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Forest ecology in a changing world: Effective ground-based methods for monitoring temperate broadleaved forest ecosystem dynamics in relation to climate change

Smith, Alison M

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Forest ecology in a changing world: Effective ground-based methods for monitoring temperate broadleaved forest ecosystem dynamics in relation to climate change

by

ALISON M. SMITH

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Author's declaration

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

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

A programme of advanced study was undertaken, which included: Postgraduate Research Skills module, An Introduction to GIS, and An Introduction to R. During the course of this research, other relevant training and experience was gained. The PhD was undertaken part-time while working, often full-time, in career-related posts. Relevant scientific seminars were attended through the university research groups. Undergraduate teaching was undertaken, including writing and delivering lectures on forest ecology and a 5-credit module on citizen science. A large number of workshops and training sessions were designed and delivered, relating to forest ecology, management and survey, through employment with Plantlife. This included presenting work at meetings and seminars with a range of forestry professionals from across south-west England.

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Abstract

The impacts of climate change on temperate forests are predicted to accelerate, with widespread implications for forest biodiversity and function. Remote sensing has provided insights into regional patterns of vegetation dynamics, and experimental studies have demonstrated impacts of specific changes on individual species. However, forests are diverse and complex ecosystems. To understand how different species in different forests respond to interacting environmental pressures, widespread ground-based monitoring is needed. The only practical way to achieve this is through the involvement of non-professional researchers, *i.e.,* with citizen science. However, many techniques used to identify subtle changes in forests require expensive equipment and professional expertise. This thesis aimed to identify practical methods for citizen scientists to collect useful data on forest ecosystem dynamics in relation to climate change. Methods for monitoring tree phenology and canopy-understorey interactions were the main focus, as tree phenology exerts strong control on understorey light and forest biodiversity, and is already responding to climate change.

The response of understorey vegetation to canopy closure in four woodlands from a single region of England (Devon) was examined in detail. These geographically close woodlands differed considerably in their composition and seasonal dynamics. The spring period was particularly important for herb-layer development, and small variations in canopy openness had important effects on herb-layer cover and composition. This work highlights the need to monitor a range of different woodlands at the regional scale, with sufficient resolution to pick up small but crucial differences through time. Citizen scientists could help to collect such data by monitoring herb-layer cover and changes in the abundance of key species, alongside monitoring the overstorey canopy.

The spring leaf phenology of four canopy trees (ash, beech, oak and sycamore) were monitored intensively in one woodland using a range of methods: counts, percentage estimates and photography. First budburst and leaf expansion dates were compared with estimates of leaf expansion timing and rate, derived from time-series data using logistic growth models. Frequently used first-event dates were potentially misleading due to high variation in leaf development rates within and between species. Percentage estimates and counts produced similar estimates of leaf expansion timing and rate. A photo-derived greenness index produced similar estimates of timing, but not rate, and was compromised by practical issues of photographing individual crowns in closed canopy woodland. Citizen science should collect time-series data instead of frequently-used first event dates—visual observations offer the most practical way to do this, but further work is needed to test reliability with citizen scientists. Given high intra- and inter-species variation in tree phenology, whole forest canopies need to be monitored to infer canopy closure timing.

Canopy openness was assessed using sophisticated hemispherical photography and a range of low-cost alternatives, across four Devon woodlands over a year. Visual estimates and ordinary photography were too coarse to identify fine-scale variation in canopies. Smartphone fisheye photography analysed with free software was identified as a reliable surrogate for estimating relative, though not absolute, canopy openness. The method has high potential as a citizen science tool, as different phone models and users gave similar canopy openness estimates.

In a detailed follow-up study, smartphone fisheye photography, hemispherical photography and visual observations of leaf expansion were used every other day to characterise spring canopy development. Logistic growth models estimated canopy closure timing and rate. Visual observations identified much earlier canopy development than either photographic method. Smartphone fisheye photography performed comparably to hemispherical photography. There is good potential for practical application of smartphone fisheye photography, as similar canopy closure estimates were gained from photos taken once every two weeks.

The research in this thesis identifies a range of methods suitable for widespread monitoring of forest ecosystem dynamics in relation to climate change. Developing a smartphone app for automatic analysis and submission of canopy images will be an important next step to enabling widespread use. A pilot project is underway to begin

testing methods with citizen scientists. Further research into data quality with citizen scientists is needed before the methods can be rolled out widely with confidence.

