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

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

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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.
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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 series
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
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 16.9 km 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, Matsui et al., 2012, Fensham and Fairfax, 2007, Rolin 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.
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 as 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.) Carrière), 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):

\[
\text{annual radial increment} = \text{radius} \times \frac{G_1 \text{GLI}}{G_2 + \text{GLI}}
\]  

(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:

\[
m_s = \frac{e^{(\alpha + \beta (DBH - DBH_s))}}{1 + e^{(\alpha + \beta (DBH - DBH_s))}}
\]  \hspace{1cm} (2.2)

where:

\(\alpha\) and \(\beta\) 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.

\[
p = z^{-y \times \text{growth}}
\]

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, $i$ ($R_i$).

$$R_i = STR \sum_{j=1}^{n} DBH_j \beta \frac{DBH_j}{30} * e^{-0.5 \left( \frac{\ln(d_{ij})/X_0}{X_\beta} \right)^2}$$  \hspace{1cm} (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

$X_\beta$ is the variance of the function

$\beta$ 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](image-url): 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) CO₂ 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:

```java
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.

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

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.

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 \((F_{(2,21)}=8.9, p=0.001; \text{figure 2.3})\), as well as the proportions of both (beech: \((F_{(2,21)}=7.2, p<0.005); \text{hemlock: } (F_{(2,21)}=8.89, p=0.001); \text{figure 2.4})\). 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

![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.](image-url)
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)

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

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:

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


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:

$$L_{ci} = \frac{L_{cai}^{it}}{L_{oat}}$$ (3.1)

Where:

$L_{cai}$ is the $i$th measurement of absolute light levels below the canopy taken at time $t$
$L_{\text{out}}$ 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/).

![Example fish-eye lens photograph of single canopy](image)

**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 serotina* (table 3.1).

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

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 15km², 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.
<table>
<thead>
<tr>
<th>Species</th>
<th>Initial number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td>4830</td>
</tr>
<tr>
<td>Beech</td>
<td>1092</td>
</tr>
<tr>
<td>Birch</td>
<td>80</td>
</tr>
<tr>
<td>Field maple</td>
<td>112</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>185</td>
</tr>
<tr>
<td>Hazel</td>
<td>202</td>
</tr>
<tr>
<td>Oak</td>
<td>1577</td>
</tr>
<tr>
<td>Sycamore</td>
<td>8908</td>
</tr>
</tbody>
</table>

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 $D_{10}$:

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

