 to2080 when calculated with rainfall since 1970.

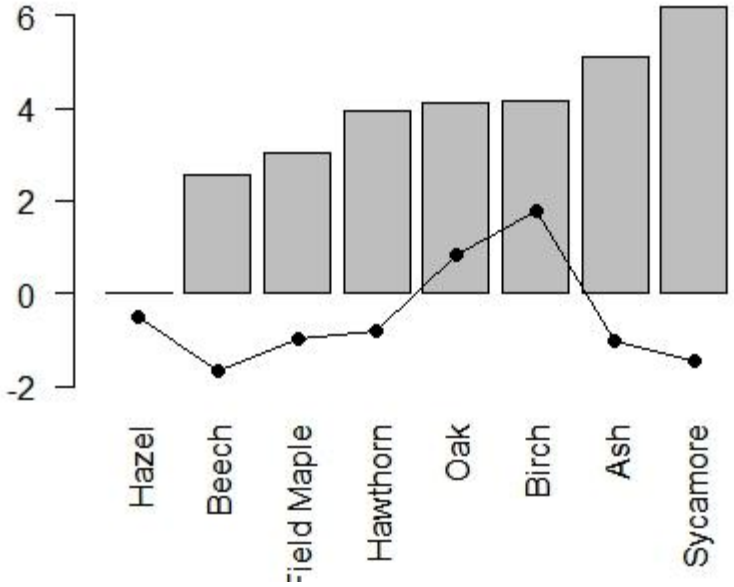


Figure 6-1: Increase in budburst date (grey bars; number of days) and drought tolerances (black line & circles; drought tolerance [phi3, see 5.3.3]) for eight species.

6.5 Model Outputs

6.5.1 Absolute numbers

With increasing intensity of climate change, the total number of individuals rises significantly from 222768 (±3561) individuals in baseline conditions to 244722 (±3656) in low emissions scenario, B1, 250708 (±3333) in medium emissions scenario, A1B, and 256883 (±3018) in high emissions scenario, A1fi (ANOVA: $F_{(3,28)}$=427, p<0.001; figure 6.2). Post-hoc analyses confirmed that there is a difference between each scenario and baseline conditions, as well as between each other (Tukey's: all p<0.001). Ash accounts for between 96.7% (A1fi) and 97.9% (B1) of the total increase in individual trees ($F_{(3,28)}$=403,p<0.0001), increasing from

195708 individuals, in baseline conditions, by 10.9% in B1 to 217071 (±2130), 13.9% to 223080 in A1B, and 16.8% in A1fi to 228722 (±1642).

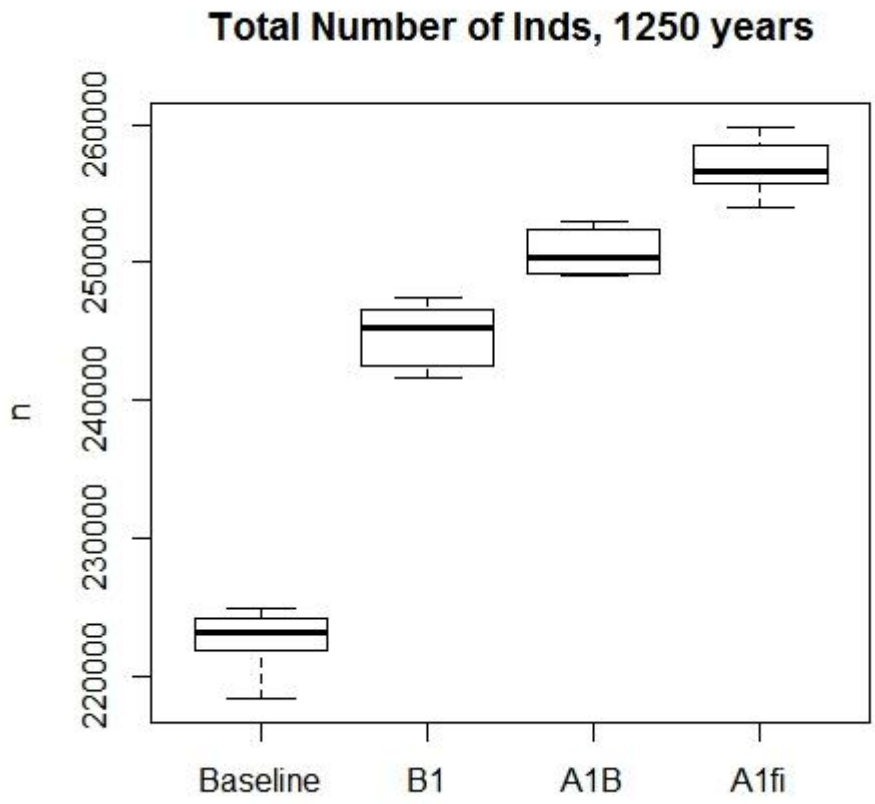


Figure 6-2: Total absolute number of individuals. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range.

The only other species to significantly increase with climate change conditions is birch, increasing their numbers by up to 37% in A1fi to 1276, from 931 in baseline conditions, with a 37% increase to 1276 in B1 and a 29% rise to 1208 individuals in A1B ($F_{(3,28)}$=5.2,p<0.01). The only species to significantly decrease between scenarios is beech, however this is not linear with increasing emissions, with the lowest number being in scenario A1B, dropping by

121 individuals from 849 (table 6.3). This compares to a reduction to 760 in B1 and 763 in A1fi ($F_{(3,28)}$=4.7,p<0.001; figure 6.3).

Absolute Number after 1250 Years

	Baseline	B1	A1B	A1fi
Ash	195708 (±2305)	217071 (±2130)	223080 (±1997)	228722 (±1642)
Beech	849 (±51)	760 (±67)	728 (±65)	763 (±85)
Birch	931 (±132)	1173 (±200)	1208 (±164)	1276 (±233)
Field Maple	519 (±68)	531 (±30)	516 (±37)	535 (±32)
Hawthorn	8268 (±380)	8546 (±525)	8419 (±529)	8701 (±493)
Hazel	2134 (±126)	2296 (±134)	2246 (±124)	2215 (±181)
Oak	12613 (±414)	12649 (±464)	12806 (±311)	12976 (±271)
Sycamore	1746 (±86)	1696 (±106)	1705 (±107)	1695 (±81)
Total	222768 (±3561)	244722 (±3656)	250708 (±3333)	256883 (±3018)

Figure 6-3: Predicted absolute numbers of each species (± SD) after 1250 years for baseline temperature and precipitation conditions and three emission scenarios.

6.5.2 Relative abundance

With its large contribution to the increase of individuals in climate scenarios, ash is the only species to increase its relative abundance in the forest, from 87.85% in baseline conditions to

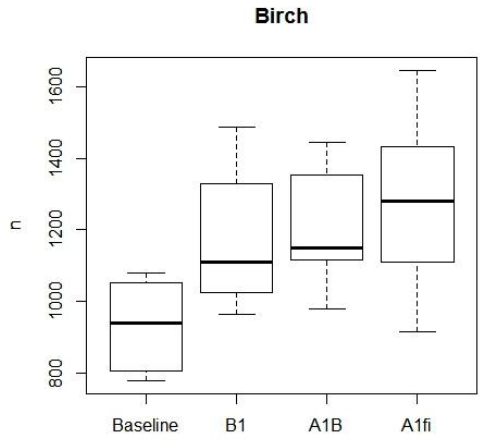
88.7%, 88.9% and 89% in B1, A1B and A1fi scenarios, respectively ($F_{(3,28)}$=36.2,p<0.0001). All other species decrease in their proportions as emissions increase (table 6.2).

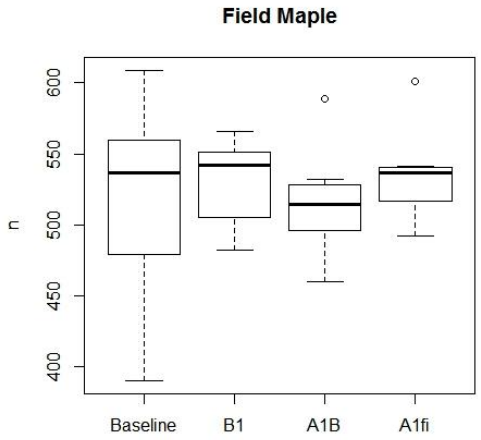
6.5.3 Age, DBH, height and adult-sapling proportions

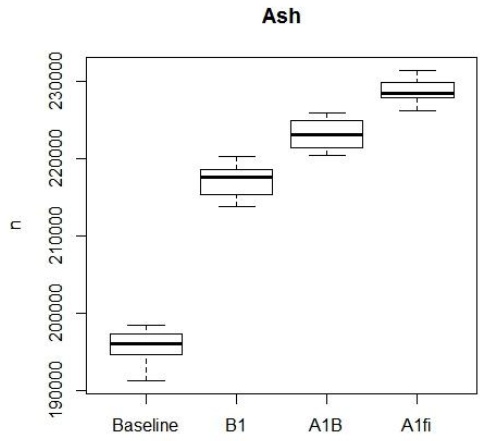
No differences were found between the scenarios in age, DBH or height. There were no differences in the proportions of saplings to adults.

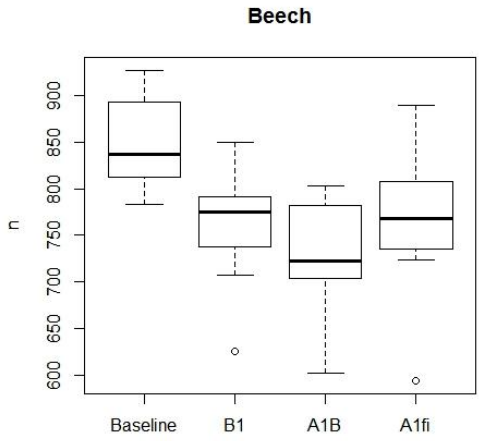
6.5.4 Comparing to the situation when only growth period changes

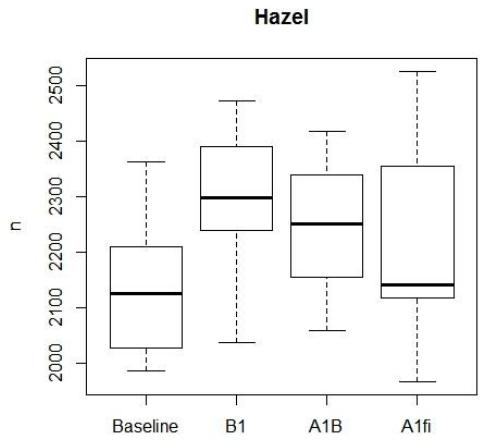
When comparing the results from this chapter to those where changes in growth period alone is considered (section 4.4) there are significant differences in the relative abundances of each species across the scenarios, apart from beech in the B1, A1B and A1fi scenarios (table 6.3). The largest increase in all scenarios is seen in ash, increasing its proportional representation in the forest by 53%, 54%, 54% and 57% trees in the forest, in A1fi, A1B, B1 and baseline conditions respectively. Modest increases are also seen in oak, hawthorn, birch and field maple. There are substantial reductions in sycamore across all scenarios, reducing from a representation of 58.57% with just growth period included in the model, to just 0.66% in highest emission scenario A1fi in these results. It reduces its representation similarly in all scenarios, losing 58.2% of its representation in A1B, 58.3% in B1 and 62% in baseline conditions. The only other species to decrease when drought is considered in addition to growing season effects is hazel, reducing its representation between 3.13% in A1fi to 3.47% in baseline (table 6.3).

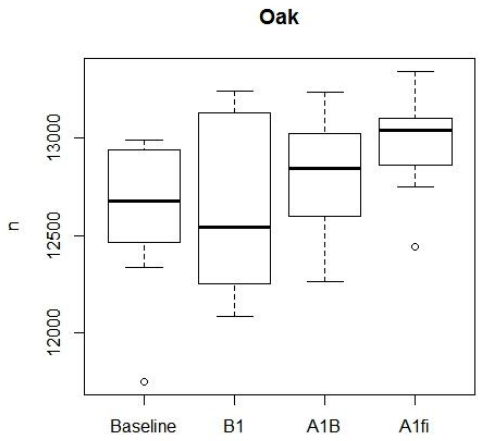

Birch
n
800
1000
1200
1400
1600
Baseline
B1
A1B
A1fi


Field Maple
n
400
450
500
550
600
Baseline
B1
A1B
A1fi


Ash
n
190000
200000
210000
220000
230000
Baseline
B1
A1B
A1fi


Beech
n
600
650
700
750
800
850
900
Baseline
B1
A1B
A1fi


Hazel
n
2000
2100
2200
2300
2400
2500
Baseline
B1
A1B
A1fi


Oak
n
12000
12500
13000
Baseline
B1
A1B
A1fi

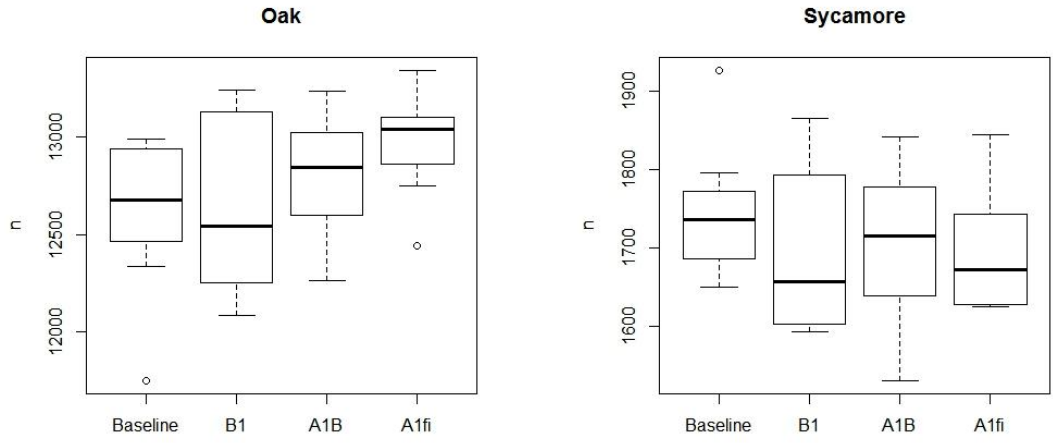


Figure 6-4: Total absolute numbers for each species after 1250 years, under baseline conditions and three emission scenarios. The dark horizontal line represents the median number of individuals from the eight runs, with top and bottom of box representing the upper and lower quartiles (25th and 75th percentile), with the end of whiskers representing the data range, or 1.5 times the interquartile range with individual outliers represented by circles.

6.5.5 Comparing to drought chapter results

When comparing relative abundances from this chapter to section 5.4, where the effect of drought alone is considered, there are no significant differences in any of the species in baseline conditions. There are however changes in the abundances of several species in the three climate scenarios (table 6.4). When both growth the period and drought-induced mortality is introduced into the model, ash is the only species to increase its relative abundance in all emission scenarios, when compared to the sole effects of drought. The differences are modest, increasing its representation by 0.69% in B1, 0.92% in A1B and 1.08% in A1fi. The only other species to increase in proportion is Hazel when both climate change impacts are considered, increasing its representation by 0.17% in B1 and 0.08% in A1B. Sycamore, oak and field maple reduce in all scenarios, with beech reducing in scenarios in B1 and A1B only (-0.05% in both). No significant differences between results are seen in

birch or hawthorn. There are however significant increases in the total absolute number of individuals in this chapter compared to the previous two.

	Proportional Representation (%)				
	Current	1250 Year Predictions			
		Baseline	B1	A1B	A1fi
Ash	26.9	87.852 (±0.0034)	88.702 (±0.0026)	88.98 (±0.0026)	89.038 (±0.0013)
Beech	1	0.381 (±0.0002)	0.311 (±0.0003)	0.29 (±0.0003)	0.297 (±0.0003)
Birch	0.4	0.418 (±0.0006)	0.48 (±0.0008)	0.482 (±0.0007)	0.496 (±0.0009)
Field Maple	0.7	0.233 (±0.0003)	0.217 (±0.0001)	0.206 (±0.0002)	0.208 (±0.0001)
Hawthorn	6.9	3.711 (±0.0017)	3.491 (±0.002)	3.358 (±0.0022)	3.386 (±0.0017)
Hazel	8.9	0.958 (±0.0006)	0.938 (±0.0006)	0.896 (±0.0005)	0.863 (±0.0007)
Oak	1.9	5.663 (±0.0021)	5.169 (±0.0019)	5.108 (±0.0013)	5.052 (±0.0011)
Sycamore	51.9	0.784 (±0.0004)	0.693 (±0.0005)	0.68 (±0.0004)	0.66 (±0.0003)

Table 6-2: Relative abundance of each species (± SD) after 1250 years under baseline conditions and three emission scenarios

Differences between climate change model with budburst model

	Baseline	B1	A1B	A1fi
Ash	+57.475	+54.255	+53.885	+53.556
Beech	+0.057	-0.003	-0.004	+0.012
Birch	+0.418	+0.480	+0.482	+0.496
Field Maple	+0.166	+0.174	+0.157	+0.153
Hawthorn	+2.145	+1.903	+1.821	+1.872
Hazel	-3.474	-3.130	-3.266	-3.207
Oak	+5.640	+5.145	+5.085	+5.030
Sycamore	-62.428	-58.824	-58.161	-57.911

Table 6-3: Changes in the proportional representation of each species in emission scenario when comparing to model considering only growth period change (section 4.4). Significant differences are shown in red.

Differences between climate change model with drought model

	Baseline	B1	A1B	A1fi
Ash	-0.21	+0.69	+0.92	+1.08
Beech	+0.02	-0.05	-0.05	-0.02
Birch	+0.03	-0.01	+0.00	-0.03
Field Maple	-0.00	-0.03	-0.03	-0.06
Hawthorn	+0.36	+0.19	+0.07	+0.26
Hazel	+0.13	+0.17	+0.08	+0.02
Oak	-0.28	-0.88	-0.92	-1.16
Sycamore	-0.03	-0.09	-0.07	-0.08

Table 6-4: Change in proportional representation of each species in emission scenario when comparing to model considering only drought (section 5.4). Significant difference are shown in red.

6.6 Discussion

In this chapter I have considered the combined effect of both budburst change and climate-induced mortality on a semi-natural ancient woodland. Overall the results are similar to those in the previous chapter (section 5.4), the most notable result being the projected changes in relative abundances of species when compared to present day.

For all emission scenarios, and the baseline conditions, ash is predicted to become the dominant species representing between 87% and 89% of all individuals in the forest, a large increase from its current abundance of 26.9%. This increases with increasing severity of climate change, with an increase in the numbers of individual trees with increasing temperature and decreasing summer rainfall. Such is the increase of individuals that ash is the only species to increase its relative abundance with increasing emissions, all other species reducing in relative abundance even with slightly higher or the same numbers of individuals. The main driver behind this increase is most likely to be the considerable reductions of current co-dominant species sycamore, which is drought intolerant, thus reducing light competition for the drought tolerant ash (Scherrer et al., 2011). As well as reducing competition, the drought induced dieback events would create new gaps in a relatively short time period that the fast growing ash can take advantage of. The reduction of sycamore reported here is consistent with previous predictions based on the Ecological Site Classification (ESC; Pyatt et al., 2001), which predicted reductions of sycamore in the South East of England in the future due to decreased rainfall (Broadmeadow et al., 2005, Read et al., 2009).