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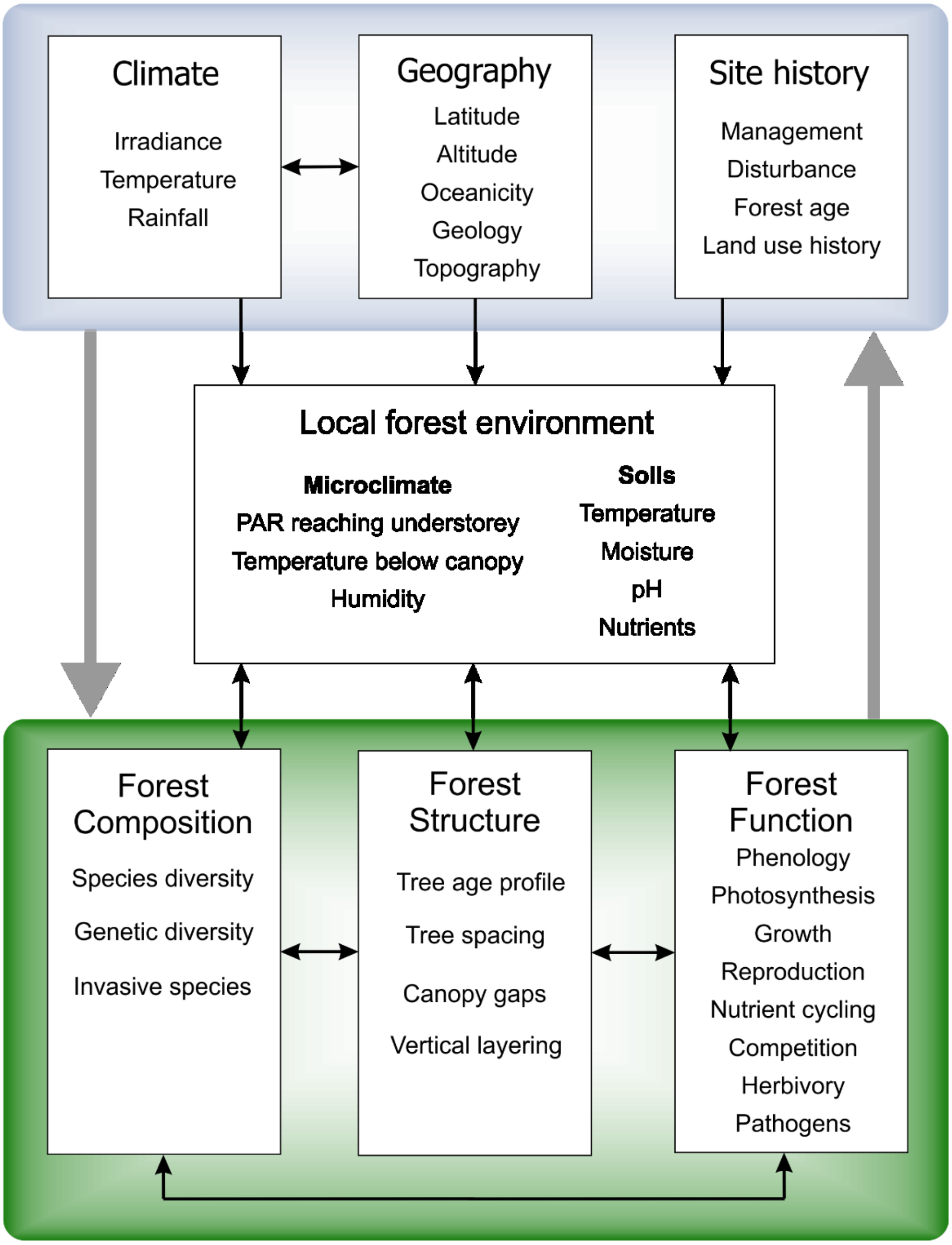
1 Introduction