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

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:

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

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

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

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 ($G_{\text{sap}}$; in cm yr$^{-1}$) was calculated using both a Michaelis-Menten function and a power function as follows:

$$G_{\text{sap}} = \frac{\alpha L}{(L + \alpha/\beta)} D_{10} \Phi$$

(3.7)
where:

\( \alpha \) is the growth rate in 100% light

\( \beta \) is the growth rate with 1% light conditions

\( L \) is the amount of light that an individual receives

\( \Phi \) is an estimated exponent which determines the size effect of the function

### 3.2.8.2 Adults

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

\[
G_{\text{adu}} = \text{MaxG} \times \text{SE} \tag{3.8}
\]

where:

\( \text{MaxG} \) (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.

\( \text{SE} \) is a size effect which is calculated by:

\[
\text{SE} = e^{-0.5 \frac{(\ln(DBH/X_0))^2}{X_b}} \tag{3.9}
\]

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:

\[ m = \frac{1 - (e^{\Phi_1} + (e^{\Phi_2} \left( \frac{DBH - meanDBH}{sdDBH} \right)} }{e^{\Phi_1} + (e^{\Phi_2} \left( \frac{DBH - meanDBH}{sdDBH} \right) )} \]  \hspace{1cm} (3.10)

where:

$\Phi_1$ and $\Phi_2$ 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, $i (R_i)$:

\[ R_i = STR \sum_{j=1}^{n} DBH_{30}^\beta * e^{-0.5(\ln(d_{ij}/X_B)^2 / X_B^2)} \]  \hspace{1cm} (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

$\beta$ 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/](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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Individuals</th>
<th>Light Transmission Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field maple</td>
<td>2</td>
<td>0.0852</td>
</tr>
<tr>
<td>Beech</td>
<td>15</td>
<td>0.1208</td>
</tr>
<tr>
<td>Hazel</td>
<td>2</td>
<td>0.1392</td>
</tr>
<tr>
<td>Sycamore</td>
<td>12</td>
<td>0.1871</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>5</td>
<td>0.2002</td>
</tr>
<tr>
<td>Oak</td>
<td>4</td>
<td>0.2062</td>
</tr>
<tr>
<td>Birch spp.</td>
<td>7</td>
<td>0.2327</td>
</tr>
<tr>
<td>Ash</td>
<td>2</td>
<td>0.3013</td>
</tr>
</tbody>
</table>

Table 3-3: Light transmission coefficients for the eight species
<table>
<thead>
<tr>
<th>Allometry Parameters (as found in Evans et al., 2015)</th>
<th>Equation no. &amp; parameter</th>
<th>Field Maple</th>
<th>Sycamore</th>
<th>Birch</th>
<th>Hazel</th>
<th>Hawthorn</th>
<th>Beech</th>
<th>Ash</th>
<th>Oak</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH to Diameter at 10 cm slope of regression</td>
<td>(3.2 a)</td>
<td>0.56</td>
<td>0.56</td>
<td>0.4</td>
<td>0.33</td>
<td>0.48</td>
<td>0.75</td>
<td>0.27</td>
<td>0.58</td>
</tr>
<tr>
<td>DBH to Diameter at 10 cm Relationship regression</td>
<td>(3.2 b)</td>
<td>2</td>
<td>2</td>
<td>2.86</td>
<td>4.25</td>
<td>2.51</td>
<td>0</td>
<td>4.74</td>
<td>1.43</td>
</tr>
<tr>
<td>Height-Diameter at 10 cm Relationship intercept</td>
<td>(3.3 a)</td>
<td>0.12</td>
<td>0.12</td>
<td>0.82</td>
<td>2.36</td>
<td>1.37</td>
<td>0.11</td>
<td>0.1</td>
<td>0.11</td>
</tr>
<tr>
<td>Height-Diameter at 10 cm Relationship slope</td>
<td>(3.3 b)</td>
<td>1.88</td>
<td>1.88</td>
<td>0.93</td>
<td>0.54</td>
<td>0.61</td>
<td>1.95</td>
<td>2.03</td>
<td>1.95</td>
</tr>
<tr>
<td>Maximum Height (m)</td>
<td>(3.4 maxht)</td>
<td>19</td>
<td>30.5</td>
<td>22.5</td>
<td>19.5</td>
<td>15</td>
<td>39</td>
<td>37.5</td>
<td>35.5</td>
</tr>
<tr>