The hypothesis that prolonged growth period may result in lower mortality in those species that are susceptible to drought was rejected, with sycamore showing the largest positive rate of increase in growth period with temperature (6.2 days $°C^{-1}$) but decreasing in abundance of

all the species, when growing season was considered in combination with drought. The significant increase in ash, which has the second most responsive change in phenology to temperature increases (5.1 days $°C^{-1}$) confirms the second hypothesis that a species that is relatively tolerant to drought will obtain an advantage from the increased productivity.

The species most tolerant to drought at Wytham was shown to be birch (figure 6.1) and was the only other to increase significantly in absolute numbers, by between 25 and 40%. This tolerance is unexpected as birch is considered to be drought intolerant, and so these results may not be replicated at other sites. one reason for their high drought tolerance displayed here may be the small numbers of individuals, which may not have been representative of the larger community. Despite a high response in budburst to temperature, the proportion of birch remains the same when budburst is considered with drought, even showing a slight decrease in proportions (table 6.4). This shows that an increase in growth period will not benefit all species that are drought tolerant, and is evidence for the indirect biotic effect of plant-plant competition.

For birch especially this may be explained by its slow growth and relatively high mortality in shade. The canopy of the forest has changed from a co-dominance of sycamore and ash, to that of mainly ash. Sycamore has a relatively dense crown when compared to ash, and so the dominance change means an increase in the light reaching below the forest canopy, and thus reducing light competition on species such as birch. This is illustrated with the predicted extinction of birch when the impact of drought was not considered on the forest, under which scenario the co-dominance of sycamore and ash was predicted to continue (section 4.4). Further evidence of biotic interactions causing changes in demography comes from hazel, which is relatively tolerant to drought. This species increases in proportions when budburst is

considered alongside drought, although it does not increase its growth period with an increase in temperature.

These results provide further compelling evidence that under climate change conditions there will be a reduction of current co-dominant species sycamore due to its drought intolerance, leading to a dominance of ash. This could be seen as a return to a more natural state, as sycamore is a non-native species, and more representative of the National Vegetation Classification (NVC) W8 *Fraxinus excelsior* - *Acer campestre* - *Mercurialis perennis* habitat that would be expected of the area (Savill et al., 2011). There has been some concern that sycamore may outcompete with native species such as ash (Morecroft et al., 2008), however this study provides evidence that climate change will prevent this at Wytham Woods. It is worth noting however that in analysing surveys undertaken between 1993 and 2005 (Morecroft et al., 2008) showed that in areas without active management at Wytham, sycamore is minimally represented or absent. This suggests that perhaps without management strategies, as in this model, ash may dominant the forest with beech or and oak as sub-dominant species.

The results presented here suggest that the reduction in sycamore will also occur in baseline conditions, which represent conditions of the previous 50 years. As well as any lack of active management, this could be a sign that climate change has already been taking effect in the area since 1970, over which period baseline conditions were taken. It has been reported that the average summer rainfall has remained the same across the UK in the past 50 years, but that this period is significantly lower than the average of the period since records began in 1766 (Jenkins et al., 2009). Shifts in populations caused by drought have been recorded since 1950 elsewhere (Allen and Breshears, 1998, Peñuelas et al., 2001, Bigler et al., 2007), and so

it may be necessary to use historic precipitation data in order to get a better baseline estimate. Temperature also plays a role in drought, and with temperatures expected to increase in South East England by 1.77°C in the next century (Jenkins et al., 2009), it could be useful to use a methodology that includes temperature when considering moisture deficits.

Sycamore is thought to be a host and food source to many species (Peterken, 2001), and there is evidence that ash seedlings may have higher survival under a sycamore canopy than under their own (Waters and Savill, 1992), although this has been contested (Morecroft et al., 2008). The reduction of sycamore will therefore have impacts on many trophic levels of the forest. The reduction of diversity could also reduce the resilience of the forest, as forests dominated by one species have greater potential for regime shifts or even ecosystem collapse (Scheffer and Carpenter, 2003, Petit and Hampe, 2006). This is especially true for UK woodlands that are dominated by ash, due to the fungus *Hymenoscyphus fraxineus* that has been causing die back events since 2012 (Mitchell et al., 2014).

For this study I have focussed on two aspects of climate change on plants: the effect of temperature on phenology, and the effect of drought-induced mortality. Future changes to temperature and rainfall caused by raised CO_2 partial pressures are thought to be the biggest threat to woodlands. However, there are further implications to consider from the direct effect of CO_2 and temperature that might alter many processes in plants from cellular reactions to growth (Bunce, 2000, Rustad et al., 2001). CO_2 enrichment is a positive force for plant species increasing productivity and diversity, and there is evidence for species-specific responses (Asshoff et al., 2006, Ainsworth and Long, 2005, Poorter and Perez-Soba, 2001). More research would be need to quantify these if they were to be included into a model, and

to take into account the limiting factors including nitrogen (Reverchon et al., 2011, Ainsworth and Long, 2005, Norby and Luo, 2004).

In chapter 4 I found that budburst was most well correlated to March temperatures, however there is evidence in some species that winter cooling can also have an effect on spring phenological events (Yu et al., 2010, Clark et al., 2014, Luedeling et al., 2009). Autumn phenological events are also controlled by temperature (Menzel, 2000, Menzel and Fabian, 1999), however these relationships are less well understood and less data are available than for spring phenology (Sparks and Menzel, 2002). Additionally, autumnal phenological events occur in the less photosynthetically active periods, and so contribute less to growth than changes in spring phenology (Menzel et al., 2006). Temperature also regulates other processes such as growth and leaf production which may have further implications for species interactions (Drobyshev et al., 2013, Lévesque et al., 2014).

Chapter 7

General Discussion

The results presented in my thesis provide evidence of the direct effects of climate change on tree species at two forests, and are able to show that abiotic interactions between individuals also have a major role in the response of some species. Here I present the first results of a model that considers the impact that increased growing seasons, due to temperature-driven earlier budburst, will have on tree communities within a woodland. For my study I considered how the increases in annual growth caused by longer growth seasons will alter the competition regimes for light. In order to do this I used a spatially-explicit individual-based model which was able to consider both the direct effects on growth and the indirect effects on light competition between individuals. My results show that it is not the species that are the most sensitive to temperature, thus having the largest increase in growing season length, but the canopy species that will see the most benefit from increased growth periods. In Wytham, the two current co-dominant species *Fraxinus excelsior* (European ash) and *Acer pseudoplatanus* (sycamore) were the only species to increase their proportional representation in the forest, impeding the increase of other species. At the GMF, however, the increase of one canopy species, *Fagus grandifolia* (American beech),was shown to impede all other species including co-dominant species *Tsuga canadensis* (Eastern hemlock).

As well as the change of phenology I also examined the effect of projected summer precipitation on the community at Wytham Woods. My results showed that the drought-intolerant canopy species sycamore will drastically reduce its representation over the next 1000 years, even under the current precipitation regime. This suggests that without active management at the site there will be significant changes to the population at Wytham, potentially leading to a dominance of ash. My research also considered the interactions of both drought together with increased growing seasons and found that when considered together, drought tolerant species can increase their proportional representation, but the

increased growth does not mitigate the effects of reduced precipitation to drought intolerant species such as sycamore. In comparing the results from previous chapters I was able to show that drought has a much more significant impact on the community at Wytham, however other impacts of climate change such as CO_2 will be important in the responses of tree populations.

It has been postulated that it is vital that interactions between plant species are considered when predicting the effects of climate change (Davis et al., 1998, Pearson and Dawson, 2003, Guisan and Thuiller, 2005, Brooker, 2006), as it is known that competition causes changes to the physiological (e.g. leaf size; van Loon et al., 2014) or functional response (e.g. stomatal conductance; Loranty et al., 2010) of species, which can ultimately drive community shifts. These interactions may also exert a stronger impact on species than the direct effects of climate change (Liancourt et al., 2013, Naithani et al., 2014). The results of my study confirm this, with the only canopy species responding to increased growing seasons, which constrained any response in sub-canopy species, even if their response to climate change is greater.

These results are consistent with an empirical study at Wytham Woods that showed that spring phenology changes affected the growth of understory species (Butt et al., 2014). This was also explained by light competition, with understory species losing their advantage of earlier budburst with the late spring events caused by low spring temperatures. I was not able to implicitly investigate effects such as these in my model, as I considered changes in growth as proportional to one other. It would however be important to include this detail in future research as the time of year that phenological events happen is important for the growth of species, for example species increasing their growth in late May or June would experience a

greater increase in growth than those earlier in the season (Morecroft et al., 2008), as it has been shown that maximum CO_2 rates occur up to 70 days after budburst (Morecroft et al., 2003) and that these differences are interspecific (Morecroft and Roberts, 1999). Also worth considering is the effect that this will have on succession of forest, if late-successional canopy species gain the most benefit within a forest then this could be a driver to accelerate succession (Bolte et al., 2014).

Given the impact that interactions have on community structure and functioning of forests it is vitally important that they are considered when predicting the effects of climate change. As well as the direct effect this will have on the individuals within the forest, changes in the functioning, productivity and survival of species has implications for vegetation-climate feedbacks, affecting important biogeochemical events such as carbon cycles (Ciais et al., 2013, Ciais et al., 2005, Dury et al., 2011). For example, drier conditions lead to a reduction in evapotranspiration which in turn leads to less evaporative cooling (Yin et al., 2014), which in turn can lead to a further warming of ecosystems (Yin et al., 2014, Seneviratne et al., 2006, Fischer et al., 2007). Increased temperatures are also expected to increase the release of CO_2 emissions from plant, leading to warmer temperatures (Cox et al., 2000, Luo, 2007), however this might be mediated through the biomass accumulation and increase in net plant productivity (Rustad et al., 2001, Melillo et al., 2002, Luo, 2007, Lin et al., 2010). If population structure is effected by interactions then this will in turn affect ecosystem functioning, and so it is important to use models that are able to consider them when considering vegetation-climate feedbacks.

My results from chapter five, showing that drought-intolerant sycamore will decrease in proportional representation in the forest, are consistent with previous predictions of the

impact on the species due to reduced rainfall (Broadmeadow et al., 2005, Morecroft et al., 2008). My results suggest that the reduction in summer precipitation over the past 50 years (Jenkins et al., 2009, Pal et al., 2004) is enough to significantly decrease their number after 1000 years. This provides a further example on a growing number of studies which relate the dieback events of species to drought events (Suarez et al., 2004, Rolim et al., 2005, Fensham and Fairfax, 2007, review: Allen et al., 2010, Ma et al., 2012), although most studies are interested in episodic drought events, whereas I considered the reduction of the mean summer precipitation values. In my study I only considered the effect that decreased precipitation will have on the mortality of species, however there will be a range of effects such as the a reduction in productivity and growth caused by an decrease of carbon caused by a reduction in stomata closing (Bréda et al., 2006, Boisvenue and Running, 2006).

Whilst my model simulations suggest that ash will become the dominant species, this has not considered the recent threat of ash dieback disease, caused by the fungus *Hymenoscyphus fraxineus*. Whilst recent surveys suggest that ash is indeed increasing its representation more than other canopy species (Kirby et al., 2014, Mihok et al., 2009), evidence from mainland Europe suggest that up to 99% of individuals are susceptible to the disease (Kjaer et al., 2012, Pautasso et al., 2013) and with potentially 68% of plots having over 20% canopy cover of ash (Kirby et al., 2014), any dieback event would be substantial. With a projected decrease of sycamore, this could lead to dominance of other canopy species such as beech or oak, although there is also concern about the threat of acute oak decline which has affected woodland populations of Britain (Denman et al., 2010). Alternatively, invasive species may become a feature of Wytham. Species are moving northwards and to higher altitudes due to changes in temperatures (Walther et al., 2002, Kullman, 2002), so it is to be expected that species will colonise new areas. Successful invasions have often been attributed to

competitive advantages to resources (Levine et al., 2003, Vilà et al., 2003, Vilà and Weiner, 2004, Gioria and Osborne, 2014), and so with reductions in sycamore and potential decreases in ash and/or oak, then new species to Wytham Woods may colonise.

Management will play a vital role in the reduction of climate change impacts in many ecosystems in the coming decades (Spittlehouse and Stewart, 2004, Noss, 2001), with a study at Wytham Woods showing that different management strategies affect the vertical canopy structure (McMahon et al., 2015). Predictions such as this help forest practitioners consider the best options in to protect current species, for example sycamores are known to be highly susceptible to squirrel (*Scirius carolingensis*) damage (Hein et al., 2009, Kirby et al., 2014), and so management to reduce this damage and aid successful regeneration under drought stress.

In this study I only considered changes to mean temperatures and precipitation, but it is thought to be extreme environmental conditions that determine the distribution, structure, productivity and survival of plant communities (Reyer et al., 2013a, Knapp et al., 2002, Chapin et al., 1993, Bokhorst et al., 2007, Van Peer et al., 2004). Phenological events, such as budburst are not only affected by the mean temperature but also by climatic events such as warm spells, drought or frosts (Rutishauser et al., 2008, Butt et al., 2014). Warm spells or heat waves can also lead to high atmospheric demands for plant transpiration, which can determine the drought tolerances of plants beyond changes in mean climate. It has been shown changes to the variability of precipitation, with constant annual amount, increases species diversity but reduces carbon turnover and annual net primary productivity (Knapp et al., 2002). Increased mortality events from extreme events can cause shifts in species distributions, community assemblages and ecosystem structures and functioning through the

creation of selective pressure of the evolution of locally adapted physiologies (Parmesan et al., 2000). Additionally, I only considered droughts caused by summer rainfall however winter rainfall also effects annual drought events by changing the water deficit (Vautard et al., 2007).

Other abiotic factors linked to climate change will also be important for the changes to diversity and functioning of ecosystems. The expected increase in carbon dioxide partial pressures will increase photosynthesis between 30% and 50% in young trees (Broadmeadow and Randle, 2002), as well as increasing the leaf-area index (LAI; Ainsworth and Long, 2005), productivity (Körner, 2006) and biomass (Stiling and Cornelissen, 2007, Kimball et al., 2007), thus having the potential to mitigate the negative effects of climate change. Increases in carbon dioxide also reduces stomatal conductance and so decreases transpiration and increases soil moisture content (Volk et al., 2000, Morgan et al., 2004), which may be essential in mediating the effects of drought on species (Holtum and Winter, 2010). Any enrichment from carbon dioxide will however be limited by the availability of other nutrients, especially nitrogen, which could become a limiting factor in some species (Broadmeadow and Jackson, 2000), and there is evidence that the enrichment from increased carbon will decrease with time (Leuzinger et al., 2011).

I used an individual based model to investigate the effect of climate change on individual growth and mortality on a tree population in a semi-natural ancient woodland. As with all modelling approaches, there are advantages and limitations. Models can only be as representative as the experimental or empirical data that is available (Leuzinger et al., 2011), and quite often the time periods that my model is based on are short and may not represent the full response of the species to environmental changes. However, data from the ECN are

some of the longest running ecological datasets which have not only been recorded methodically, but replicated at other sites across the UK meaning that my research could be extended to other sites across the UK with relative ease. Using this method I was also able to consider not only the direct effect of climate change on forest but how interactions will mediate these effects. It would be useful to be able to quantify these biotic interactions, as the data is made available through the use of a spatially-explicit model. My results have been shown to be consistent with other models and empirical studies at Wytham, which helps to validate their accuracy.

References

ABER, J. D., OLLINGER, S. V., FEDERER, C. A., REICH, P. B., GOULDEN, M. L., KICKLIGHTER, D. W., MELILLO, J. M. & LATHROP, R. G. 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States.

ADLER, P. B., DALGLEISH, H. J. & ELLNER, S. P. 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology,* 100**,** 478-487.

AINSWORTH, E. A. & LONG, S. P. 2005. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. *New Phytol,* 165**,** 351-71.

ALEXANDER, J. M., DIEZ, J. M. & LEVINE, J. M. 2015. Novel competitors shape species/' responses to climate change. *Nature*, advance online publication.

ALEXANDER, L. V. & JONES, P. D. 2001. Updated precipitation series for the U.K. and discussion of recent extremes. *Atmospheric Science Letters*.

ALLEN, C. D. 2009. Climate-induced forest dieback: An escalating global phenomenon? *Unasylva,* 231/232**,** 43-49.

ALLEN, C. D. & BRESHEARS, D. D. 1998. Drought-induced shift of a forest–woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences,* 95**,** 14839-14842.

ALLEN, C. D., MACALADY, A. K., CHENCHOUNI, H., BACHELET, D., MCDOWELL, N., VENNETIER, M., KITZBERGER, T., RIGLING, A., BRESHEARS, D. D., HOGG, E. H., GONZALEZ, P., FENSHAM, R., ZHANG, Z., CASTRO, J., DEMIDOVA, N., LIM, J.-H., ALLARD, G., RUNNING, S. W., SEMERCI, A. & COBB, N. 2010. A global overview of drought and heat-induced tree mortality

reveals emerging climate change risks for forests. *Forest Ecology and Management,* 259**,** 660-684.

AMEZTEGUI, A., COLL, L. & MESSIER, C. 2015. Modelling the effect of climate-induced changes in recruitment and juvenile growth on mixed-forest dynamics: The case of montane–subalpine Pyrenean ecotones. *Ecological Modelling,* 313**,** 84-93.

ARANDA, I., GIL, L. & PARDOS, J. A. 2000. Water relations and gas exchange in Fagus sylvatica L. and Quercus petraea (Mattuschka) Liebl. in a mixed stand at their southern limit of distribution in Europe. *Trees-Structure and Function,* 14**,** 344-352.

ASSHOFF, R., ZOTZ, G. & KORNER, C. 2006. Growth and phenology of mature temperate forest trees in elevated CO2. *Global Change Biology,* 12**,** 848-861.

BAI, E., LI, S., XU, W., LI, W., DAI, W. & JIANG, P. 2013. A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist,* 199**,** 441-451.

BALVANERA, P., PFISTERER, A. B., BUCHMANN, N., HE, J. S., NAKASHIZUKA, T., RAFFAELLI, D. & SCHMID, B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol Lett,* 9**,** 1146-56.

BARNOSKY, A. D., MATZKE, N., TOMIYA, S., WOGAN, G. O., SWARTZ, B., QUENTAL, T. B., MARSHALL, C., MCGUIRE, J. L., LINDSEY, E. L., MAGUIRE, K. C., MERSEY, B. & FERRER, E. A. 2011. Has the Earth's sixth mass extinction already arrived? *Nature,* 471**,** 51-7.

BARRIOPEDRO, D., FISCHER, E. M., LUTERBACHER, J., TRIGO, R. & GARCIA-HERRERA, R. 2011. The Hot Summer of 2010: Redrawing the Temperature Record Map of Europe. *Science,* 332**,** 220-224.

BART, J. 1995. ACCEPTANCE CRITERIA FOR USING INDIVIDUAL-BASED MODELS TO MAKE MANAGEMENT DECISIONS. *Ecological Applications,* 5**,** 411-420.

BAUER, S., WYSZOMIRSKI, T., BERGER, U., HILDENBRANDT, H. & GRIMM, V. 2004. Asymmetric competition as a natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. *Plant Ecology,* 170**,** 135-145.

BEAUDET, M., HARVEY, B. D., MESSIER, C., COATES, K. D., POULIN, J., KNEESHAW, D. D., BRAIS, S. & BERGERON, Y. 2011. Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *Forest Ecology and Management,* 261**,** 84-94.

BEIER, C., BEIERKUHNLEIN, C., WOHLGEMUTH, T., PENUELAS, J., EMMETT, B., KORNER, C., DE BOECK, H., CHRISTENSEN, J. H., LEUZINGER, S., JANSSENS, I. A. & HANSEN, K. 2012. Precipitation manipulation experiments--challenges and recommendations for the future. *Ecol Lett,* 15**,** 899-911.

BELLARD, C., BERTELSMEIER, C., LEADLEY, P., THUILLER, W. & COURCHAMP, F. 2012. Impacts of climate change on the future of biodiversity. *Ecol Lett*.

BENITO-GARZON, M., RUIZ-BENITO, P. & ZAVALA, M. A. 2013. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. *Global Ecology and Biogeography,* 22**,** 1141-1151.

BERTIN, R. I. 2008. Plant phenology and distribution in relation to recent climate change. *Journal of the Torrey Botanical Society*, 135**,** 126-146.

BIASI, C., MEYER, H., RUSALIMOVA, O., HÄMMERLE, R., KAISER, C., BARANYI, C., DAIMS, H., LASHCHINSKY, N., BARSUKOV, P. & RICHTER, A. 2008. Initial effects of experimental warming on carbon exchange rates, plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil,* 307**,** 191-205.

BIGLER, C., GAVIN, D. G., GUNNING, C. & VEBLEN, T. T. 2007. Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos,* 116**,** 1983-1994.

BILELA, S., DOUNAVI, A., FUSSI, B., KONNERT, M., HOLST, J., MAYER, H., RENNENBERG, H. & SIMON, J. 2012. Natural regeneration of Fagus sylvatica L. adapts with maturation to warmer and drier microclimatic conditions. *Forest Ecology and Management,* 275**,** 60-67.

BINGGELI, P. 1993. The Conservation Value of Sycamore. *Quarterly Review of Forestry*.

BITHELL, M. & BRASINGTON, J. 2009. Coupling agent-based models of subsistence farming with individual-based forest models and dynamic models of water distribution. *Environmental Modelling & Software,* 24**,** 173-190.

BOISVENUE, C. & RUNNING, S. W. 2006. Impacts of climate change on natural forest productivity - evidence since the middle of the 20th century. *Global Change Biology,* 12**,** 862-882.

BOKHORST, S., BJERKE, J. W., DAVEY, M. P., TAULAVUORI, K., TAULAVUORI, E., LAINE, K., CALLAGHAN, T. V. & PHOENIX, G. K. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. *Physiologia Plantarum,* 140**,** 128-140.

BOKHORST, S., HUISKES, A., CONVEY, P. & AERTS, R. 2007. The effect of environmental change on vascular plant and cryptogam communities from the Falkland Islands and the Maritime Antarctic. *BMC Ecology,* 7**,** 15.

BOLNICK, D. I., AMARASEKARE, P., ARAUJO, M. S., BUERGER, R., LEVINE, J. M., NOVAK, M., RUDOLF, V. H. W., SCHREIBER, S. J., URBAN, M. C. & VASSEUR, D. A. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution,* 26**,** 183-192.

BOLTE, A., HILBRIG, L., GRUNDMANN, B. & ROLOFF, A. 2014. Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. *Annals of Forest Science,* 71**,** 139-147.

BONAN, G. B. 2008a. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science,* 320**,** 1444-1449.

BONAN, G. B. 2008b. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science,* 320**,** 1444-9.

BONAN, G. B., LEVIS, S., SITCH, S., VERTENSTEIN, M. & OLESON, K. W. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biology,* 9**,** 1543-1566.

BOSE, A. K., HARVEY, B. D., COATES, K. D., BRAIS, S. & BERGERON, Y. 2015. Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. *Ecological Modelling,* 300**,** 123-136.

BOTH, C., BOUWHUIS, S., LESSELLS, C. M. & VISSER, M. E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature,* 441**,** 81-83.

BOTH, C., VAN ASCH, M., BIJLSMA, R. G., VAN DEN BURG, A. B. & VISSER, M. E. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *Journal of Animal Ecology,* 78**,** 73-83.

BOTKIN, D. B., JANAK, J. F. & WALLIS, J. R. 1972. Rationale, limitation and assumptions of a northeastern forest growth simulator. *IBM Journal of Research and Development,* 16**,** 101-&.

BOULANGEAT, I., GRAVEL, D. & THUILLER, W. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology letters,* 15**,** 584-593.

BOZDOGAN, H. 1987. MODEL SELECTION AND AKAIKE INFORMATION CRITERION (AIC) - THE GENERAL-THEORY AND ITS ANALYTICAL EXTENSIONS. *Psychometrika,* 52**,** 345-370.

BRESHEARS, D. D., COBB, N. S., RICH, P. M., PRICE, K. P., ALLEN, C. D., BALICE, R. G., ROMME, W. H., KASTENS, J. H., FLOYD, M. L., BELNAP, J., ANDERSON, J. J., MYERS, O. B. & MEYER, C. W. 2005. Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci U S A,* 102**,** 15144-8.

BROADMEADOW, M. S. J. & JACKSON, S. B. 2000. Growth responses of Quercus petraea, Fraxinus excelsior and Pinus sylvestris to elevated carbon dioxide, ozone and water supply. *New Phytologist,* 146**,** 437-451.

BROADMEADOW, M. S. J. & RANDLE, T. 2002. The impacts of increased CO2 concentrations on tree growth and function. *In:* BROADMEADOW, M. S. J. (ed.) *Forestry Commission Bulletin No 125.* Edinburgh: Forestry Commision.

BROADMEADOW, M. S. J., RAY, D. & SAMUEL, C. J. A. S. 2005. Climate change and the future for broadleaved tree species in Britain. *Forestry,* 78**,** 145-161.

BROOKER, R. W. 2006. Plant-plant interactions and environmental change. *New Phytol,* 171**,** 271-84.

BRUNO, J. F., STACHOWICZ, J. J. & BERTNESS, M. D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution,* 18**,** 119-125.

BRÉDA, N., HUC, R., GRANIER, A. & DREYER, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science,* 63**,** 625-644.

BUNCE, J. A. 2000. Responses of stomatal conductance to light, humidity and temperature in winter wheat and barley grown at three concentrations of carbon dioxide in the field. *Global Change Biology,* 6**,** 371-382.

BURKE, E. J., BROWN, S. J. & CHRISTIDIS, N. 2006. Modeling the recent evolution of global drought and projections for the twenty-first century with the hadley centre climate model. *Journal of Hydrometeorology,* 7**,** 1113-1125.

BURTHE, S., DAUNT, F., BUTLER, A., ELSTON, D. A., FREDERIKSEN, M., JOHNS, D., NEWELL, M., THACKERAY, S. J. & WANLESS, S. 2012. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series,* 454**,** 119-+.

BUTT, N., BEBBER, D. P., RIUTTA, T., CROCKATT, M., MORECROFT, M. D. & MALHI, Y. 2014. Relationships between tree growth and weather extremes: Spatial and interspecific comparisons in a temperate broadleaf forest. *Forest Ecology and Management,* 334**,** 209-216.

CANHAM, C. D., FINZI, A. C., PACALA, S. W. & BURBANK, D. H. 1994. CAUSES AND CONSEQUENCES OF RESOURCE HETEROGENEITY IN FORESTS - INTERSPECIFIC VARIATION IN LIGHT TRANSMISSION BY CANOPY TREES. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 24**,** 337-349.

CANNELL, M. G. R., THORNLEY, J. H. M., MOBBS, D. C. & FRIEND, A. D. 1998. UK conifer forests may be growing faster in response to increased N deposition, atmospheric CO2 and temperature. *Forestry,* 71**,** 277-296.

CARNICER, J., COLL, M., NINYEROLA, M., PONS, X., SANCHEZ, G. & PENUELAS, J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proc Natl Acad Sci U S A,* 108**,** 1474-1478.

CASPER, B. B. & JACKSON, R. B. 1997. Plant Competition Underground. *Annual Review of Ecology and Systematics,* 28**,** 545-570.

CAVIN, L., MOUNTFORD, E. P., PETERKEN, G. F., JUMP, A. S. & WHITEHEAD, D. 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology,* 27**,** 1424-1435.

CHAPIN, F., RINCON, E. & HUANTE, P. 1993. Environmental responses of plants and ecosystems as predictors of the impact of global change. *Journal of Biosciences,* 18**,** 515-524.

CHAPIN III, F. S., ZAVALETA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALA, O. E., HOBBIE, S. E., MACK, M. C. & DIAZ, S. 2000. Consequences of changing biodiversity. *Nature,* 405**,** 234-242.

CHEN, I. C., HILL, J. K., OHLEMUELLER, R., ROY, D. B. & THOMAS, C. D. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science,* 333**,** 1024-1026.

CHOAT, B., JANSEN, S., BRODRIBB, T. J., COCHARD, H., DELZON, S., BHASKAR, R., BUCCI, S. J., FEILD, T. S., GLEASON, S. M., HACKE, U. G., JACOBSEN, A. L., LENS, F., MAHERALI, H., MARTINEZ-VILALTA, J., MAYR, S.,

MENCUCCINI, M., MITCHELL, P. J., NARDINI, A., PITTERMANN, J., PRATT, R. B., SPERRY, J. S., WESTOBY, M., WRIGHT, I. J. & ZANNE, A. E. 2012. Global convergence in the vulnerability of forests to drought. *Nature,* 491**,** 752-+.

CHOLER, P., MICHALET, R. & CALLAWAY, R. M. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology,* 82**,** 3295-3308.

CHUINE, I. 2010. Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B-Biological Sciences,* 365**,** 3149-3160.

CHUINE, I., MORIN, X. & BUGMANN, H. 2010. Warming, Photoperiods, and Tree Phenology. *Science,* 329**,** 277-278.

CHURKINA, G., SCHIMEL, D., BRASWELL, B. H. & XIAO, X. 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology,* 11**,** 1777-1787.

CIAIS, P., REICHSTEIN, M., VIOVY, N., GRANIER, A., OGEE, J., ALLARD, V., AUBINET, M., BUCHMANN, N., BERNHOFER, C., CARRARA, A., CHEVALLIER, F., DE NOBLET, N., FRIEND, A. D., FRIEDLINGSTEIN, P., GRUNWALD, T., HEINESCH, B., KERONEN, P., KNOHL, A., KRINNER, G., LOUSTAU, D., MANCA, G., MATTEUCCI, G., MIGLIETTA, F., OURCIVAL, J. M., PAPALE, D., PILEGAARD, K., RAMBAL, S., SEUFERT, G., SOUSSANA, J. F., SANZ, M. J., SCHULZE, E. D., VESALA, T. & VALENTINI, R. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature,* 437**,** 529-533.

CIAIS, P., SABINE, C., BALA, G., BOPP, L., BROVKIN, V., CANADELL, J., CHHABRA, A., DEFRIES, R., GALLOWAY, J., HEIMANN, M., JONES, C., LE QUÉRÉ, C., MYNENI, R. B., PIAO, S. & THORNTON, P. 2013. Carbon and Other Biogeochemical Cycles. *In:* STOCKER, T. F., QIN, D., PLATTNER, G. K.,

TIGNOR, M., ALLEN, S. K., BOSCHUNG, J., NAUELS, A., XIA, Y., BEX, V. & MIDGLEY, P. M. (eds.) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

CLARK, J. S., SALK, C., MELILLO, J., MOHAN, J. & ANTEN, N. 2014. Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology,* 28**,** 1344-1355.

CLAUSSEN, M., BROVKIN, V., GANOPOLSKI, A., KUBATZKI, C. & PETOUKHOV, V. 1998. *Modelling global terrestrial vegetation–climate interaction*.

COATES, K. D., BOLDOR, M., HALL, E. & ASTRUP, R. 2009. Evaluation of the complex stand simulation model SORTIE-ND for time supply review in sub-boreal forests of Northern BC. *Technical Report for Forest Science Program Project Y093187.*

COX, P. M., BETTS, R. A., JONES, C. D., SPALL, S. A. & TOTTERDELL, I. J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature,* 408**,** 184-187.

CRAMER, W., BONDEAU, A., WOODWARD, F. I., PRENTICE, I. C., BETTS, R. A., BROVKIN, V., COX, P. M., FISHER, V., FOLEY, J. A., FRIEND, A. D., KUCHARIK, C., LOMAS, M. R., RAMANKUTTY, N., SITCH, S., SMITH, B., WHITE, A. & YOUNG-MOLLING, C. 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. *Global Change Biology,* 7**,** 357-373.

CRAWFORD, R. M. M. 2008. *Plants at the margin: ecological limits and climate chagne,* Cambridge, Cambridge University Press.

DAVIS, A. J., LAWTON, J. H., SHORROCKS, B. & JENKINSON, L. S. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology,* 67**,** 600-612.

DEKKER, S. C., DE BOER, H. J., BROVKIN, V., FRAEDRICH, K., WASSEN, M. J. & RIETKERK, M. 2010. Biogeophysical feedbacks trigger shifts in the modelled vegetation-atmosphere system at multiple scales. *Biogeosciences,* 7**,** 1237-1245.

DENMAN, S., KIRK, S. & WEBBER, J. 2010. Managing Acute Oak Decline. Forestry Commission.

DIAZ, S., FARGIONE, J., CHAPIN, F. S., III & TILMAN, D. 2006. Biodiversity loss threatens human well-being. *Plos Biology,* 4**,** 1300-1305.

DIELEMAN, C. M., BRANFIREUN, B. A., MCLAUGHLIN, J. W. & LINDO, Z. 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology,* 21**,** 388-395.

DIELEMAN, W. I., VICCA, S., DIJKSTRA, F. A., HAGEDORN, F., HOVENDEN, M. J., LARSEN, K. S., MORGAN, J. A., VOLDER, A., BEIER, C., DUKES, J. S., KING, J., LEUZINGER, S., LINDER, S., LUO, Y., OREN, R., DE ANGELIS, P., TINGEY, D., HOOSBEEK, M. R. & JANSSENS, I. A. 2012. Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO2 and temperature. *Glob Chang Biol,* 18**,** 2681-93.

DIJKSTRA, J. A., WESTERMAN, E. L. & HARRIS, L. G. 2011. The effects of climate change on species composition, succession and phenology: a case study. *Global Change Biology,* 17**,** 2360-2369.

DIXON, R. K., SOLOMON, A. M., BROWN, S., HOUGHTON, R. A., TREXIER, M. C. & WISNIEWSKI, J. 1994. Carbon Pools and Flux of Global Forest Ecosystems. *Science,* 263**,** 185-190.

DROBYSHEV, I., GEWEHR, S., BERNINGER, F., BERGERON, Y. & MCGLONE, M. 2013. Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. *Journal of Ecology,* 101**,** 231-242.

DUFFY, J. E. 2009. Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment,* 7**,** 437-444.

DUNNETT, N. P. & GRIME, J. P. 1999. Competition as an amplifier of short-term vegetation responses to climate: an experimental test. *Functional Ecology,* 13**,** 388-395.

DURY, M., HAMBUCKERS, A., WARNANT, P., HENROT, A., FAVRE, E., OUBERDOUS, M. & FRANÇOIS, L. 2011. Responses of European forest ecosystems to 21st century climate: assessing changes in interannual variability and fire intensity. *iForest - Biogeosciences and Forestry,* 4**,** 82-99.

EDWARDS, M. & RICHARDSON, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature,* 430**,** 881-884.

ELLISON, A. M., BANK, M. S., CLINTON, B. D., COLBURN, E. A., ELLIOTT, K., FORD, C. R., FOSTER, D. R., KLOEPPEL, B. D., KNOEPP, J. D., LOVETT, G. M., MOHAN, J., ORWIG, D. A., RODENHOUSE, N. L., SOBCZAK, W. V., STINSON, K. A., STONE, J. K., SWAN, C. M., THOMPSON, J., VON HOLLE, B. & WEBSTER, J. R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment,* 3**,** 479-486.

ELMQVIST, T., FOLKE, C., NYSTROM, M., PETERSON, G., BENGTSSON, J., WALKER, B. & NORBERG, J. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment,* 1**,** 488-494.

ENGELBRECHT, B. M. J., COMITA, L. S., CONDIT, R., KURSAR, T. A., TYREE, M. T., TURNER, B. L. & HUBBELL, S. P. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature,* 447**,** 80-U2.

EVANS, M. R. 2012. Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 367**,** 181-190.

EVANS, M. R., BENTON, T. G., GRIMM, V., LESSELLS, C. M., O'MALLEY, M. A., MOUSTAKAS, A. & WEISBERG, M. 2014. Data availability and model complexity, generality, and utility: a reply to Lonergan. *Trends in Ecology & Evolution,* 29**,** 302-303.

EVANS, M. R., MOUSTAKAS, A., CAREY, G., MALHI, Y., BUTT, N., BENHAM, S., PALLETT, D. & SCHÄFER, S. 2015. Allometry and growth of eight tree taxa in United Kingdom woodlands. *Scientific Data,* 2.

EVANS, M. R., NORRIS, K. J. & BENTON, T. G. 2012. Predictive ecology: systems approaches. *Philos Trans R Soc Lond B Biol Sci,* 367**,** 163-9.

FENSHAM, R. J. & FAIRFAX, R. J. 2007. Drought-related tree death of savanna eucalypts: Species susceptibility, soil conditions and root architecture. *Journal of Vegetation Science,* 18**,** 71-80.

FISCHER, E. M., SENEVIRATNE, S. I., VIDALE, P. L., LÜTHI, D. & SCHÄR, C. 2007. Soil Moisture–Atmosphere Interactions during the 2003 European Summer Heat Wave. *Journal of Climate,* 20**,** 5081-5099.

FRECKLETON, R. P. & WATKINSON, A. R. 2001. Asymmetric competition between plant species. *Functional Ecology,* 15**,** 615-623.

FU, Y. H., CAMPIOLI, M., DECKMYN, G. & JANSSENS, I. A. 2012. The Impact of Winter and Spring Temperatures on Temperate Tree Budburst Dates: Results from an Experimental Climate Manipulation. *PLoS One,* 7**,** e47324.

FULTON, M., KAMMAN, J. & COYLE, M. 2014. Hydraulic limitation on maximum height of Pinus strobus trees in northern Minnesota, USA. *Trees,* 28**,** 841-848.

GASTON, K. J. 2005. Biodiversity and extinction: species and people. *Progress in Physical Geography***,** 239-247.