<td>Adult height slope</td>
<td>(3.4 b)</td>
<td>0.046</td>
<td>0.041</td>
<td>0.049</td>
<td>0.069</td>
<td>0.051</td>
<td>0.007</td>
<td>0.007</td>
<td>0.016</td>
</tr>
<tr>
<td>Crown radius slope of regression</td>
<td>(3.5 a)</td>
<td>0.19</td>
<td>0.36</td>
<td>0.04</td>
<td>0.01</td>
<td>0.16</td>
<td>0.29</td>
<td>0.11</td>
<td>0.22</td>
</tr>
<tr>
<td>Crown radius exponent</td>
<td>(3.5 b)</td>
<td>0.83</td>
<td>0.72</td>
<td>1.37</td>
<td>2.15</td>
<td>0.99</td>
<td>0.77</td>
<td>1.06</td>
<td>0.78</td>
</tr>
<tr>
<td>Crown height slope</td>
<td>(3.6 a)</td>
<td>0.13</td>
<td>0.24</td>
<td>0.21</td>
<td>0.21</td>
<td>0.31</td>
<td>0.13</td>
<td>0.01</td>
<td>0.02</td>
</tr>
<tr>
<td>Crown Height parameter b</td>
<td>(3.6 b)</td>
<td>1.53</td>
<td>1.28</td>
<td>1.28</td>
<td>1.44</td>
<td>1.3</td>
<td>1.47</td>
<td>2.48</td>
<td>2.01</td>
</tr>
<tr>
<td>Growth Parameters (as found in Evans et al., 2015)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth D10 exponent</td>
<td>(3.7 Φ)</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
<td>0.845</td>
</tr>
<tr>
<td>High light growth</td>
<td>(3.7 a)</td>
<td>0.1250</td>
<td>0.0118</td>
<td>0.1690</td>
<td>-0.0160</td>
<td>0.0264</td>
<td>0.1520</td>
<td>0.0082</td>
<td>0.0546</td>
</tr>
<tr>
<td>Low light growth</td>
<td>(3.7 β)</td>
<td>0.1590</td>
<td>0.0215</td>
<td>0.1370</td>
<td>0.0680</td>
<td>0.0055</td>
<td>0.0750</td>
<td>0.0001</td>
<td>0.0348</td>
</tr>
<tr>
<td>Max Growth rate (cm yr⁻¹)</td>
<td>(3.8 MaxG)</td>
<td>0.59</td>
<td>0.48</td>
<td>0.77</td>
<td>0.54</td>
<td>0.62</td>
<td>0.97</td>
<td>1.47</td>
<td>1.81</td>
</tr>
<tr>
<td>Size effect parameter x0</td>
<td>(3.9 x₀)</td>
<td>20.13</td>
<td>20.56</td>
<td>15.68</td>
<td>9.62</td>
<td>12.93</td>
<td>31.87</td>
<td>19.9</td>
<td>26.45</td>
</tr>
<tr>
<td>Size effect parameter xb</td>
<td>(3.9 x₀)</td>
<td>93.12</td>
<td>135.25</td>
<td>66.26</td>
<td>12.74</td>
<td>55.06</td>
<td>1013.79</td>
<td>58.52</td>
<td>495.06</td>
</tr>
</tbody>
</table>
### Mortality Parameters (as in Moustakas & Evans, 2014)

<table>
<thead>
<tr>
<th>Equation &amp; parameter</th>
<th>Field</th>
<th>Maple</th>
<th>Sycamore</th>
<th>Birch</th>
<th>Hazel</th>
<th>Hawthorn</th>
<th>Beech</th>
<th>Ash</th>
<th>Oak</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual mortality rate parameter $\phi_1^2$</td>
<td>$(3.10 , \phi_1)$</td>
<td>5.5700</td>
<td>5.6200</td>
<td>3.4000</td>
<td>5.6500</td>
<td>4.8300</td>
<td>4.6800</td>
<td>5.3600</td>
<td>4.2300</td>
</tr>
<tr>
<td>Annual mortality rate parameter $\phi_2^2$</td>
<td>$(3.10 , \phi_2)$</td>
<td>-0.2070</td>
<td>5.2300</td>
<td>0.1430</td>
<td>-0.1900</td>
<td>-0.0900</td>
<td>-0.2270</td>
<td>0.4400</td>
<td>1.8300</td>
</tr>
<tr>
<td>Mean DBH</td>
<td>$(3.10 , \text{meanDBH})$</td>
<td>18.7000</td>
<td>19.9300</td>
<td>27.5800</td>
<td>10.8300</td>
<td>14.7300</td>
<td>27.5100</td>
<td>20.8300</td>
<td>37.3900</td>
</tr>
</tbody>
</table>

### Recruitment Parameters (taken from Swift, 2005)$^3$

| Recruitment parameter $STR$ | $(3.11 \, STR)$ | 725 | 725 | 10249 | 1976 | 1976 | 224 | 946 | 224 |
| Recruitment parameter $\theta$ | $(3.11 \, \theta)$ | 2.95 | 2.95 | 1.3 | 0.72 | 0.72 | 3.55 | 5.65 | 3.55 |
| Recruitment parameter $x_0$ | $(3.11 \, x_0)$ | 4.67 | 4.67 | 38.29 | 7.84 | 7.84 | 4.01 | 29.71 | 4.01 |
| Recruitment parameter $xb$ | $(3.11 \, xb)$ | 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 nineteenth 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 occurring 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 25km² 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:

```java
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.
<table>
<thead>
<tr>
<th>Mean Canopy Openness</th>
<th>Time to 3m in Full Sun (Years)</th>
<th>3m in 1% light</th>
<th>5-Yr survivorship of 1cm diameter sapling 1% sun</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak</td>
<td>20.62</td>
<td>6</td>
<td>135</td>
</tr>
<tr>
<td>Hazel</td>
<td>13.92</td>
<td>4</td>
<td>248</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>20.02</td>
<td>5</td>
<td>266</td>
</tr>
<tr>
<td>Birch</td>
<td>23.27</td>
<td>240</td>
<td>528</td>
</tr>
<tr>
<td>Field Maple</td>
<td>8.52</td>
<td>323</td>
<td>571</td>
</tr>
<tr>
<td>Sycamore</td>
<td>18.71</td>
<td>19</td>
<td>609</td>
</tr>
<tr>
<td>Ash</td>
<td>30.13</td>
<td>8</td>
<td>768</td>
</tr>
<tr>
<td>Beech</td>
<td>12.08</td>
<td>269</td>
<td>796</td>
</tr>
</tbody>
</table>

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).
<table>
<thead>
<tr>
<th></th>
<th>February Average</th>
<th>March Average</th>
<th>April Average</th>
<th>February-March Average</th>
<th>March-April Average</th>
<th>February-April Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td>*</td>
<td></td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>.</td>
<td></td>
<td></td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hawthorn</td>
<td>**</td>
<td>**</td>
<td>***</td>
<td>*</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Hazel</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oak</td>
<td>*</td>
<td>***</td>
<td>*</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Birch</td>
<td>.</td>
<td></td>
<td>*</td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Sycamore</td>
<td>.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field Maple</td>
<td>*</td>
<td>*</td>
<td></td>
<td>**</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th></th>
<th>Change in budburst date (days °C⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field maple</td>
<td>3.035</td>
</tr>
<tr>
<td>Sycamore</td>
<td>6.2</td>
</tr>
<tr>
<td>Birch</td>
<td>4.165</td>
</tr>
<tr>
<td>Hazel</td>
<td>0</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>3.944</td>
</tr>
<tr>
<td>Beech</td>
<td>2.545</td>
</tr>
<tr>
<td>Ash</td>
<td>5.1</td>
</tr>
<tr>
<td>Oak</td>
<td>4.1</td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>Proportional Representation (%)</th>
<th>Current</th>
<th>After 1250 Years</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Baseline</td>
<td>B1</td>
</tr>
<tr>
<td>Ash</td>
<td>26.9</td>
<td>30.2</td>
</tr>
<tr>
<td>Beech</td>
<td>0.325</td>
<td>0.303</td>
</tr>
<tr>
<td>Birch</td>
<td>0.4</td>
<td>0</td>
</tr>
<tr>
<td>Field Maple</td>
<td>0.7</td>
<td>0.07</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>6.9</td>
<td>1.562</td>
</tr>
<tr>
<td>Hazel</td>
<td>8.9</td>
<td>4.502</td>
</tr>
<tr>
<td>Oak</td>
<td>1.9</td>
<td>0.024</td>
</tr>
<tr>
<td>Sycamore</td>
<td>51.9</td>
<td>63.317</td>
</tr>
</tbody>
</table>

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: F3,24 = 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).

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

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.
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 CO₂ 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 CO₂ 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.

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, its 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°C (Butt et al., 2014). Forty-one 10m² 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:

\[
SPI = \frac{(\text{monthly precipitation} - \text{average precipitation})}{\text{s.d. precipitation}}
\]  

(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-km² 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 ($\phi$), 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).