GILMAN, S. E., URBAN, M. C., TEWKSBURY, J., GILCHRIST, G. W. & HOLT, R. D. 2010. A framework for community interactions under climate change. *Trends Ecol Evol,* 25**,** 325-31.

GIORIA, M. & OSBORNE, B. A. 2014. Resource competition in plant invasions: emerging patterns and research needs. *Frontiers in Plant Science,* 5.

GITLIN, A. R., STHULTZ, C. M., BOWKER, M. A., STUMPF, S., PAXTON, K. L., KENNEDY, K., MUNOZ, A., BAILEY, J. K. & WHITHAM, T. G. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conservation Biology,* 20**,** 1477-1486.

GOULDEN, M. L., MUNGER, J. W., FAN, S.-M., DAUBE, B. C. & WOFSY, S. C. 1996. Exchange of Carbon Dioxide by a Deciduous Forest: Response to Interannual Climate Variability. *Science,* 271**,** 1576-1578.

GRANIER, A., REICHSTEIN, M., BREDA, N., JANSSENS, I. A., FALGE, E., CIAIS, P., GRUNWALD, T., AUBINET, M., BERBIGIER, P., BERNHOFER, C., BUCHMANN, N., FACINI, O., GRASSI, G., HEINESCH, B., ILVESNIEMI, H., KERONEN, P., KNOHL, A., KOSTNER, B., LAGERGREN, F., LINDROTH, A., LONGDOZ, B., LOUSTAU, D., MATEUS, J., MONTAGNANI, L., NYS, C., MOORS, E., PAPALE, D., PEIFFER, M., PILEGAARD, K., PITA, G.,

PUMPANEN, J., RAMBAL, S., REBMANN, C., RODRIGUES, A., SEUFERT, G., TENHUNEN, J., VESALA, I. & WANG, Q. 2007. Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology,* 143**,** 123-145.

GRIME, J. P. 1979. *Plant Strategies and Vegetation Processes,* Chichester, UK, Wiley.

GRIMM, V. & RAILSBACK, S. F. 2005. *Individual-based modeling and ecology,* Princeton, Princeton university press.

GRIMM, V., REVILLA, E., BERGER, U., JELTSCH, F., MOOIJ, W. M., RAILSBACK, S. F., THULKE, H. H., WEINER, J., WIEGAND, T. & DEANGELIS, D. L. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science,* 310**,** 987-91.

GU, L., HANSON, P. J., MAC POST, W., KAISER, D. P., YANG, B., NEMANI, R., PALLARDY, S. G. & MEYERS, T. 2008. The 2007 eastern US spring freezes: Increased cold damage in a warming world? *BioScience,* 58**,** 253-262.

GUISAN, A. & THUILLER, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol Lett,* 8**,** 993-1009.

HANEWINKEL, M., CULLMANN, D. A., SCHELHAAS, M.-J., NABUURS, G.-J. & ZIMMERMANN, N. E. 2013. Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change,* 3**,** 203-207.

HARTMANN, H. 2011. Will a 385 million year-struggle for light become a struggle for water and for carbon? - How trees may cope with more frequent climate change-type drought events. *Global Change Biology,* 17**,** 642-655.

HAWKINS, C. D. B., DHAR, A., BALLIET, N. A. & RUNZER, K. D. 2012. Residual mature trees and secondary stand structure after mountain pine beetle attack in central British Columbia. *Forest Ecology and Management,* 277**,** 107-115.

HE, J.-S., ZHANG, Q.-B. & BAZZAZ, F. A. 2005. Differential drought responses between saplings and adult trees in four co-occurring species of New England. *Trees,* 19**,** 442-450.

HE, Q., BERTNESS, M. D. & ALTIERI, A. H. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecol Lett,* 16**,** 695-706.

HEGLAND, S. J., NIELSEN, A., LÁZARO, A., BJERKNES, A.-L. & TOTLAND, Ø. 2009. How does climate warming affect plant-pollinator interactions? *Ecology Letters,* 12**,** 184-195.

HEIN, S., COLLET, C., AMMER, C., GOFF, N. L., SKOVSGAARD, J. P. & SAVILL, P. 2009. A review of growth and stand dynamics of Acer pseudoplatanus L. in Europe: implications for silviculture. *Forestry,* 82**,** 361-385.

HENRY, H. A. L. 2007. Soil freeze-thaw cycle experiments: Trends, methodological weaknesses and suggested improvements. *Soil Biology & Biochemistry,* 39**,** 977-986.

HIPFNER, J. M. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series,* 368**,** 295-304.

HOGG, E. H., BRANDT, J. P. & KOCHTUBAJDA, B. 2002. Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research,* 32**,** 823-832.

HOLTUM, J. A. M. & WINTER, K. 2010. Elevated CO2 and forest vegetation: more a water issue than a carbon issue? *Functional Plant Biology,* 37**,** 694-702.

HOOPER, D. U., CHAPIN, F. S., EWEL, J. J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J. H., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETALA, H., SYMSTAD, A. J., VANDERMEER, J. & WARDLE, D. A. 2005.

Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs,* 75**,** 3-35.

HULME, M., JENKINS, G. J., LU, X., TURNPENNY, J. R., MITCHELL, T. D., JONES, R. G., LOWE, J., MURPHY, J. M., HASSELL, D., BOORMAN, P. M., MCDONALD, R. E. & HILL, S. 2002. Climate Change Scenarios for the United Kingdom: The UKCIP02 Scientific Report. Norwich, UK: Tyndall Centre for Climate Change Research, School of Environmental Sciences, University of Easst Anglia.

HURVICH, C. M. & TSAI, C. L. 1989. REGRESSION AND TIME-SERIES MODEL SELECTION IN SMALL SAMPLES. *Biometrika,* 76**,** 297-307.

HYNYNEN, J., NIEMISTO, P., VIHERA-AARNIO, A., BRUNNER, A., HEIN, S. & VELLING, P. 2009. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. *Forestry,* 83**,** 103-119.

HYNYNEN, J., NIEMISTÖ, P., VIHERÄ-AARNIO, A., BRUNNER, A., HEIN, S. & VELLING, P. 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe. *Forestry,* 83**,** 103-119.

IBANEZ, I., CLARK, J. S., DIETZE, M. C., FEELEY, K., HERSH, M., LADEAU, S., MCBRIDE, A., WELCH, N. E. & WOLOSIN, M. S. 2006. Predicting biodiversity change: Outside the climate envelope, beyond the species-area curve. *Ecology,* 87**,** 1896-1906.

IBANEZ, I., PRIMACK, R. B., MILLER-RUSHING, A. J., ELLWOOD, E., HIGUCHI, H., LEE, S. D., KOBORI, H. & SILANDER, J. A. 2010. Forecasting phenology under global warming. *Philos Trans R Soc Lond B Biol Sci,* 365**,** 3247-60.

INOUYE, D. W. 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology,* 89**,** 353-362.

IPCC 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,* Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

IPCC 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.

JENKINS, G. J., PERRY, M. & PRIOR, J. 2009. The climate of the United Kingdom and recent trends. Exeter, UK.: Met Office Hadley Centre.

JENTSCH, A., KREYLING, J. & BEIERKUHNLEIN, C. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment,* 5**,** 365-374.

JEONG, S.-J., HO, C.-H., GIM, H.-J. & BROWN, M. E. 2011. Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. *Global Change Biology,* 17**,** 2385-2399.

JEONG, S.-J., MEDVIGY, D., SHEVLIAKOVA, E. & MALYSHEV, S. 2012. Uncertainties in terrestrial carbon budgets related to spring phenology. *Journal of Geophysical Research,* 117.

JOHNSTON, A. S. A., HOLMSTRUP, M., HODSON, M. E., THORBEK, P., ALVAREZ, T. & SIBLY, R. M. 2014. Earthworm distribution and abundance predicted by a process-based model. *Applied Soil Ecology,* 84**,** 112-123.

JUEZ, L., GONZALEZ-MARTINEZ, S. C., NANOS, N., DE-LUCAS, A. I., ORDONEZ, C., DEL PESO, C. & BRAVO, F. 2014. Can seed production and restricted dispersal limit recruitment in Pinus pinaster Aiton from the Spanish Northern Plateau? *Forest Ecology and Management,* 313**,** 329-339.

JULIEN, Y. & SOBRINO, J. A. 2009. Global land surface phenology trends from GIMMS database. *International Journal of Remote Sensing,* 30**,** 3495-3513.

JUMP, A. S. & PENUELAS, J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol Lett,* 8**,** 1010-1020.

KEARNEY, M. & PORTER, W. P. 2004. MAPPING THE FUNDAMENTAL NICHE: PHYSIOLOGY, CLIMATE, AND THE DISTRIBUTION OF A NOCTURNAL LIZARD. *Ecology,* 85**,** 3119-3131.

KELLY, A. E. & GOULDEN, M. L. 2008. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences,* 105**,** 11823-11826.

KERBY, J. T., WILMERS, C. C. & POST, E. 2012. Climate change, phenology and the nature of consumer-resource itneractions: advancing the match/mismatch hypothesis. *In:* TAKAYUKI, O., SCHMITZ, O. J. & HOLT, R. D. (eds.) *Trait-Mediated Indirect Interactions: Ecological and Evolutionary Perspectives.* Cambridfge: Cambridge University Press.

KHALIL, A. A. M. & GRACE, J. 1992. ACCLIMATION TO DROUGHT IN ACER-PSEUDOPLATANUS L (SYCAMORE) SEEDLINGS. *Journal of Experimental Botany,* 43**,** 1591-1602.

KIERS, T. E., PALMER, T. M., IVES, A. R., BRUNO, J. F. & BRONSTEIN, J. L. 2010. Mutualisms in a changing world: an evolutionary perspective. *Ecol Lett,* 13**,** 1459-74.

KIMBALL, B. A., IDSO, S. B., JOHNSON, S. & RILLIG, M. C. 2007. Seventeen years of carbon dioxide enrichment of sour orange trees: final results. *Global Change Biology,* 13**,** 2171-2183.

KIRBY, K. J., BAZELY, D. R., GOLDBERG, E. A., HALL, J. E., ISTED, R., PERRY, S. C. & THOMAS, R. C. 2014. Changes in the tree and shrub layer of Wytham Woods

(Southern England) 1974-2012: local and national trends compared. *Forestry,* 87**,** 663-673.

KJAER, E. D., MCKINNEY, L. V., NIELSEN, L. R., HANSEN, L. N. & HANSEN, J. K. 2012. Adaptive potential of ash (Fraxinus excelsior) populations against the novel emerging pathogen Hymenoscyphus pseudoalbidus. *Evol Appl,* 5**,** 219-28.

KLANDERUD, K. 2005. Climate change effects on species interactions in an alpine plant community. *Journal of Ecology,* 93**,** 127-137.

KLANDERUD, K. & TOTLAND, Ø. 2005. The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology,* 93**,** 493-501.

KLANDERUD, K., VANDVIK, V. & GOLDBERG, D. 2015. The Importance of Biotic vs. Abiotic Drivers of Local Plant Community Composition Along Regional Bioclimatic Gradients. *PLoS One,* 10**,** e0130205.

KLEIN, J. A., HARTE, J. & ZHAO, X.-Q. 2004. Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters,* 7**,** 1170-1179.

KLEIN, J. A., HARTE, J. & ZHAO, X. Q. 2007. Experimental warming, not grazing, decreases rangeland quality on the Tibetan Plateau. *Ecol Appl,* 17**,** 541-57.

KNAPP, A. K., FAY, P. A., BLAIR, J. M., COLLINS, S. L., SMITH, M. D., CARLISLE, J. D., HARPER, C. W., DANNER, B. T., LETT, M. S. & MCCARRON, J. K. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science,* 298**,** 2202-2205.

KOBE, R. K., PACALA, S. W., SILANDER, J. A., JR. & CANHAM, C. D. 1995. Juvenile Tree Survivorship as a Component of Shade Tolerance. *Ecological Applications,* 5**,** 517-532.

KOH, L. P., DUNN, R. R., SODHI, N. S., COLWELL, R. K., PROCTOR, H. C. & SMITH, V. S. 2004. Species coextinctions and the biodiversity crisis. *Science,* 305**,** 1632-4.

KORNER, C. & BASLER, D. 2010. Plant science. Phenology under global warming. *Science,* 327**,** 1461-2.

KREYLING, J., HAEI, M. & LAUDON, H. 2012. Absence of snow cover reduces understory plant cover and alters plant community composition in boreal forests. *Oecologia,* 168**,** 577-587.

KUDO, G. & IDA, T. Y. 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology,* 94**,** 2311-2320.

KULLMAN, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology,* 90**,** 68-77.

KUNSTLER, G., ALLEN, R. B., COOMES, D. A. & CANHAM, C. D. W., E.F. 2011. SORTIE/NZ model development. Landcare Research New Zealand Ltd.

KUNSTLER, G., COOMES, D. A. & CANHAM, C. D. 2009. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *Journal of Ecology,* 97**,** 685-695.

KURZ, W. A., STINSON, G., RAMPLEY, G. J., DYMOND, C. C. & NEILSON, E. T. 2008. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences of the United States of America,* 105**,** 1551-1555.

KÉRY, M. & SCHMID, H. 2005. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology,* 43**,** 101-110.

KÖRNER, C. 2006. Plant CO2 responses: an issue of definition, time and resource supply. *New Phytologist,* 172**,** 393-411.

LAMB, E. G. 2008. DIRECT AND INDIRECT CONTROL OF GRASSLAND COMMUNITY STRUCTURE BY LITTER, RESOURCES, AND BIOMASS. *Ecology,* 89**,** 216-225.

LAURANCE, W. F., OLIVEIRA, A. A., LAURANCE, S. G., CONDIT, R., NASCIMENTO, H. E. M., SANCHEZ-THORIN, A. C., LOVEJOY, T. E., ANDRADE, A., D'ANGELO, S., RIBEIRO, J. E. & DICK, C. W. 2004. Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature,* 428**,** 171-175.

LEITH, H. 1974. *Phenology and seasonality modeling,* Berlin, Springer.

LEMOINE, D., PELTIER, J. P. & MARIGO, G. 2001. Comparative studies of the water relations and the hydraulic characteristics in Fraxinus excelsior, Acer pseudoplatanus and A-opalus trees under soil water contrasted conditions. *Annals of Forest Science,* 58**,** 723-731.

LEUZINGER, S., LUO, Y., BEIER, C., DIELEMAN, W., VICCA, S. & KORNER, C. 2011. Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol Evol,* 26**,** 236-41.

LEUZINGER, S., ZOTZ, G., ASSHOFF, R. & KORNER, C. 2005. Responses of deciduous forest trees to severe drought in Central Europe. *Tree Physiol,* 25**,** 641-650.

LEVINE, J. M., VILÀ, M., D'ANTONIO, C. M., DUKES, J. S., GRIGULIS, K. & LAVOREL, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences,* 270**,** 775-781.

LIANCOURT, P., SPENCE, L. A., SONG, D. S., LKHAGVA, A., SHARKHUU, A., BOLDGIV, B., HELLIKER, B. R., PETRAITIS, P. S. & CASPER, B. B. 2013. Plant response to climate change varies with topography, interactions with neighbors, and ecotype. *Ecology,* 94**,** 444-453.

LIN, D., XIA, J. & WAN, S. 2010. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytol,* 188**,** 187-98.

LIN, J., HARCOMBE, P. A., FULTON, M. R. & HALL, R. W. 2004. Sapling Growth and Survivorship as Affected by Light and Flooding in a River Floodplain Forest of Southeast Texas. *Oecologia,* 139**,** 399-407.

LIU, J. & ASHTON, P. S. 1995. Individual-based simulation models for forest succession and management. *Forest Ecology and Management,* 73**,** 157-175.

LORANTY, M. M., MACKAY, D. S., EWERS, B. E., TRAVER, E. & KRUGER, E. L. 2010. Competition for light between individual trees lowers reference canopy stomatal conductance: Results from a model. *Journal of Geophysical Research,* 115.

LORTIE, C. J., BROOKER, R. W., CHOLER, P., KIKVIDZE, Z., MICHALET, R., PUGNAIRE, F. I. & CALLAWAY, R. M. 2004. Rethinking plant community theory. *Oikos,* 107**,** 433-438.

LUEDELING, E., ZHANG, M. H. & GIRVETZ, E. H. 2009. Climatic Changes Lead to Declining Winter Chill for Fruit and Nut Trees in California during 1950-2099. *PLoS One,* 4.

LUKAC, M., CALFAPIETRA, C., LAGOMARSINO, A. & LORETO, F. 2010. Global climate change and tree nutrition: effects of elevated CO2 and temperature. *Tree Physiol,* 30**,** 1209-20.

LUO, Y. 2007. Terrestrial Carbon–Cycle Feedback to Climate Warming. *Annual Review of Ecology, Evolution, and Systematics,* 38**,** 683-712.

LUYSSAERT, S., SCHULZE, E. D., BORNER, A., KNOHL, A., HESSENMOLLER, D., LAW, B. E., CIAIS, P. & GRACE, J. 2008. Old-growth forests as global carbon sinks. *Nature,* 455**,** 213-215.

LÉVESQUE, M., RIGLING, A., BUGMANN, H., WEBER, P. & BRANG, P. 2014. Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. *Agricultural and Forest Meteorology,* 197**,** 1-12.

MA, T. & ZHOU, C. G. 2012. Climate-associated changes in spring plant phenology in China. *International Journal of Biometeorology,* 56**,** 269-275.

MA, Z., PENG, C., ZHU, Q., CHEN, H., YU, G., LI, W., ZHOU, X., WANG, W. & ZHANG, W. 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences,* 109**,** 2423-2427.

MAESTRE, F. T., VALLADARES, F. & REYNOLDS, J. F. 2005. Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology,* 93**,** 748-757.

MARTINEZ-VILALTA, J., LLORET, F. & BRESHEARS, D. D. 2012. Drought-induced forest decline: causes, scope and implications. *Biol Lett,* 8**,** 689-91.

MASON, T. H. E., STEPHENS, P. A., APOLLONIO, M. & WILLIS, S. G. 2014. Predicting potential responses to future climate in an alpine ungulate: interspecific interactions exceed climate effects. *Global Change Biology,* 20**,** 3872-3882.

MATSUIK, G., RUTHROF, K. X. & HARDY, G. S. J. 2012. Drought and heat triggers sudden and severe dieback in a dominant mediterranean-type woodland species. 2**,** 183-186.

MCDOWELL, N., POCKMAN, W. T., ALLEN, C. D., BRESHEARS, D. D., COBB, N., KOLB, T., PLAUT, J., SPERRY, J., WEST, A., WILLIAMS, D. G. & YEPEZ, E. A. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol,* 178**,** 719-39.

MCKEE, T. B., DOESKEN, N. J. & KLEIST, J. 1993. The relationship of drought frequency and duration to time scales. *Eighth Conference on Applied Climatology.* Anaheim, California.

MCMAHON, S. M., BEBBER, D. P., BUTT, N., CROCKATT, M., KIRBY, K., PARKER, G. G., RIUTTA, T. & SLADE, E. M. 2015. Ground based LiDAR demonstrates the legacy of management history to canopy structure and composition across a fragmented temperate woodland. *Forest Ecology and Management,* 335**,** 255-260.

MEDIAVILLA, S. & ESCUDERO, A. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. *Forest Ecology and Management,* 187**,** 281-294.

MEDVIGY, D., WOFSY, S. C., MUNGER, J. W., HOLLINGER, D. Y. & MOORCROFT, P. R. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research,* 114.

MELILLO, J. M., RICHMOND, T. C. & YOHE, G. 2014. Climate Change Impacts in the United States: The Third National Climate Assessment. *U.S. Global Change Research Program*

MELILLO, J. M., STEUDLER, P. A., ABER, J. D., NEWKIRK, K., LUX, H., BOWLES, F. P., CATRICALA, C., MAGILL, A., AHRENS, T. & MORRISSEAU, S. 2002. Soil Warming and Carbon-Cycle Feedbacks to the Climate System. *Science,* 298**,** 2173-2176.

MENZEL, A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int J Biometeorol,* 44**,** 76-81.

MENZEL, A. & FABIAN, P. 1999. Growing season extended in Europe. *Nature,* 397**,** 659-659.

MENZEL, A., SPARKS, T. H., ESTRELLA, N., KOCH, E., AASA, A., AHAS, R., ALM-KUBLER, K., BISSOLLI, P., BRASLAVSKA, O., BRIEDE, A., CHMIELEWSKI, F. M., CREPINSEK, Z., CURNEL, Y., DAHL, A., DEFILA, C., DONNELLY, A., FILELLA, Y., JATCZA, K., MAGE, F., MESTRE, A., NORDLI, O., PENUELAS, J., PIRINEN, P., REMISOVA, V., SCHEIFINGER, H., STRIZ, M., SUSNIK, A., VAN VLIET, A. J. H., WIELGOLASKI, F. E., ZACH, S. & ZUST, A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biology,* 12**,** 1969-1976.

METTE, T., DOLOS, K., MEINARDUS, C., BRÄUNING, A., REINEKING, B., BLASCHKE, M., PRETZSCH, H., BEIERKUHNLEIN, C., GOHLKE, A. & WELLSTEIN, C. 2013. Climatic turning point for beech and oak under climate change in Central Europe. *Ecosphere,* 4**,** art145.

MIGLIAVACCA, M., SONNENTAG, O., KEENAN, T. F., CESCATTI, A., O'KEEFE, J. & RICHARDSON, A. D. 2012. On the uncertainty of phenological responses to climate change, and implications for a terrestrial biosphere model. *Biogeosciences,* 9**,** 2063-2083.

MIHOK, B., KENDERES, K., KIRBY, K. J., PAVIOUR-SMITH, K. & ELBOURN, C. A. 2009. Forty-year changes in the canopy and the understorey in Wytham Woods. *Forestry,* 82**,** 515-527.

MILLENIUM ECOSYSTEM ASSESSMENT 2005. Ecosystems and Human Well-being: Synthesis. Washington, D.C.

MILLER-RUSHING, A. J. & PRIMACK, R. B. 2008. Global Warming and Flowering Times in Thoreau's Concord: A Community Perspective. *Ecology,* 89**,** 332-341.

MITCHELL, R. J., BEATON, J. K., BELLAMY, P. E., BROOME, A., CHETCUTI, J., EATON, S., ELLIS, C. J., GIMONA, A., HARMER, R., HESTER, A. J., HEWISON, R. L., HODGETTS, N. G., IASON, G. R., KERR, G., LITTLEWOOD, N. A., NEWEY, S., POTTS, J. M., POZSGAI, G., RAY, D., SIM, D. A., STOCKAN, J. A., TAYLOR, A. F. S. & WOODWARD, S. 2014. Ash dieback in the UK: A review of the ecological and conservation implications and potential management options. *Biological Conservation,* 175**,** 95-109.

MONTOYA, J. M. & RAFFAELLI, D. 2010. Climate change, biotic interactions and ecosystem services. *Philos Trans R Soc Lond B Biol Sci,* 365**,** 2013-8.

MOORCROFT, P. R., HURTT, G. C. & PACALA, S. W. 2001. A method for scaling vegetation dynamics: The ecosystem demography model (ED). *Ecological Monographs,* 71**,** 557-585.

MORAVIE, M. A., PASCAL, J. P. & AUGER, P. 1997. Investigating canopy regeneration processes through individual-based spatial models: application to a tropical rain forest. *Ecological Modelling,* 104**,** 241-260.

MORECROFT, M. D., BEALEY, C. E., BEAUMONT, D. A., BENHAM, S., BROOKS, D. R., BURT, T. P., CRITCHLEY, C. N. R., DICK, J., LITTLEWOOD, N. A., MONTEITH, D. T., SCOTT, W. A., SMITH, R. I., WALMSEY, C. & WATSON, H. 2009. The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation,* 142**,** 2814-2832.

MORECROFT, M. D. & ROBERTS, J. M. 1999. Photosynthesis and stomatal conductance of mature canopy Oak (Quercus robur) and Sycamore (Acer pseudoplatanus) trees throughout the growing season. *Functional Ecology,* 13**,** 332-342.

MORECROFT, M. D., STOKES, V. J. & MORISON, J. I. L. 2003. Seasonal changes in the photosynthetic capacity of canopy oak (Quercus robur) leaves: the impact of slow development on annual carbon uptake. *Int J Biometeorol,* 47**,** 221-226.

MORECROFT, M. D., STOKES, V. J., TAYLOR, M. E. & MORISON, J. I. L. 2008. Effects of climate and management history on the distribution and growth of sycamore (Acer pseudoplatanus L.) in a southern British woodland in comparison to native competitors. *Forestry,* 81**,** 59-74.

MORGAN, J. A., PATAKI, D. E., KÖRNER, C., CLARK, H., DEL GROSSO, S. J., GRÜNZWEIG, J. M., KNAPP, A. K., MOSIER, A. R., NEWTON, P. C. D., NIKLAUS, P. A., NIPPERT, J. B., NOWAK, R. S., PARTON, W. J., POLLEY, H. W. & SHAW, M. R. 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO2. *Oecologia,* 140**,** 11-25.

MORIN, X., LECHOWICZ, M. J., AUGSPURGER, C., O'KEEFE, J., VINER, D. & CHUINE, I. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology,* 15**,** 961-975.

MORISETTE, J. T., RICHARDSON, A. D., KNAPP, A. K., FISHER, J. I., GRAHAM, E. A., ABATZOGLOU, J., WILSON, B. E., BRESHEARS, D. D., HENEBRY, G. M., HANES, J. M. & LIANG, L. 2009. Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment,* 7**,** 253-260.

MOUSTAKAS, A. & EVANS, M. R. 2015. Effects of growth rate, size, and light availability on tree survival across life stages: a demographic analysis accounting for missing values and small sample sizes. *BMC Ecology,* 15.

MUELLER, R. C., SCUDDER, C. M., PORTER, M. E., TROTTER, R. T., GEHRING, C. A. & WHITHAM, T. G. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal of Ecology,* 93**,** 1085-1093.

MUNSON, S. M., WEBB, R. H., BELNAP, J., ANDREW HUBBARD, J., SWANN, D. E. & RUTMAN, S. 2012. Forecasting climate change impacts to plant community composition in the Sonoran Desert region. *Global Change Biology,* 18**,** 1083-1095.

MURPHY, J. M., SEXTON, D. M. H., JENKINS, G. J., BOOTH, B., BROWN, C. C., CLARK, R. T., COLLINS, M., HARRIS, G. R., KENDON, E. J., BETTS, R. A., BROWN, S. J., HUMPHREY, K. A., MCCARTHY, M. P., MCDONALD, R. E., STEPHENS, A., WALLACE, C., WARREN, R., WILBY, R. & WOOD, R. A. 2009. UK Climate projections science report: climate change projections. Exeter: Met Office Hadley Centre.

NAEEM, S. & WRIGHT, J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters,* 6**,** 567-579.

NAITHANI, K. J., EWERS, B. E., ADELMAN, J. D. & SIEMENS, D. H. 2014. Abiotic and biotic controls on local spatial distribution and performance of Boechera stricta. *Frontiers in Plant Science,* 5.

NAKASHIZUKA, T. 2001. Species coexistence in temperate, mixed deciduous forests. *Trends Ecol Evol,* 16**,** 205-210.

NAKICENOVIC, N. & SWART, R. (eds.) 2000. *Emission scenarios.,* Cambridge: Cambridge University Press.

NEILSON, R. P., PITELKA, L. F., SOLOMON, A. M., NATHAN, R., MIDGLEY, G. F., FRAGOSO, J. M. V., LISCHKE, H. & THOMPSON, K. 2005. Forecasting Regional to Global Plant Migration in Response to Climate Change. *BioScience,* 55**,** 749-759.

NEWNHAM, R. M. 1964. *The development of a stand model for Douglas fir.* University of British Columbia, Canada.

NIINEMETS, Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management,* 260**,** 1623-1639.

NORBY, R. J., DELUCIA, E. H., GIELEN, B., CALFAPIETRA, C., GIARDINA, C. P., KING, J. S., LEDFORD, J., MCCARTHY, H. R., MOORE, D. J., CEULEMANS, R., DE ANGELIS, P., FINZI, A. C., KARNOSKY, D. F., KUBISKE, M. E., LUKAC, M., PREGITZER, K. S., SCARASCIA-MUGNOZZA, G. E., SCHLESINGER, W. H. & OREN, R. 2005. Forest response to elevated CO2 is conserved across a broad range of productivity. *Proc Natl Acad Sci U S A,* 102**,** 18052-6.

NORBY, R. J. & LUO, Y. Q. 2004. Evaluating ecosystem responses to rising atmospheric CO(2) and global warming in a multi-factor world. *New Phytologist,* 162**,** 281-293.

NORBY, R. J., OGLE, K., CURTIS, P. S., BADECK, F. W., HUTH, A., HURTT, G. C., KOHYAMA, T. & PENUELAS, J. 2001. Aboveground growth and competition in forest gap models: An analysis for studies of climatic change. *Climatic Change,* 51**,** 415-447.

NORRIS, K. 2012. Biodiversity in the context of ecosystem services: the applied need for systems approaches. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 367**,** 191-199.

NORTHFIELD, T. D. & IVES, A. R. 2013. Coevolution and the Effects of Climate Change on Interacting Species. *PLoS Biol,* 11**,** e1001685.

NOSS, R. F. 2001. Beyond Kyoto: Forest Management in a Time of Rapid Climate Change Después de Kyoto: Manejo Forestal en Tiempos de Cambio Climático Acelerado. *Conservation Biology,* 15**,** 578-590.

O'KEEFE, J. 2012. Phenology of Woody Species at Harvard Forest since 1990. Harvard Forest Data Archive: HF003.

PACALA, S. W., CANHAM, C. D., SAPONARA, J., SILANDER, J. A., KOBE, R. K. & RIBBENS, E. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs,* 66**,** 1-43.

PACALA, S. W., CANHAM, C. D. & SILANDER, J. A. 1993. FOREST MODELS DEFINED BY FIELD-MEASUREMENTS .1. THE DESIGN OF A NORTHEASTERN FOREST SIMULATOR. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 23**,** 1980-1988.

PACALA, S. W., CANHAM, C. D., SILANDER JR, J. A. & KOBE, R. K. 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research,* 24**,** 2172-2183.

PACALA, S. W. & REES, M. 1998. Models Suggesting Field Experiments to Test Two Hypotheses Explaining Successional Diversity. *The American Naturalist,* 152**,** 729-737.

PAL, J. S., GIORGI, F. & BI, X. 2004. Consistency of recent European summer precipitation trends and extremes with future regional climate projections. *Geophysical Research Letters,* 31**,** n/a-n/a.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics.* Palo Alto: Annual Reviews.

PARMESAN, C., ROOT, T. L. & WILLIG, M. R. 2000. Impacts of Extreme Weather and Climate on Terrestrial Biota. *Bulletin of the American Meteorological Society,* 81**,** 443-450.

PARMESAN, C. & YOHE, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* 421**,** 37-42.

PAUTASSO, M., AAS, G., QUELOZ, V. & HOLDENRIEDER, O. 2013. European ash (Fraxinus excelsior) dieback – A conservation biology challenge. *Biological Conservation,* 158**,** 37-49.

PEARSON, R. G. & DAWSON, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* 12**,** 361-371.

PELLERIN, M., DELESTRADE, A., MATHIEU, G., RIGAULT, O. & YOCCOZ, N. G. 2012. Spring tree phenology in the Alps: effects of air temperature, altitude and local topography. *European Journal of Forest Research,* 131**,** 1957-1965.

PENUELAS, J., GORDON, C., LLORENS, L., NIELSEN, T., TIETEMA, A., BEIER, C., BRUNA, P., EMMETT, B., ESTIARTE, M. & GORISSEN, A. 2004. Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north-south European gradient. *Ecosystems,* 7**,** 598-612.

PETERKEN, G. F. 2001. Ecological effects of introduced tree species in Britain. *Forest Ecology and Management,* 141**,** 31-42.

PETERKEN, G. F. & MOUNTFORD, E. P. 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry,* 69**,** 125-136.

PETERSON, T. C. & BARINGER, M. O. 2009. State of the State in 2008. Bullleting of the American Meteorological Society.

PETIT, R. J. & HAMPE, A. 2006. Some Evolutionary Consequences of Being a Tree. *Annual Review of Ecology, Evolution, and Systematics,* 37**,** 187-214.

PEÑUELAS, J., FILELLA, I. & COMAS, P. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology,* 8**,** 531-544.

PEÑUELAS, J., LLORET, F. & MONTOYA, R. 2001. Severe drought effects on Mediterranean woody flora in Spain. *Forest Science,* 47**,** 214-218.

PHILLIPS, P. D., DE AZEVEDO, C. P., DEGEN, B., THOMPSON, I. S., SILVA, J. N. M. & VAN GARDINGEN, P. R. 2004. An individual-based spatially explicit simulation model for strategic forest management planning in the eastern Amazon. *Ecological Modelling,* 173**,** 335-354.

PIAO, S., FANG, J., ZHOU, L., CIAIS, P. & ZHU, B. 2006. Variations in satellite-derived phenology in China's temperate vegetation. *Global Change Biology,* 12**,** 672-685.

POLASKY, S., NELSON, E., PENNINGTON, D. & JOHNSON, K. A. 2010. The Impact of Land-Use Change on Ecosystem Services, Biodiversity and Returns to Landowners: A Case Study in the State of Minnesota. *Environmental and Resource Economics,* 48**,** 219-242.

POLGAR, C. A. & PRIMACK, R. B. 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist,* 191**,** 926-941.

POORTER, H. & PEREZ-SOBA, M. 2001. The growth response of plants to elevated CO2 under non-optimal environmental conditions. *Oecologia,* 129**,** 1-20.

PORTÉ, A. & BARTELINK, H. H. 2002. Modelling mixed forest growth: a review of models for forest management. *Ecological Modelling,* 150**,** 141-188.

POST, E. & FORCHHAMMER, M. C. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363**,** 2369-2375.

POST, E., PEDERSEN, C., WILMERS, C. C. & FORCHHAMMER, M. C. 2008. Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society of London B: Biological Sciences,* 275**,** 2005-2013.

PURVES, D. & PACALA, S. 2008. Predictive models of forest dynamics. *Science,* 320**,** 1452-3.

PURVES, D. W., LICHSTEIN, J. W., STRIGUL, N. & PACALA, S. W. 2008. Predicting and understanding forest dynamics using a simple tractable model. *Proc Natl Acad Sci U S A,* 105**,** 17018-22.

PYATT, D. G., RAY, D. & FLETCHER, J. 2001. An ecological site classification for forestry in Great britain. *Forestry Commission Bulletin 124.* Edinburgh: Forestry Commission.

QIAO, M., ZHANG, Z., LI, Y., XIAO, J., YIN, H., YUE, B. & LIU, Q. 2015. Experimental warming effects on root nitrogen absorption and mycorrhizal infection in a subalpine coniferous forest. *Scandinavian Journal of Forest Research***,** 1-8.

RAFFAELLI, D. G. 2006. Biodiversity and ecosystem functioning: issues of scale and trophic complexity. *Marine Ecology Progress Series,* 311**,** 285-294.

RAFFERTY, N. E. & IVES, A. R. 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecol Lett,* 14**,** 69-74.

RAHMSTORF, S. & COUMOU, D. 2012. Increase of extreme events in a warming world (vol 108, pg 17905, 2011). *Proc Natl Acad Sci U S A,* 109**,** 4708-4708.

READ, D. J., FREER-SMITH, P. H., MORISON, J. I. L., HANLEY, N., WEST, C. C. & SNOWDON, P. 2009. Combating climate change - a role for UK forests. An assessment of the potential of the UK's trees and woodlands to mitigate and adapt to climate change. Edinburgh: The Stationery Office.

REES, M., CONDIT, R., CRAWLEY, M., PACALA, S. & TILMAN, D. 2001. Long-Term Studies of Vegetation Dynamics. *Science,* 293**,** 650-655.

REHFELDT, G. E., FERGUSON, D. E. & CROOKSTON, N. L. 2009. Aspen, climate, and sudden decline in western USA. *Forest Ecology and Management,* 258**,** 2353-2364.

REVERCHON, F., XU, Z., BLUMFIELD, T. J., CHEN, C. & ABDULLAH, K. M. 2011. Impact of global climate change and fire on the occurrence and function of

understorey legumes in forest ecosystems. *Journal of Soils and Sediments,* 12**,** 150-160.

REYER, C. P., LEUZINGER, S., RAMMIG, A., WOLF, A., BARTHOLOMEUS, R. P., BONFANTE, A., DE LORENZI, F., DURY, M., GLONING, P., ABOU JAOUDE, R., KLEIN, T., KUSTER, T. M., MARTINS, M., NIEDRIST, G., RICCARDI, M., WOHLFAHRT, G., DE ANGELIS, P., DE DATO, G., FRANCOIS, L., MENZEL, A. & PEREIRA, M. 2013a. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Glob Chang Biol,* 19**,** 75-89.

REYER, C. P. O., LEUZINGER, S., RAMMIG, A., WOLF, A., BARTHOLOMEUS, R. P., BONFANTE, A., DE LORENZI, F., DURY, M., GLONING, P., ABOU JAOUDE, R., KLEIN, T., KUSTER, T. M., MARTINS, M., NIEDRIST, G., RICCARDI, M., WOHLFAHRT, G., DE ANGELIS, P., DE DATO, G., FRANCOIS, L., MENZEL, A. & PEREIRA, M. 2013b. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology,* 19**,** 75-89.

RICH, P. M., BRESHEARS, D. D. & WHITE, A. B. 2008. Phenology of Mixed Woody-Herbaceous Ecosystems following Extreme Events: Net and Differential Responses. *Ecology,* 89**,** 342-352.