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Description</th>
<th>Survival Probability (Φ)</th>
<th>Relocation probability (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Φ: DBH; p: c</td>
<td>Constant between years; varies with DBH</td>
<td>Constant between years</td>
<td></td>
</tr>
<tr>
<td>Φ: SPI; p: c</td>
<td>Constant between years; varies with SPI</td>
<td>Constant between years</td>
<td></td>
</tr>
<tr>
<td>Φ: DBH + SPI;</td>
<td>Constant between years; varies with SPI and DBH independently</td>
<td>Constant between years</td>
<td></td>
</tr>
<tr>
<td>p: c</td>
<td>Constant between years; varies with SPI and DBH dependently</td>
<td>Constant between years</td>
<td></td>
</tr>
</tbody>
</table>

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 25m² 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:

```r
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:

\( \text{dam} \) is the mortality probability for an individual at a single time step

\( \text{params[kind].phi1} \) is the first mortality parameter

\( \text{params[kind].phi2} \) is the parameter relating mortality to DBH

\( \text{params[kind].phi3} \) 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 QAICc but these also have very low difference in QAICc 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Best Model</th>
<th>2nd Best Model</th>
<th>3rd Best Model</th>
<th>4th Best Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field Maple</td>
<td>DBH + SPI</td>
<td>DBH*SPI</td>
<td>DBH</td>
<td>SPI</td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>2.209</td>
<td>2.7354</td>
<td>5.0511</td>
<td></td>
</tr>
<tr>
<td>Sycamore</td>
<td>SPI</td>
<td>DBH + SPI</td>
<td>DBH</td>
<td>DBH*SPI</td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>0.5584</td>
<td>0.608</td>
<td>1.7052</td>
<td></td>
</tr>
<tr>
<td>Birch</td>
<td>DBH</td>
<td>DBH*SPI</td>
<td>SPI</td>
<td>DBH*SPI</td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>0.2277</td>
<td>0.566</td>
<td>2.3382</td>
<td></td>
</tr>
<tr>
<td>Hazel</td>
<td>DBH</td>
<td>SPI</td>
<td>DBH*SPI</td>
<td></td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>0.5607</td>
<td>2.0256</td>
<td>3.9964</td>
<td></td>
</tr>
<tr>
<td>Hawthorn</td>
<td>SPI</td>
<td>DBH + SPI</td>
<td>DBH*SPI</td>
<td></td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>0.2275</td>
<td>2.1111</td>
<td>3.9388</td>
<td></td>
</tr>
<tr>
<td>Beech</td>
<td>DBH*SPI</td>
<td>DBH + SPI</td>
<td>SPI</td>
<td>DBH</td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>9.15</td>
<td>11.115</td>
<td>11.4922</td>
<td></td>
</tr>
<tr>
<td>Ash</td>
<td>DBH*SPI</td>
<td>SPI</td>
<td>DBH + SPI</td>
<td></td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>4.6759</td>
<td>5.3489</td>
<td>6.5877</td>
<td></td>
</tr>
<tr>
<td>Oak</td>
<td>SPI</td>
<td>DBH + SPI</td>
<td>DBH*SPI</td>
<td></td>
</tr>
<tr>
<td>ΔQAICc</td>
<td>0.0218</td>
<td>1.8311</td>
<td>3.8845</td>
<td></td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>Years</th>
<th>SPI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993-1996</td>
<td>-1.0728</td>
</tr>
<tr>
<td>1997-1999</td>
<td>0.2020</td>
</tr>
<tr>
<td>2000-2002</td>
<td>0.0029</td>
</tr>
<tr>
<td>2003-2005</td>
<td>0.2830</td>
</tr>
<tr>
<td>2006-2008</td>
<td>0.8103</td>
</tr>
<tr>
<td>2009-2012</td>
<td>1.0476</td>
</tr>
</tbody>
</table>

*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*

<table>
<thead>
<tr>
<th>Years</th>
<th>SPI</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012-2020</td>
<td>-0.0440</td>
</tr>
<tr>
<td>2021-2030</td>
<td>-0.1874</td>
</tr>
<tr>
<td>2031-2040</td>
<td>-0.2484</td>
</tr>
<tr>
<td>2041-2050</td>
<td>-0.4314</td>
</tr>
<tr>
<td>2051-2060</td>
<td>-0.5325</td>
</tr>
<tr>
<td>2061-2070</td>
<td>-0.6168</td>
</tr>
<tr>
<td>2071-2080</td>
<td>-0.6960</td>
</tr>
</tbody>
</table>

*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).

<table>
<thead>
<tr>
<th>Proportions (%)</th>
<th>Current</th>
<th>After 1250 Years</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Baseline</td>
<td>B1</td>
</tr>
<tr>
<td>Ash</td>
<td>26.9</td>
<td>83.6</td>
</tr>
<tr>
<td>Beech</td>
<td>1</td>
<td>0.7</td>
</tr>
<tr>
<td>Birch</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Field Maple</td>
<td>0.7</td>
<td>0.3</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>6.9</td>
<td>3.7</td>
</tr>
<tr>
<td>Hazel</td>
<td>8.9</td>
<td>1.2</td>