RICHARDSON, A. D., KEENAN, T. F., MIGLIAVACCA, M., RYU, Y., SONNENTAG, O. & TOOMEY, M. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology,* 169**,** 156-173.

ROLIM, S. G., JESUS, R. M., NASCIMENTO, H. E. M., DO COUTO, H. T. Z. & CHAMBERS, J. Q. 2005. Biomass change in an Atlantic tropical moist forest: the ENSO effect in permanent sample plots over a 22-year period. *Oecologia,* 142**,** 238-246.

ROOT, T. L., PRICE, J. T., HALL, K. R., SCHNEIDER, S. H., ROSENZWEIG, C. & POUNDS, J. A. 2003. Fingerprints of global warming on wild animals and plants. *Nature,* 421**,** 57-60.

ROSE, L., LEUSCHNER, C., KOECKEMANN, B. & BUSCHMANN, H. 2009. Are marginal beech (Fagus sylvatica L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research,* 128**,** 335-343.

ROSENZWEIG, C., IGLESIAS, A., YANG, X. B., EPSTEIN, P. & CHIVIAN, E. 2001. Climate Change and Extreme Weather Events; Implications for Food Production, Plant Diseases, and Pests. *Global Change and Human Health,* 2**,** 90-104.

RUSANEN, M. & MYKING, T. 2003. EUFORGEN Technical Guidelines for Genetic Conservation and Use for Sycamore (Acer pseudoplatanus). Rome, Italy: International Plant Genetic Resources Institute.

RUSTAD, L. E., CAMPBELL, J. L., MARION, G. M., NORBY, R. J., MITCHELL, M. J., HARTLEY, A. E., CORNELISSEN, J. H. C., GUREVITCH, J. & GCTE, N. 2001. A Meta-Analysis of the Response of Soil Respiration, Net Nitrogen Mineralization, and Aboveground Plant Growth to Experimental Ecosystem Warming. *Oecologia,* 126**,** 543-562.

RUTISHAUSER, T., LUTERBACHER, J., DEFILA, C., FRANK, D. & WANNER, H. 2008. Swiss spring plant phenology 2007: Extremes, a multi-century perspective, and changes in temperature sensitivity. *Geophysical Research Letters,* 35**,** n/a-n/a.

SALA, A., PIPER, F. & HOCH, G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytologist,* 186**,** 274-281.

SALA, O. E. 2000. Global Biodiversity Scenarios for the Year 2100 . *Science,* 287**,** 1770-1774.

SALESKA, S. R., SHAW, M. R., FISCHER, M. L., DUNNE, J. A., STILL, C. J., HOLMAN, M. L. & HARTE, J. 2002. Plant community composition mediates both large transient decline and predicted long-term recovery of soil carbon under climate warming. *Global Biogeochemical Cycles,* 16.

SAMUELSSON, P., JONES, C. G., WILLÉN, U., ULLERSTIG, A., GOLLVIK, S., HANSSON, U. L. F., JANSSON, C., KJELLSTRÖM, E., NIKULIN, G. & WYSER, K. 2011. The Rossby Centre Regional Climate model RCA3: model description and performance. *Tellus A,* 63**,** 4-23.

SAVILL, P. S., PERRINS, C., KIRBY, K. J. & FISHER, N. 2011. *Wytham Woods: Oxford's Ecological Laboratory,* Oxford, OUP.

SCHAR, C., VIDALE, P. L., LUTHI, D., FREI, C., HABERLI, C., LINIGER, M. A. & APPENZELLER, C. 2004. The role of increasing temperature variability in European summer heatwaves. *Nature,* 427**,** 332-336.

SCHEFFER, M. & CARPENTER, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol,* 18**,** 648-656.

SCHERRER, D., BADER, M. K.-F. & KÖRNER, C. 2011. Drought-sensitivity ranking of deciduous tree species based on thermal imaging of forest canopies. *Agricultural and Forest Meteorology,* 151**,** 1632-1640.

SCHWARTZ, M. D., AHAS, R. & AASA, A. 2006. Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology,* 12**,** 343-351.

SCHWARTZ, M. D. & HANES, J. M. 2010. Intercomparing multiple measures of the onset of spring in eastern North America. *International Journal of Climatology,* 30**,** 1614-1626.

SCHWINNING, S. & WEINER, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia,* 113**,** 447-455.

SEIDL, R., RAMMER, W., SCHELLER, R. M. & SPIES, T. A. 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling,* 231**,** 87-100.

SEMCHENKO, M., LEPIK, M., GÖTZENBERGER, L. & ZOBEL, K. 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? *Journal of Ecology,* 100**,** 459-466.

SENEVIRATNE, S. I., LUTHI, D., LITSCHI, M. & SCHAR, C. 2006. Land-atmosphere coupling and climate change in Europe. *Nature,* 443**,** 205-209.

SHEVTSOVA, A., OJALA, A., NEUVONEN, S., VIENO, M. & HAUKIOJA, E. 1995. Growth and Reproduction of Dwarf Shrubs in a Subarctic Plant Community: Annual Variation and Above-Ground Interactions with Neighbours. *Journal of Ecology,* 83**,** 263-275.

SIMPSON, I. R. & JONES, P. D. 2012. Updated precipitation series for the UK derived from Met Office gridded data. *International Journal of Climatology,* 32**,** 2271-2282.

SMITH, B., SAMUELSSON, P., WRAMNEBY, A. & RUMMUKAINEN, M. 2011. A model of the coupled dynamics of climate, vegetation and terrestrial ecosystem biogeochemistry for regional applications. *Tellus A,* 63**,** 87-106.

SMITH, M. J. & SIBLY, R. M. 2008. Identification of trade-offs underlying the primary strategies of plants. *Evolutionary Ecology Research,* 10**,** 45-60.

SMITH, S. J., EDMONDS, J., HARLIN, C. A., MUNDRA, A. & CALVIN, K. 2015. Near-term acceleration in the rate of temperature change. *Nature Climate Change,* 5**,** 333-336.

SOJA, A. J., TCHEBAKOVA, N. M., FRENCH, N. H. F., FLANNIGAN, M. D., SHUGART, H. H., STOCKS, B. J., SUKHININ, A. I., PARFENOVA, E. I., CHAPIN, F. S. & STACKHOUSE, P. W. 2007. Climate-induced boreal forest

change: Predictions versus current observations. *Global and Planetary Change,* 56**,** 274-296.

SPARKS, T. H. & MENZEL, A. 2002. Observed changes in seasons: an overview. *International Journal of Climatology,* 22**,** 1715-1725.

SPITTLEHOUSE, D. L. & STEWART, R. B. 2004. *Adaptation to climate change in forest management*.

STILING, P. & CORNELISSEN, T. 2007. How does elevated carbon dioxide (CO2) affect plant–herbivore interactions? A field experiment and meta-analysis of CO2-mediated changes on plant chemistry and herbivore performance. *Global Change Biology,* 13**,** 1823-1842.

SUAREZ, M. L., GHERMANDI, L. & KITZBERGER, T. 2004. Factors predisposing episodic drought-induced tree mortality in Nothofagus - site, climatic sensitivity and growth trends. *Journal of Ecology,* 92**,** 954-966.

SUAREZ, M. L. & KITZBERGER, T. 2008. Recruitment patterns following a severe drought: long-term compositional shifts in Patagonian forests. *Canadian Journal of Forest Research,* 38**,** 3002-3010.

SULLIVAN, P. F., ARENS, S. J. T., CHIMNER, R. A. & WELKER, J. M. 2008. Temperature and microtopography interact to control carbon cycling in a high arctic fen. *Ecosystems,* 11**,** 61-76.

SUTHERST, R. W., MAYWALD, G. F. & BOURNE, A. S. 2007. Including species interactions in risk assessments for global change. *Global Change Biology,* 13**,** 1843-1859.

SUTTLE, K. B., THOMSEN, M. A. & POWER, M. E. 2007. Species interactions reverse grassland responses to changing climate. *Science,* 315**,** 640-2.

SWIFT, L. C. 2005. Carlibrating SORTIE's recruitment subroutine for southeastern Qubec: verifying the consistency of paramters. Department of Biology, Concordia University, Montreal, Quebec, Canada.

SYKES, J. M. & LANE, A. M. J. 1996. The United Kingdom Environmental Change Network: Protocols for Standard Measurements at Terrestrial Sites. London: The Stationery Office.

TANSLEY, A. G. 1917. On competition between Glaium Saxatile L. (G. Hercynicum Weig.) and Galium Sylvestre Poll. (G. Asperum Schreb.) on different types of soil. *Journal of Ecology,* 5**,** 173-179.

TEAM, R. C. 2013. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

TERRADAS, J., PEÑUELAS, J. & LLORET, F. 2009. The Fluctuation Niche in Plants. *International Journal of Ecology*, 2009**,** 1-5.

THACKERAY, S. J., SPARKS, T. H., FREDERIKSEN, M., BURTHE, S., BACON, P. J., BELL, J. R., BOTHAM, M. S., BRERETON, T. M., BRIGHT, P. W., CARVALHO, L., CLUTTON-BROCK, T. I. M., DAWSON, A., EDWARDS, M., ELLIOTT, J. M., HARRINGTON, R., JOHNS, D., JONES, I. D., JONES, J. T., LEECH, D. I., ROY, D. B., SCOTT, W. A., SMITH, M., SMITHERS, R. J., WINFIELD, I. J. & WANLESS, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology,* 16**,** 3304-3313.

THIBAULT, K. M. & BROWN, J. H. 2008. Impact of an extreme climatic event on community assembly. *Proc Natl Acad Sci U S A,* 105**,** 3410-5.

THOMAS, C. D., CAMERON, A., GREEN, R. E., BAKKENES, M., BEAUMONT, L. J., COLLINGHAM, Y. C., ERASMUS, B. F. N., DE SIQUEIRA, M. F., GRAINGER,

A., HANNAH, L., HUGHES, L., HUNTLEY, B., VAN JAARSVELD, A. S., MIDGLEY, G. F., MILES, L., ORTEGA-HUERTA, M. A., PETERSON, A. T., PHILLIPS, O. L. & WILLIAMS, S. E. 2004. Extinction risk from climate change. *Nature,* 427**,** 145-148.

THOMSON, J. D. 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society of London B: Biological Sciences,* 365**,** 3187-3199.

THORPE, A. S., ASCHEHOUG, E. T., ATWATER, D. Z. & CALLAWAY, R. M. 2011. Interactions among plants and evolution. *Journal of Ecology,* 99**,** 729-740.

THUILLER, W., LAVOREL, S., ARAUJO, M. B., SYKES, M. T. & PRENTICE, I. C. 2005. Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci U S A,* 102**,** 8245-50.

TIERNEY, G. L., FAHEY, T. J., GROFFMAN, P. M., HARDY, J. P., FITZHUGH, R. D., DRISCOLL, C. T. & YAVITT, J. B. 2003. Environmental control of fine root dynamics in a northern hardwood forest. *Global Change Biology,* 9**,** 670-679.

TILMAN, D. & LEHMAN, C. 2001. Human-caused environmental change: Impacts on plant diversity and evolution. *Proc Natl Acad Sci U S A,* 98**,** 5433-5440.

TOMIOLO, S., VAN DER PUTTEN, W. H. & TIELBORGER, K. 2015. Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change. *Ecology,* 96**,** 1298-1308.

TYLIANAKIS, J. M., DIDHAM, R. K., BASCOMPTE, J. & WARDLE, D. A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol Lett,* 11**,** 1351-1363.

URBAN, M. C., TEWKSBURY, J. J. & SHELDON, K. S. 2012a. On a collision course: competition and dispersal differences create no-analogue communities and cause

extinctions during climate change. *Proceedings of the Royal Society of London B: Biological Sciences*.

URBAN, M. C., TEWKSBURY, J. J. & SHELDON, K. S. 2012b. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society of London B: Biological Sciences,* 279**,** 2072-2080.

VAN LOON, M. P., SCHIEVING, F., RIETKERK, M., DEKKER, S. C., STERCK, F. & ANTEN, N. P. 2014. How light competition between plants affects their response to climate change. *New Phytol,* 203**,** 1253-65.

VAN MANTGEM, P. J. & STEPHENSON, N. L. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecological Society of America Annual Meeting Abstracts*.

VAN MANTGEM, P. J., STEPHENSON, N. L., BYRNE, J. C., DANIELS, L. D., FRANKLIN, J. F., FULE, P. Z., HARMON, M. E., LARSON, A. J., SMITH, J. M., TAYLOR, A. H. & VEBLEN, T. T. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. *Science,* 323**,** 521-524.

VAN PEER, L., NIJS, I., REHEUL, D. & DE CAUWER, B. 2004. Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. *Functional Ecology,* 18**,** 769-778.

VAUTARD, R., YIOU, P., D'ANDREA, F., DE NOBLET, N., VIOVY, N., CASSOU, C., POLCHER, J., CIAIS, P., KAGEYAMA, M. & FAN, Y. 2007. Summertime European heat and drought waves induced by wintertime Mediterranean rainfall deficit. *Geophysical Research Letters,* 34.

VILÀ, M., GÓMEZ, A. & MARON, J. 2003. Are alien plants more competitive than their native conspecifics? A test using Hypericum perforatum L. *Oecologia,* 137**,** 211-215.

VILÀ, M. & WEINER, J. 2004. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. *Oikos,* 105**,** 229-238.

VISSER, M., TE MARVELDE, L. & LOF, M. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology,* 153**,** 75-84.

VISSER, M. E. & BOTH, C. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proc Biol Sci,* 272**,** 2561-9.

VISSER, M. E. & HOLLEMAN, L. J. 2001. Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc Biol Sci,* 268**,** 289-94.

VITASSE, Y., PORTE, A. J., KREMER, A., MICHALET, R. & DELZON, S. 2009. Responses of canopy duration to temperature changes in four temperate tree species: relative contributions of spring and autumn leaf phenology. *Oecologia,* 161**,** 187-98.

VOLK, M., NIKLAUS, P. A. & KÖRNER, C. 2000. Soil moisture effects determine CO2 responses of grassland species. *Oecologia,* 125**,** 380-388.

WALTER, J., JENTSCH, A., BEIERKUHNLEIN, C. & KREYLING, J. 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environmental and Experimental Botany,* 94**,** 3-8.

WALTHER, G. R., BERGER, S. & SYKES, M. T. 2005. An ecological 'footprint' of climate change. *Proceedings of the Royal Society B-Biological Sciences,* 272**,** 1427-1432.

WALTHER, G. R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J. M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature,* 416**,** 389-395.

WAN, S. Q., HUI, D. F., WALLACE, L. & LUO, Y. Q. 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. *Global Biogeochemical Cycles,* 19.

WANG, G., YU, M., PAL, J., MEI, R., BONAN, G., LEVIS, S. & THORNTON, P. 2015. On the development of a coupled regional climate–vegetation model RCM–CLM–CN–DV and its validation in Tropical Africa. *Climate Dynamics***,** 1-25.

WANG, Q., WANG, C. H., ZHAO, B., MA, Z. J., LUO, Y. Q., CHEN, J. K. & LI, B. 2006. Effects of growing conditions on the growth of and interactions between salt marsh plants: implications for invasibility of habitats. *Biological Invasions,* 8**,** 1547-1560.

WATERS, T. L. & SAVILL, P. S. 1992. ASH AND SYCAMORE REGENERATION AND THE PHENOMENON OF THEIR ALTERNATION. *Forestry,* 65**,** 417-433.

WATSON, D. J. 1947. Comparative Physiological Studies on the Growth of Field Crops: I. Variation in Net Assimilation Rate and Leaf Area between Species and Varieties, and within and between Years. *Annals of Botany,* 11**,** 41-76.

WATT, A. S. 1947. Pattern and process in the plant community. *The Journal of Ecology,* 35**,** 1-22

WEINER, J. 1990. Asymmetric Competition in Plant Populations. *Trends Ecol Evol,* 5**,** 360-364.

WENT, F. W. 1942. The Dependence of Certain Annual Plants on Shrubs in Southern Californi Deserts. *Bulletin of the Torrey Botanical Club,* 69**,** 100-114.

WHITE, G. C. & BURNHAM, K. P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study,* 46**,** 120-139.

WILLIAMS, J. W. & JACKSON, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment,* 5**,** 475-482.

WILLIS, C. G., RUHFEL, B., PRIMACK, R. B., MILLER-RUSHING, A. J. & DAVIS, C. C. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc Natl Acad Sci U S A,* 105**,** 17029-33.

WINDER, M. & SCHINDLER, D. E. 2004. CLIMATE CHANGE UNCOUPLES TROPHIC INTERACTIONS IN AN AQUATIC ECOSYSTEM. *Ecology,* 85**,** 2100-2106.

WINN, J., TIERNEY, M., HEATHWAITE, A. L., JONES, L., PATERSON, J., SIMPSON, L., THOMSON, A. & TURLEY, C. 2011. The Drivers of Change in UK Ecosystems and Ecosystem Services. *The UK National Ecosystem Assessment Technical Report.* Cambridge: UK National Ecosystem Assessment, UNEP-WCMC.

WORLD METEOROLOGIAL ORGANIZATION 2013. Standardized Precipitation Index User Manual. Geneva, Switzerland.

WORRALL, J. J., EGELAND, L., EAGER, T., MASK, R. A., JOHNSON, E. W., KEMP, P. A. & SHEPPERD, W. D. 2008. Rapid mortality of Populus tremuloides in southwestern Colorado, USA. *Forest Ecology and Management,* 255**,** 686-696.

WU, Z. T., DIJKSTRA, P., KOCH, G. W. & HUNGATE, B. A. 2012. Biogeochemical and ecological feedbacks in grassland responses to warming. *Nature Clim. Change,* 2**,** 458-461.

WU, Z. T., DIJKSTRA, P., KOCH, G. W., PENUELAS, J. & HUNGATE, B. A. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology,* 17**,** 927-942.

YANG, H. J., WU, M. Y., LIU, W. X., ZHANG, Z., ZHANG, N. L. & WAN, S. Q. 2011. Community structure and composition in response to climate change in a temperate steppe. *Global Change Biology,* 17**,** 452-465.

YANG, L. H. & RUDOLF, V. H. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol Lett,* 13**,** 1-10.

YIN, D., RODERICK, M. L., LEECH, G., SUN, F. & HUANG, Y. 2014. The contribution of reduction in evaporative cooling to higher surface air temperatures during drought. *Geophysical Research Letters,* 41**,** 7891-7897.

YODA , K., KIRA, T., OGAWA, H. & HOZUMI, H. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of the Institute of Polytechnics,* 14**,** 107-29.

YU, H., LUEDELING, E. & XU, J. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc Natl Acad Sci U S A,* 107**,** 22151-6.

Appendices

SCIENTIFIC DATA

OPEN

SUBJECT CATEGORIES

» Forest ecology

» Plant ecology

» Climate-change ecology

» Light responses

Received: 06 January 2015
Accepted: 10 February 2015
Published: 03 March 2015

Allometry and growth of eight tree taxa in United Kingdom woodlands

Matthew R. Evans[1], Aristides Moustakas[1], Gregory Carey[1], Yadvinder Malhi[2], Nathalie Butt[3], Sue Benham[4], Denise Pallett[5] & Stefanie Schäfer[5]

As part of a project to develop predictive ecosystem models of United Kingdom woodlands we have collated data from two United Kingdom woodlands - Wytham Woods and Alice Holt. Here we present data from 582 individual trees of eight taxa in the form of summary variables relating to the allometric relationships between trunk diameter, height, crown height, crown radius and trunk radial growth rate to the tree's light environment and diameter at breast height. In addition the raw data files containing the variables from which the summary data were obtained. Large sample sizes with longitudinal data spanning 22 years make these datasets useful for future studies concerned with the way trees change in size and shape over their life-span.

Design Type(s)	time series design
Measurement Type(s)	diameter • height • crown radius • crown height • incident light • canopy
Technology Type(s)	Measuring Tape • Hypsometer; Laser Vertex; Laser Range Meter • Vernier Caliper • Laser Range Meter • PAR Quantum sensor • software
Factor Type(s)	
Sample Characteristic(s)	Woodland • Wytham Woods • Acer pseudoplatanus • Fraxinus excelsior • Quercus robur • Fagus sylvatica • Corylus avellana • Crataegus monogyna • Acer campestre • Betula • Alice Holt Forest

[1]School of Biological and Chemical Sciences, Queen Mary University of London, Mile End Road, London E1 4NS, UK. [2]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK. [3]ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, The University of Queensland, St Lucia 4072, Australia. [4]Centre for Ecosystem, Society and Biosecurity, Forest Research, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH, UK. [5]CEH-Wallingford, Maclean Building, Benson Lane, Crowmarsh, Gifford, Wallingford, Oxfordshire OX10 8BB, UK.
Correspondence and requests for materials should be addressed to M.E. (email: m.evans@qmul.ac.uk)

Background & Summary

Prediction is a basic, possibly defining, feature of scientific disciplines[1]. To develop ecological models that are capable of being projected into the future, possibly into novel conditions outside the parameter space within which the data were collected, process-based models are required. Such process-based models are extremely demanding of data, as there are often many interacting processes each requiring parameterisation[2,3]. For long-lived species, such as trees, parameterisation is especially demanding as most processes occur slowly, and so require long-term datasets to ensure that robust estimates of the relevant rates can be obtained[4]. It is rare that datasets exist for the purposes of creating such models, and so data, the collection of which was originally motivated by some other purpose, usually need to be identified and processed in a manner that makes them suitable for inclusion in such models. At present in ecology, prediction is attempted relatively rarely[5,6] and for example the recent United Kingdom National Ecosystem Assessment struggled to find suitable models or empirical examples on which to base its scenarios of likely future states of ecosystems[7].

We are developing predictive ecosystem models initially with the intention of providing projections of the future state of United Kingdom woodlands. As our underlying computational model we have implemented SORTIE—an established forest model[8]. We chose SORTIE over the many competing models because it is conceptually simple (based on trees competing for one resource, i.e. light), it is based on ecological information that can be parameterised from field data, it has been extensively and successfully used in North America[8–11] and New Zealand[12–14], and it is individual-based, which allows for us to plan for coupling between trophic levels more easily than if individuals were aggregated. In SORTIE, trees compete for light by intercepting incident sunlight and modifying the light environment beneath their crown. Sapling growth depends on their light environment while adult growth depends on their size. For adult trees, traits (height, crown height and radius) vary with diameter at breast height (DBH); while for saplings, traits vary with diameter at 10 cm above ground level. We have parameterised these functions by collating three datasets, and by collecting data specifically for this project where they did not previously exist. Here we make available these data and the summary variables for the eight commonest tree taxa (Table 1).

This information is most obviously of utility for those, who like ourselves, are planning to use individual-based models of trees, and who may be interested in the allometry and growth of the taxa included here (Table 1). However, allometric relationships such as these are extremely important in understanding the biology of the species concerned[15,16] and so will be of interest to those with more fundamental ecological interests. Similarly practitioners, e.g. foresters, may find these data of use if they wish to understand how timber production changes as trees grow. DBH has long been the measurement of choice among foresters—for good reason as it is both straightforward to measure and interpret in terms of timber volume[17]. The data presented here allow estimation of other aspects of tree size and shape from DBH.

Since 1992 the Environmental Change Network has measured DBH and height of focal trees at two woodland sites—Wytham Woods (Oxfordshire) and Alice Holt (Surrey) using standard protocols[18]. The DBH of an additional set of trees was also measured in Wytham Woods in 2008 and 2010 (by two of us—Malhi and Butt). We have collated these data and combined them into a single dataset, which we have supplemented with data on the crown height and crown radius of the adult trees, diameter at 10 cm above ground level, and on the local light environment of saplings. The workflow used to generate the output is shown in Figure 1.

Methods

Study sites

Data were collected from two United Kingdom woodlands—Wytham Woods and Alice Holt. Wytham Woods (51°46′N, 1°20′W, UK National Grid: SP 46 08) has been a research site (owned and managed by Oxford University) since the 1940s. It is approximately 400 Ha in extent, ranging in height from 60–165 m above sea level. The site has been extensively managed, mainly by coppicing, although this has

Latin name	Common name	Taxonomic code
Acer pseudoplatanus	Sycamore	ACERPS
Fraxinus excelsior	European ash	FRAXEX
Quercus robur	Pedunculate oak	QUERRO
Fagus sylvatica	European beech	FAGUSY
Corylus avellana	Common hazel	CORYAV
Crataegus monogyna	Common hawthorn	CRATMO
Acer campestre	Field maple	ACERCA
Betula spp.	Birch	BETUSP

Table 1. List of taxa included in the data files, including the taxonomic code used in all data files, Latin name and common name of each taxon.

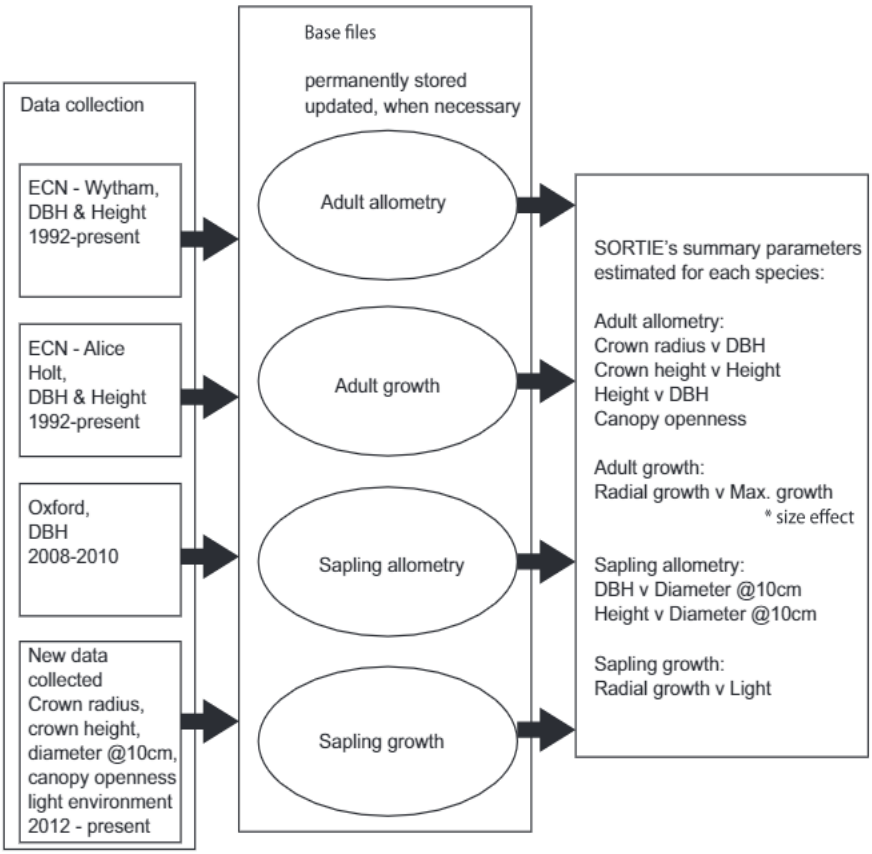


Figure 1. Workflow for database construction and parameter estimation. Base files and files containing SORTIE's parameters are contained in this database release. Both types of files can be refreshed when new data are included by re-running analyses on updated base files.

not been conducted since the early 20th Century. There are regions of ancient woodland, secondary woodland and plantation; only the plantation areas are still managed today. Alice Holt (51°10′N, 0°50′W, UK National Grid: SU80 42) is in northern Hampshire and managed by the Forest Commission. The entire site is about 850 Ha, the majority planted with Corsican pine (*Pinus nigra*), but 140 Ha of old-growth oak (*Quercus robur*) woodland remain, in which the data used here were collected. The site varies in altitude from 70–125 m. These two sites are the two woodland sites in the Environmental Change Network (ECN) in the United Kingdom.

Data collection

Three datasets have been collated here:

- Environmental Change Network (Wytham Woods) (ECN-W), the ECN has monitored a fixed set of sites in Wytham Woods since 1992. In this dataset we have data on 250 individual trees in 41 plots that have had DBH measured on seven occasions (1993, 1996, 1999, 2002, 2005, 2008, 2012), and height measured three times (1993, 2002, 2012).
- Environmental Change Network (Alice Holt) (ECN-AH), the ECN has monitored a fixed set of sites in Alice Holt since 1994. In this dataset we have data on 216 individual trees in 51 plots that have DBH measured seven times (1994, 1997, 2000, 2002, 2005, 2008, 2011). Height was measured on the same trees on three occasions (1994, 2002, 2011). Another set of 56 trees on nine plots had DBH measured five times (2004, 2005, 2007, 2012 and 2013), and height measured twice (2004 and 2012).
- Oxford University plot (OXF), two of the authors (Malhi and Butt) have established an 18 Ha plot containing about 20,000 individual trees, which have had DBH measured on two occasions (2008 and 2010).

Since 2011 three of the authors (Evans, Moustakas and Carey) have supplemented these three datasets by:

- Measuring diameter at 10 cm above ground level on all saplings (defined here as trees with DBH < 10 cm) in ECN-W, ECH-AH, and a sample of 88 from OXF.
- Measuring the light environment around all saplings in ECN-W, ECH-AH and a sample of 88 from OXF.

- Measuring the height of a sample of 88 saplings from OXF.
- Measuring crown radius and crown height for all adults in ECN-W and ECH-AH.
- Measuring canopy openness for a sample of 165 trees in Wytham Woods.

It would have been desirable to have estimates of the age of trees in the datasets. Unfortunately none of trees in datasets have been cored to determine tree age. In a separate publication we have estimated tree mortality for the same taxa as are included here using the ECN-W dataset through the application of a Cormack Jolly Seber model[19].

Measurement methods

Diameter at Breast Height (DBH). DBH is a measurement that is routinely included in the datasets collated here. The three datasets ECN-W, ECN-AH and OXF include a measurement of DBH which is taken following standardised methods, by measuring trunk circumference using a tape to the nearest 0.1 cm at 1.3 m above ground level[18]. To ensure that DBH was measured at the same point on subsequent surveys trees were marked with paint at the point at which DBH was measured.

Growth. Mean growth rates of individual trees were estimated by taking a series of DBH measurements and subtracting the measurement at time point t from the measurement at t+1 to calculate the change in DBH between the two time points and then to divide this value by the number of years between the two time points. If for any tree there were more than two measurements, the values were averaged to produce a single value per tree.

Height (*H*). Tree height is measured in the two ECN datasets, and was measured by Evans and Moustakas for a number of further trees, as described above. Height is measured by ECN using a hypsometer to the nearest 0.5 m at Wytham Woods following[18], and using a laser Vertex (Haglof Vertex III, Långsele, Sweden) to the nearest 0.1 m at Alice Holt. Height measurements taken by Evans and Moustakas used a Laser Range Meter (Hilti PD40, Hilti, Schaan, Liechtenstein) to the nearest 0.1 m. The use of three different devices to assess height is likely to have increased measurement error in this parameter, at least if one was concerned with differences between the sites at which measurements were taken. A good test to determine the extent of this error would have been directly to compare measures of tree height taken using the three different instruments, unfortunately this was not possible. However, if a single measure of tree height is taken for each tree there are no significant difference in the measurements taken by the different instruments, once taxon and stage (adult or sapling) were taken into account ($F = 5.43$, $N = 465$, with eight taxa and 2 stages, $P = 0.98$).

Diameter 10 cm above ground level (D_{10}). D_{10} was measured for saplings in all three datasets: two measurements were made on each sapling using vernier callipers to the nearest 0.1 cm. The two measurements were taken, as far as practically possible, perpendicular to one other and averaged to produce one measurement per tree. A tape was not used to measure D_{10} as vegetation and debris at the base of the trees made inserting a tape round the tree against its trunk extremely difficult to achieve in a consistent manner. As D_{10} was not a repeated measure the point at which it was measured was not permanently marked as was DBH. The measurements were taken at a point that was determined to be 10 cm above ground level (using vernier callipers).

Crown radius (CRad). CRad was measured for adults in the ECN-W and ECN-AH datasets by visually projecting the crown margin onto the ground and measuring the two longest perpendicular diameters to the nearest cm using a measuring tape. The two measurements were halved and averaged to produce a single measurement per tree[14,20].

Crown height (CH). CH was established for adults in the ECN-W and ECN-AH datasets by measuring the distance from the ground to the point where foliage occupied at least three of the four quadrants round the trunk[20], using a Laser Range Meter (Hilti PD40) to the nearest 0.1 m. These data were combined with height data for the same trees to estimate crown height (the distance between the top of the tree and the base of the crown), by subtracting the distance from the base of the crown from tree height[14,20].

Light environment. Light meter readings were taken on cloudy days (so that light arriving at the trees was as scattered as possible) during September 2012 for saplings in the ECN-W dataset, July-August 2013 for saplings in the ECN-AH dataset and September 2014 for a sample of 90 saplings in the OXF dataset[13]. We measured the percentage of incident light at the canopy reaching each tree (L_c) by measuring the light intensity beneath the canopy at three positions within 1 m of the trunk of each tree at a height of 1.3 m (L_{cait}—the ith measurement of absolute light levels below the canopy taken at time t, where $i = 1$–3), and simultaneously in a large open gap nearby (L_{oat}—the absolute light levels in the open at time t). To measure light levels we used two PAR Quantum sensors (SKP215, Skye Instruments Ltd, Llandrindod Wells, United Kingdom) that were both calibrated against the same reference lamp. The sensor used to measure light levels under the canopy was used in conjunction with a meter (SKP 200, Skye Instruments Ltd, Llandrindod Wells, United Kingdom) recording to one decimal place; the one measuring light levels

in the open was used with a datalogger (SDL5050 DataHog 2, Skye Instruments Ltd, Llandrindod Wells, United Kingdom). Measurements from the sensor in the open gap were made every 10 s with the mean of these more frequent values recorded every 10 min. We calculated three light intensity values for each tree, which are the proportion of the available light that reached each tree's position (L_{ci}, where $i = 1$–3):

$$L_{ci} = L_{cait}/L_{oat} \quad (1)$$

L_{c1}, L_{c2} and L_{c3} for each tree were averaged to produce a single value (L_c) for each individual tree.

Canopy openness. This light transmission coefficient is estimated using fish-eye-lens photographs taken under canopies that are dominated by a single taxon. The fish-eye-lens photographs are taken at 1.35 m above the ground and orientated to magnetic North. The percentage of canopy openness was analysed for individual circular sections of canopy using Gap Light Analyzer software (http://www.ecostudies.org/gla/), following the method described in ref. 20. The gap light analyser software allows the crown of a tree to be identified in the photograph by the operator and then estimates the percentage of canopy openness for circular sections of the crown. The degree of canopy openness depends on the structure of the crown and the size and shape of the leaves, this variable is used in SORTIE to filter out light hitting the canopy and so modify the light environment below the tree. Differences in canopy openness and canopy dimensions between taxa create a patchy light environment in the forest.

Summary variables

We generated the taxon-specific summary statistics relating to the allometry and growth equations required by SORTIE[8]. These are:

Allometry. Taxon-specific allometric functions describe the tree's size and shape.

Saplings (trees with DBH < 10 cm)

To describe the allometry of saplings, two relationships are used—a linear one between D_{10} (trunk diameter at 10 cm above ground level) and DBH, and a power function between D_{10} and height (H).

$$\mathrm{DBH} = a + bD_{10} \quad (2)$$

$$H = aD_{10}^{b} \text{ or } \log H = \log a + b \log\ D_{10} \quad (3)$$

Adults (trees with DBH>10 cm)

To adequately describe the size and shape of adult trees requires three allometric relationships to be parameterised, power relationships between crown radius (CRad) and DBH, crown height (CH) and tree height; and an exponential relationship between height and DBH, with an asymptote at maxH.

$$\mathrm{CRad} = a\mathrm{DBH}^{b}, \text{ or } \log \mathrm{CRad} = \log a + b \log \mathrm{DBH} \quad (4)$$

$$\mathrm{CH} = aH^{b}, \text{ or } \log \mathrm{CH} = \log a + b \log H \quad (5)$$

$$H = 1.35 + (\mathrm{max}H - 1.35)\left(1 - e^{-b\mathrm{DBH}}\right) \quad (6)$$

Growth

Saplings

Radial growth is assumed to be described by a Michaelis-Menten function that relates growth in DBH (G_{sap}, in cm yr^{-1}) to light availability (L, expressed as a percentage of daylight), combined with a power function of the effect of size. Michaelis-Menten functions are specific forms of dose-response curves where the rate of a response variable depends on the concentration of a substrate. Here sapling growth is the response variable and the intensity of light is the substrate on which growth depends[13].

$$G_{\mathrm{sap}} = (\alpha L/(L + (\alpha/\beta)))D_{10}^{\phi} \quad (7)$$

α is the asymptotic growth a high light levels, β is the slope of the growth function at zero light. D_{10}^{ϕ} is the size effect to determine the most appropriate value of ϕ we fitted models with $\phi = 0$–1, and report the best fitting model (as determined by the lowest residual standard error) which was $\phi = 0.845$ (which gave a residual standard error of 0.005 with 116 degrees of freedom).

Adults

Adult radial growth rate was assumed to be related to maximum radial growth rate that a taxon can attain devalued by a size effect, so that in general trees grow more slowly as they get larger.

$$G_{\mathrm{adult}} = \mathrm{Max}G \times \mathrm{SE} \quad (8)$$

The size effect SE is given by:

$$\mathrm{SE} = e^{-0.5(\ln(\mathrm{DBH}/x_0)/x_b)^2} \quad (9)$$

x_0 and x_b are estimated parameters.