</tr>
<tr>
<td>Oak</td>
<td>1.9</td>
<td>7.5</td>
</tr>
<tr>
<td>Sycamore</td>
<td>51.9</td>
<td>2.6</td>
</tr>
</tbody>
</table>

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).
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 ($\chi^2=0$, df=3, p=1).

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

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.
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 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 CO₂ 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, Rehfelt 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), pendulate 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:

$$SPI = \frac{\text{monthly precipitation} - \text{average precipitation}}{\text{s.d. precipitation}}$$  \hspace{1cm} (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 that 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).

<table>
<thead>
<tr>
<th>Years</th>
<th>SPI</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012-2020</td>
<td>-0.0440</td>
</tr>
<tr>
<td>2021-2030</td>
<td>-0.1874</td>
</tr>
<tr>
<td>2031-2040</td>
<td>-0.2484</td>
</tr>
<tr>
<td>2041-2050</td>
<td>-0.4314</td>
</tr>
<tr>
<td>2051-2060</td>
<td>-0.5325</td>
</tr>
<tr>
<td>2061-2070</td>
<td>-0.6168</td>
</tr>
<tr>
<td>2071-2080</td>
<td>-0.6960</td>
</tr>
</tbody>
</table>

Table 6-1: Forecasted standardised precipitation index (SPI) for the years 2012 to 2080 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 $[\phi_3$, 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).

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

![Total Number of Inds, 1250 years](image)

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.
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**

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

**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).
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 (%)

<table>
<thead>
<tr>
<th></th>
<th>Current</th>
<th>1250 Year Predictions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Baseline</td>
<td>B1</td>
</tr>
<tr>
<td>Ash</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>26.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0034)</td>
<td>(±0.0026)</td>
</tr>
<tr>
<td></td>
<td>0.381</td>
<td>0.311</td>
</tr>
<tr>
<td>Beech</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0002)</td>
<td>(±0.0003)</td>
</tr>
<tr>
<td></td>
<td>0.418</td>
<td>0.48</td>
</tr>
<tr>
<td>Birch</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0006)</td>
<td>(±0.0008)</td>
</tr>
<tr>
<td></td>
<td>0.233</td>
<td>0.217</td>
</tr>
<tr>
<td>Field Maple</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0003)</td>
<td>(±0.0001)</td>
</tr>
<tr>
<td></td>
<td>3.711</td>
<td>3.491</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>6.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0017)</td>
<td>(±0.002)</td>
</tr>
<tr>
<td></td>
<td>0.958</td>
<td>0.938</td>
</tr>
<tr>
<td>Hazel</td>
<td>8.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0006)</td>
<td>(±0.0006)</td>
</tr>
<tr>
<td></td>
<td>5.663</td>
<td>5.169</td>
</tr>
<tr>
<td>Oak</td>
<td>1.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0021)</td>
<td>(±0.0019)</td>
</tr>
<tr>
<td></td>
<td>0.784</td>
<td>0.693</td>
</tr>
<tr>
<td>Sycamore</td>
<td>51.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(±0.0004)</td>
<td>(±0.0005)</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Baseline</th>
<th>B1</th>
<th>A1B</th>
<th>A1fi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td>+57.475</td>
<td>+54.255</td>
<td>+53.885</td>
<td>+53.556</td>
</tr>
<tr>
<td>Beech</td>
<td>+0.057</td>
<td>-0.003</td>
<td>-0.004</td>
<td>+0.012</td>
</tr>
<tr>
<td>Birch</td>
<td>+0.418</td>
<td>+0.480</td>
<td>+0.482</td>
<td>+0.496</td>
</tr>
<tr>
<td>Field Maple</td>
<td>+0.166</td>
<td>+0.174</td>
<td>+0.157</td>
<td>+0.153</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>+2.145</td>
<td>+1.903</td>
<td>+1.821</td>
<td>+1.872</td>
</tr>
<tr>
<td>Hazel</td>
<td>-3.474</td>
<td>-3.130</td>
<td>-3.266</td>
<td>-3.207</td>
</tr>
<tr>
<td>Oak</td>
<td>+5.640</td>
<td>+5.145</td>
<td>+5.085</td>
<td>+5.030</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Species</th>
<th>Baseline</th>
<th>B1</th>
<th>A1B</th>
<th>A1fi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ash</td>
<td>-0.21</td>
<td>+0.69</td>
<td>+0.92</td>
<td>+1.08</td>