Data analysis

As both the dependent and the independent variables were subject to sampling error, ranged major axis (RMA) model II regression[21] was used to analyse the relationships between sapling D_{10} and height (equation 3), sapling D_{10} and DBH (equation 2), adult CRad and DBH (equation 4), and adult CH and height (equation 5). We used the lmodel2 procedure in the lmodel2 library[22] implemented in R 2.15.2 (ref. 23). As we had longitudinal data on both adult height and DBH (equation 6) we used repeated measures ANOVA with DBH as the independent variable and height as the dependent variable and individual code as a random effect to avoid pseudo-replication of trees that had been measured more than once. For this analysis we used the lmer procedure in the lme4 library[24] in R 2.15.2 (ref. 23). To analyse the relationship between sapling growth rates and light (equation 7) we used the MM2 procedure in the drc library[25] of R to fit a two parameter Michaelis-Menten function to the relationship between the growth rate and the light environment of individual saplings.

Equation 9 is a two-parameter (x_0 and x_b) negative exponential distribution. In order to estimate x_0 and x_b inverse modelling was employed (identifying the parameters of a distribution from data). Maximum likelihood estimation was used for fitting the two parameters of the negative exponential distribution[26] using data on adult tree growth rates in ECN-W and ECN-AH.

Data Records

The data contained in this data descriptor have been deposited in Dryad (Data Citation 1). All data include codes to identify the individual trees: for ECN-W these are derived by adding (tree number) to (plot number ×100); for ECH-AH they are derived by adding (cell identity code) to (plot identity code ×100); for OXF all trees have individual coded tags and these numbers were used as the identity codes. Individual codes can be used to identify individual trees within a given dataset but may be replicated between datasets. Our study is primarily concerned with allometric relationships of saplings and adult trees. We also provide the original data needed to derive these data. The majority of the DBH and height data are publicly available: All ECN data used here (DBH and height data for datasets ECN-W and ECN-AH) are available on request from Centre for Ecology and Hydrology (http://data.ecn.ac.uk/access.asp); the DBH records associated with dataset OXF have been published at http://ctfs.arnarb.harvard.edu/Public/plotdataaccess/index.php from where they can be freely downloaded.

Sapling allometry DBH, D_{10} & Height—data record 1

Contains data on DBH (cm), D_{10} (cm) and Height (m) for a total of 145 saplings for the eight taxa under consideration. Data are drawn from three datasets (ECN-W, ECN-AH and OXF). The year in which the DBH and height and D_{10} data were recorded is reported for each individual. Data record 1 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated October 16 2014.

Adult allometry DBH, Height & Crown height—data record 2

Contains data on DBH (cm), Height (m), Crown height (m) and Crown radius (m) for a total of 297 adult trees for the eight taxa under consideration. Data are drawn from two datasets (ECN-W and ECN-AH). The year in which DBH, height and crown height and radius were recorded are reported for each individual. Data record 2 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated October 16 2014.

All trees height v DBH—data record 3

Contains data on DBH (cm) and Height (m) for 481 individuals for the eight taxa under consideration. Data are drawn from two datasets (ECN-W and ECN-AH). Repeated measures on each individual results in 1211 records, the year of each measurement is reported. Data record 3 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated February 5 2015.

Sapling growth—data record 4

Contains data on DBH growth rates (cm yr^{-1}) for the periods between measurements, the mean growth rate, D_{10} (cm), and the fraction of ambient light in the tree's environment for 129 individuals representing seven of the eight taxa under consideration to parameterise equation 7. Data are drawn from two datasets (ECN-W and OXF). The year in which D_{10} and light were measured is reported. Data record 4 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated October 16 2014.

All trees growth—data record 5

Contains data on DBH growth rates (cm yr^{-1}) for both adults and saplings for the periods between measurements and the mean growth rate for 439 individuals of the eight taxa under consideration. Data are drawn from three datasets (ECN-W, OXF and ECN-AH). Data record 5 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated February 5 2015.

Canopy openness—data record 6

Contains data on canopy openness for 165 single taxon stands of the eight taxa under consideration. Data record 6 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated October 16 2014.

SORTIE parameter file—data record 7

Contains data on 16 parameters for each of the eight taxa considered here. These allow the instantiation of the equation 1,2,3,4,5,6,7,8 listed above. In conjunction with parameters on mortality and dispersal they also allow SORTIE to be run to produce projections of United Kingdom lowland woodlands. Data record 7 is stored as a tab delimited text file (Data Citation 1), and is available from the Dryad Digital Repository, an up-to-date file is maintained at www.predictivecology.com. The dataset was last updated February 5 2015.

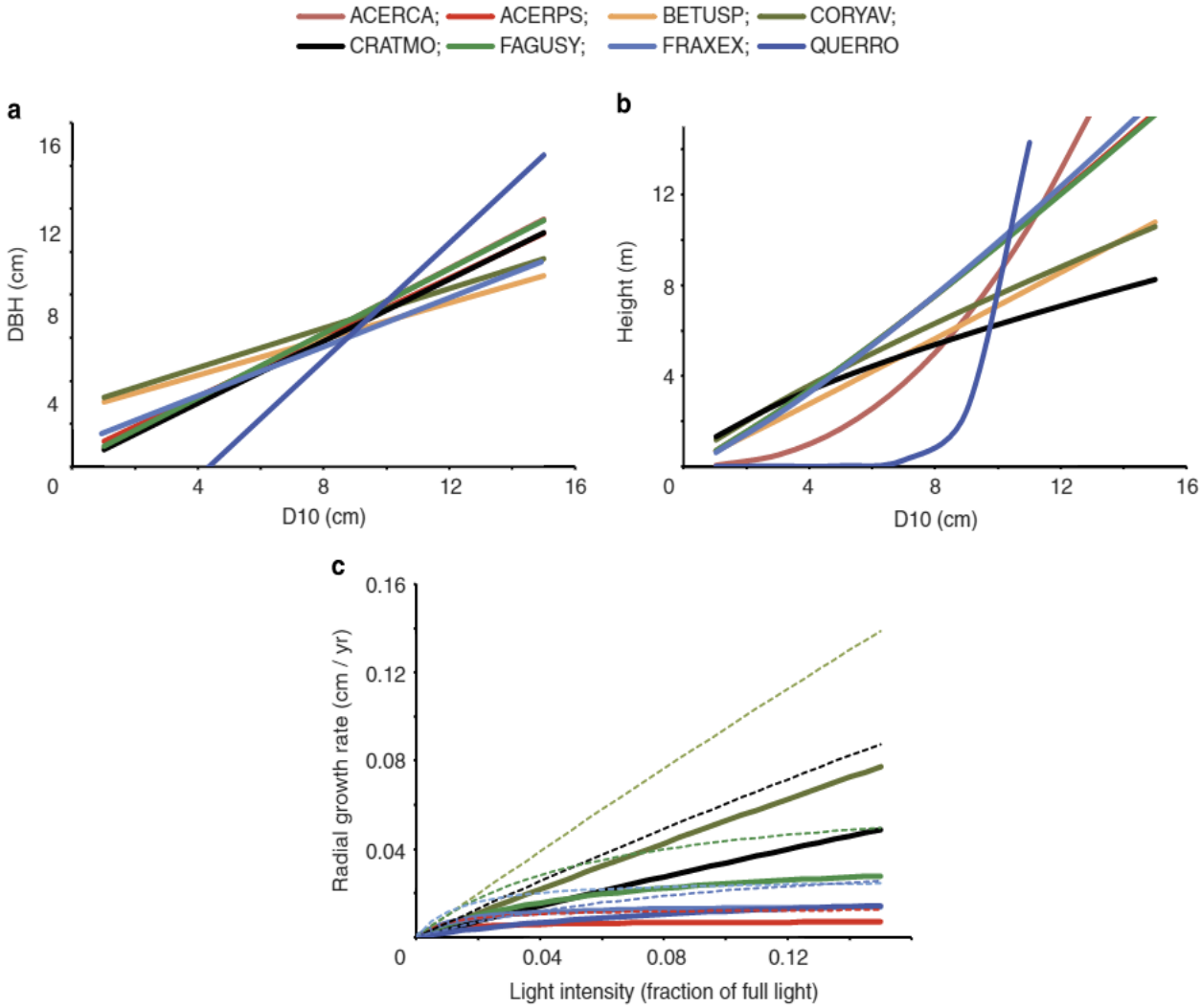


Figure 2. Allometric relationships and growth rates for saplings trees. (**a**) Allometric relationships between D_{10} and DBH for the eight tree taxa considered here, estimated using parameters in data record 7 in equation 2. (**b**) Allometric relationships between D_{10} and height for the eight tree taxa considered here, estimated using the parameters in data record 7 in equation 3. (**c**) Allometric growth in different light environments for the six taxa for which the relevant parameters could be estimated. Functions estimated using parameters in data record 7 in equation 7. Solid lines are for 5 cm DBH trees, dotted lines for 10 cm DBH trees. ACERCA—Field Maple (*Acer campestre*); ACERPS—Sycamore (*Acer pseudoplatanus*); BETUSP—Birch (*Betula* spp.); CORYAV—Hazel (*Corylus avellana*); FAGUSY—Beech (*Fagus sylvatica*); FRAXEX—Ash (*Fraxinus excelsior*), QUERRO—Pedunculate Oak (*Quercus robur*).

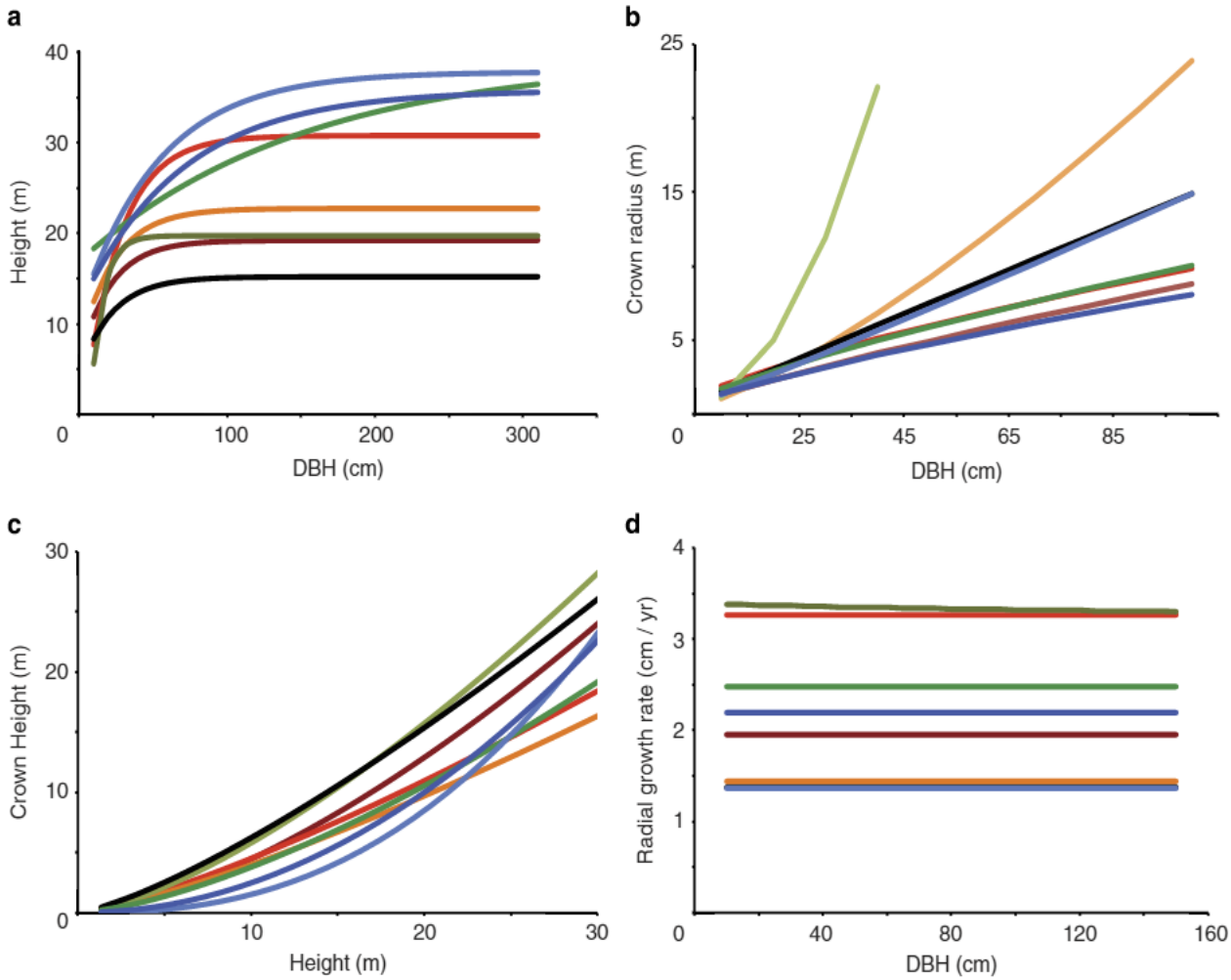


Figure 3. Allometric relationships and growth rates for adult trees. (**a**) Allometric relationships between DBH and height for the eight tree taxa considered here, estimated using parameters in data record 7 in equation 6. (**b**) Allometric relationships between DBH and crown radius for the eight tree taxa considered here, estimated using parameters in data record 7 in equation 4. (**c**) Allometric relationships between crown height and height for the eight tree taxa considered here, estimated using parameters in data record 7 in equation 5. (**d**) Allometric annual diameter growth rate for each of the eight taxa considered here, estimated using parameters in data record 7 in equation 8. For legend see Figure 2.

Technical Validation

Once we had compiled data into the collated files, data entries were completed and verified using a number of techniques:

1. Any missing data were checked by examining the original data files obtained from ECN or Malhi and Butt and field notebooks.
2. Taxonomic codes were standardised and checked by counting the frequency with which each code appeared, examining any which were represented by few entries, and correcting any typographical errors that were revealed.
3. Maxima, minima, means and variances were calculated for all variables and outliers, and checked against original data records.
4. Each file was created from the original data twice separated by at least one month, the sequence of data in at least one column per dataset was used as an index variable, and the order obtained in the two datasets compared against each other. Any discrepancies were checked against the original datasets.
5. We have plotted the summary parameters in data record 7, to determine whether the predicted relationships are reasonable and in accordance with the most complete set of similar relationships found in ref. 14. These can be seen in Figures 2 and 3, and will be updated along with data record 7 and new versions posted at www.predictivecology.com.

References

1. Medawar, P. *The Limits Of Science* (Oxford University Press, 1984).
2. Lonergan, M. Data availability constrains model complexity, generality, and utility: a response to Evans *et al. Trends Ecol. Evol.* **29,** 301–302 (2014).
3. Evans, M. R. *et al.* Data availability and model complexity, generality, and utility: a reply to Lonergan. *Trends Ecol. Evol.* **29,** 302–303 (2014).
4. Moustakas, A. *et al.* Long-term mortality patterns of the deep-rooted Acacia erioloba: The middle class shall die!. *J. Veg. Sci.* **17,** 473–480 (2006).
5. Evans, M. R. *et al.* Predictive systems ecology. *Proc. R. Soc. Ser. B* **280,** 20131452 (2013).
6. Evans, M. R. *et al.* Do simple models lead to generality in ecology? *TREE* **28,** 578–583 (2013).
7. DEFRA. *The UK National Ecosystem Assessment: Synthesis Of The Key Findings* (Department for the Environment, Food and Rural Affairs, 2011).
8. Pacala, S. W. *et al.* Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* **66,** 1–43 (1996).
9. Purves, D. & Pacala, S. Predictive models of forest dynamics. *Science* **320,** 1452–1453 (2008).
10. Strigul, N., Pristinski, D., Purves, D., Dushoff, J. & Pacala, S. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecol. Monogr.* **78,** 523–545 (2008).
11. Purves, D. W., Lichstein, J. W., Strigul, N. & Pacala, S. W. Predicting and understanding forest dynamics using a simple tractable model. *Proc. Natl. Acad. Sci. USA* **105,** 17018–17022 (2008).
12. Kunstler, G., Coomes, D. A. & Canham, C. D. Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *J. Ecol.* **97,** 685–695 (2009).
13. Coomes, D. A., Kunstler, G., Canham, C. D. & Wright, E. A greater range of shade-tolerance niches in nutrient-rich forests: an explanation for positive richness–productivity relationships? *J. Ecology* **97,** 705–717 (2009).
14. Kunstler, G., Allen, R. B., Coomes, D. A., Canham, C. D. & Wright, E. F. *SORTIE/NZ Model Development* 55 (Landcare Research New Zealand Ltd, 2011).
15. Schmidt-Nielsen, K. *Scaling: Why Is Animal Size So Important?* (Cambridge University Press, 1984).
16. Bonner, J. T. *Why Size Matters: From Bacteria To Blue Whales* (Princeton University Press, 2006).
17. Mackie, E. D. & Matthews, R. W. *Forest Mensuration, A Handbook For Practitioners* (HMSO, 2006).
18. Sykes, J. M. & Lane, A. M. J. *The United Kingdom Environmental Change Network: Protocols For Standard Measurements At Terrestrial Sites* (The Stationery Office, 1996).
19. Moustakas, A. & Evans, M. R. Effects of growth rate, size, and light availability on tree survival across life stages: a demographic analysis accounting for missing values and small sample sizes. *BMC Ecology* doi:10.1186/s12898-015-0038-8 (2015).
20. Canham, C. D., Coates, K. D., Bartemucci, P. & Quaglia, S. Measurement and modeling of spatially-explicit variation in light transmission through interior cedar-hemlock forests of British Columbia. *Can. J. For. Res* **29,** 1775–1783 (1999).
21. Sokal, R. R. & Rohlf, F. J. *Biometry - The Principles And Practice Of Statistics In Biological Research* 3rd edn, (W.H. Freeman, 1995).
22. Legendre, P. lmodel2: Model II Regression. *R package version* **1,** 7–0 (2011).
23. R Development Core Team. *R; A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2008).
24. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0 (2012).
25. Ritz, C. & Streibig, J. C. Bioassay analysis using R. *J. Statist. Software* **12,** 1–22 (2005).
26. Harris, C. M. & Sykes, E. A. Likelihood estimation for generalized mixed exponential distributions. *Naval Research Logistics* **34,** 251–279 (1987).

Data Citations

1. Evans, M. R. *et al. Dryad* http://dx.doi.org/10.5061/dryad.2c1s7 (2015).

Acknowledgements

We thank the University of Oxford for access to Wytham Woods and Forest Research for access to Alice Holt. Michelle Taylor and Mike Morecroft collected much of the original ECN data at Wytham Woods.

Author Contributions

M.R.E. collected data on D_{10}, crown height, crown radius, light environment around trees, conducted the statistical analyses, collated the datasets and drafted the manuscript. A.M. collected data on D10, crown height, crown radius, light environment around trees, calculated x_0 and x_b and drafted the manuscript. G.C. collected data on canopy openness, and commented on the manuscript. Y.M. and N.B. collected data in dataset OXF on DBH and height, NB commented on the manuscript. D.P. and S.S. collected data in dataset ECN-W, and commented on the manuscript. S.B. collected data in dataset EN-AH, and commented on the manuscript.

Additional information

Competing financial interests: The authors declare no competing financial interest.

How to cite this article: Evans, M. R. *et al.* Allometry and growth of eight tree taxa in United Kingdom woodlands. *Sci. Data* 2:150006 doi: 10.1038/sdata.2015.6 (2015).