</tr>
<tr>
<td>Beech</td>
<td>+0.02</td>
<td>-0.05</td>
<td>-0.05</td>
<td>-0.02</td>
</tr>
<tr>
<td>Birch</td>
<td>+0.03</td>
<td>-0.01</td>
<td>+0.00</td>
<td>-0.03</td>
</tr>
<tr>
<td>Field Maple</td>
<td>-0.00</td>
<td>-0.03</td>
<td>-0.03</td>
<td>-0.06</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>+0.36</td>
<td>+0.19</td>
<td>+0.07</td>
<td>+0.26</td>
</tr>
<tr>
<td>Hazel</td>
<td>+0.13</td>
<td>+0.17</td>
<td>+0.08</td>
<td>+0.02</td>
</tr>
<tr>
<td>Oak</td>
<td>-0.28</td>
<td>-0.88</td>
<td>-0.92</td>
<td>-1.16</td>
</tr>
<tr>
<td>Sycamore</td>
<td>-0.03</td>
<td>-0.09</td>
<td>-0.07</td>
<td>-0.08</td>
</tr>
</tbody>
</table>

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 CO₂ 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 CO₂ 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 affected 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.
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Appendices
Allometry and growth of eight tree taxa in United Kingdom woodlands

Matthew R. Evans, Aristides Moustakas, Gregory Carey, Yadavinder Malhi, Nathalie Butt, Sue Benham, Denise Pallett & Stefanie Schäfer

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.

<table>
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<tr>
<th>Design Type(s)</th>
<th>time series design</th>
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<tr>
<td>Measurement Type(s)</td>
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</tr>
<tr>
<td>Technology Type(s)</td>
<td>Measuring Tape • Hypsometer; Laser Vertex; Laser Range Meter • Vernier Caliper • Laser Range Meter • PAR Quantum sensor • software</td>
</tr>
<tr>
<td>Factor Type(s)</td>
<td>Woodland • Wytham Woods • Acer pseudoplatanus • Fraxinus excelsior • Quercus robur • Fagus sylvatica • Corylus avellana • Crataegus monogyna • Acer campestre • Betula • Alice Holt Forest</td>
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Background & Summary
Prediction is a basic, possibly defining, feature of scientific disciplines. 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. 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. 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 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.

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. 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 and New Zealand, 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 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. 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. 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

<table>
<thead>
<tr>
<th>Latin name</th>
<th>Common name</th>
<th>Taxonomic code</th>
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<tbody>
<tr>
<td>Acer pseudoplatanus</td>
<td>Sycamore</td>
<td>ACERPS</td>
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<tr>
<td>Picea abies</td>
<td>European spruce</td>
<td>PICEAE</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>Pedunculate oak</td>
<td>QUIERO</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>European beech</td>
<td>FAGUSY</td>
</tr>
<tr>
<td>Corylus avellana</td>
<td>Common hazel</td>
<td>CORAYV</td>
</tr>
<tr>
<td>Chamaecyparis lawsoniana</td>
<td>Common Lawson cypress</td>
<td>CRATOM</td>
</tr>
<tr>
<td>Acer campestre</td>
<td>Field maple</td>
<td>ACERCA</td>
</tr>
<tr>
<td>Betula spp.</td>
<td>Birch</td>
<td>BETUSP</td>
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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.
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 850ha, the majority planted with Corsican pine (Pinus nigra), but 140ha of old-growth oak (Quercus robur) woodland remain, in which the data used here were collected. The site varies in altitude from 70–125m. 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:


- Oxford University plot (OXF), two of the authors (Mallik and Butt) have established an 18ha 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 10cm above ground level on all saplings (defined here as trees with DBH < 10cm) in ECN-W, ECN-AH, and a sample of 88 from OXF.
- Measuring the light environment around all saplings in ECN-W, ECN-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\textsuperscript{15}.

**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, ECH-AH and OXF\textsuperscript{1} 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\textsuperscript{14}. 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\textsuperscript{15}, and using a laser Vertex (Haglof Vertex III, Längele, 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 differences in the measurements taken by the different instruments, once taxon and stage (adult or sapling) were taken into account (\( \Gamma = 5.43, N = 465, \) with eight taxa and 2 stages, \( P = 0.98 \)).

**Diameter 10 cm above ground level (D\textsubscript{10}).** \( D\textsubscript{10} \) 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 another and averaged to produce one measurement per tree. A tape was not used to measure \( D\textsubscript{10} \) 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 \( D\textsubscript{10} \) 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 ECH-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\textsuperscript{14,20}.

**Crown height (CH).** CH was established for adults in the ECN-W and ECH-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\textsuperscript{15}, 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\textsuperscript{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\textsuperscript{15}. We measured the percentage of incident light at the canopy reaching each tree (\( L_i \)) 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 (\( L_{i\text{canopy}} \)), the 8th measurement of absolute light levels below the canopy taken at time \( t \), where \( i = 1 \ldots 3 \), and simultaneously in a large open gap nearby (\( L_{i\text{open}} \), 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 \( (L_{ci}, \text{ where } i = 1-3) \): 

\[
L_{ci} = L_{\text{avail}}/L_{\text{out}}
\]  

\( L_{c1}, L_{c2} \) 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\(^a\). 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 (\( H \)).

\[
DBH = a + bD_{10}
\]

\( aD_{10}^p \) or \( \log H = \log a + b \log D_{10} \)

\[
H = aD_{10}^p \quad \text{or} \quad \log H = \log a + b \log D_{10}
\]

**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.

\[
\text{CRad} = aDBH^p, \quad \text{or} \quad \log \text{CRad} = \log a + b \log DBH
\]

\[
\text{CH} = aH^p, \quad \text{or} \quad \log \text{CH} = \log a + b \log H
\]

\[
H = 1.35 + (\max H - 1.35)(1 - e^{-DBH})
\]

**Growth**

**Saplings**

Radial growth is assumed to be described by a Michaelis-Menten function that relates growth in DBH \( (G_{\text{sap}}, \text{cm yr}^{-1}) \) to light availability \( (L_c, \text{expressed as a percentage of daylight}) \), 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.\(^{13} \) \( \phi \)

\[
G_{\text{sap}} = \frac{(aL_c/(L_c + (\alpha/\beta)))D_{10}^p}{(aL_c/(L_c + (\alpha/\beta)))D_{10}^p}
\]

\( \alpha \) is the asymptotic growth at high light levels, \( \beta \) is the slope of the growth function at zero light, \( D_{10}^p \) is the size effect to determine the most appropriate value of \( \phi \) 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.

\[
G_{\text{adult}} = \text{Max}G \times SE
\]

The size effect \( SE \) is given by:

\[
SE = e^{-0.5[(\ln(DBH/x_0)/x_0)]^2}
\]

\( x_0 \) and \( x_0 \) 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 CIRad 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\(^{23}\) 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 \(\times 100\)); for ECN-AH they are derived by adding (cell identity code) to (plot identity code \(\times 100\)); 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.ararab.harvard.edu/Public/plotdatabas/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.predictiveecology.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.predictiveecology.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.predictiveecology.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.predictiveecology.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.predictiveecology.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.predictiveecology.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.predictiveecology.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.predictiveecology.com.
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Data Citations

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Author Contributions
M.R.E. collected data on D10, 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 $x_2$ and $x_3$ 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.


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