1.1 Ecosystem dynamics in temperate broadleaved forests

Forest ecosystems are generally described in terms of their composition, structure and function (Franklin, 1988; Packham et al., 1992; Thomas and Packham, 2007). Composition refers to constituent organisms and their diversity (both at the species and genetic level). Forest composition is highly related to forest structure, which is the horizontal arrangement of trees and shrubs (degree of clumping, gap sizes etc.), and the vertical arrangement of foliage in the canopy, shrub and field layers. Together with environmental factors, composition and structure determine forest ecosystem functions, such as photosynthesis, growth, reproduction and nutrient cycling (McElhinny et al., 2005). Clearly, these functions are not static, but are dynamic processes that change through time. Indeed, the structure and composition of forests also change through time, albeit over longer timescales. Therefore, it is useful to include ecosystem dynamics—the study of change in an ecosystem through time—in our understanding of forest ecosystems (Packham et al., 1992). These ecosystem dynamics operate at many levels, from the scale of individual plant cells to whole forested landscapes, and from milliseconds to millennia (Chapin et al., 2002). Here I refer to 'ecosystem dynamics' in terms of the relationship between forest canopies and understories, both in terms of seasonal (intra-annual) changes, and year-to-year (inter-annual) changes. Key factors that determine forest ecosystem dynamics and their interrelatedness are summarised in Fig. 1.1.

Temperate broadleaved forests are found in mid-latitude regions, specifically western and central Europe, North America, eastern Asia, Australasia and small areas of South America (Archibold, 1995). Across their range they vary greatly in terms of composition, structure and function. In the UK alone, 18 distinct woodland communities have been described, with a further 73 sub-communities defined (Hall et al., 2004). As temperate forests are diverse and complex ecosystems, which vary greatly from place to place even over small spatial scales, there is a need for widespread monitoring to understand impacts of environmental change (Chudomelova et al., 2017; Fraterrigo et al., 2006; Gazol and Ibanez, 2010; Verstraeten et al., 2013).

Fig 1.1. Conceptual model showing key factors influencing forest ecosystem dynamics.



Light is one of the key factors influencing temperate forest ecosystem dynamics (Whigham, 2004). Temperate forests are characterised by their seasonality, as growth is limited by the availability of photosynthetically active radiation (PAR) and low temperatures during winter. To conserve energy, forest canopies senesce and lose their leaves in autumn, adding a nutrient influx to the soil. In spring, the forest canopy grows leaves and begins its annual growth period, exerting strong control on the understorey light environment (Kato and Komiyama, 2002). The early spring period prior to canopy closure is therefore critical for the growth of tree saplings and many herbaceous plants (Rothstein and Zak, 2001). As well as light availability in spring, the size, position and frequency of canopy gaps influences growth and production in the understorey (Chazdon and Pearcy, 1991). Canopy gaps are often associated with tree regeneration and high levels of herb-layer and insect diversity (Muscolo et al., 2014; Ohwaki et al., 2017; Proctor et al., 2012; Sabatini et al., 2014). In addition, shade is important for specialist flora, and the varying degrees of sun and shade, resulting from patterns of overstorey composition and structure, shape the understorey microclimate, providing a range of niches for flora adapted to different conditions (Valladares et al., 2016).

Old-growth forests or Ancient Semi-Natural Woodlands (ASNW) are forests that have existed since 1600 AD, and they are the most important temperate forests from a conservation perspective (Peterken, 1993). While temperate broadleaved forests vary greatly in terms of composition, in general terms old growth forests are characterised by structural heterogeneity, with a mixed age structure giving rise to a diverse range of light environments and microclimates (Franklin and Van Pelt, 2004; Ishii et al., 2004; Sabatini et al., 2014). In addition, they typically have nutrient-poor soils as they have never been improved for agriculture (Rackham, 2006). These soils have developed over long time-scales, and contain diverse communities of mycorrhizal fungi, important in aiding nutrient uptake (Siddiqui et al., 2008). All species of woodland ground flora that have been studied have been found to form associations with mycorrhizae (Whigham, 2004), and these associations are thought to be important in increasing resilience to stress factors, including climate change (Pickles and Simard, 2017; Zhu et al., 2018). Together, these characteristics of old-growth forests contribute to their biodiversity and resilience.

However, temperate forest ecosystems have experienced widespread change over the past century, leading to structural and taxonomic homogenisation (Keith et al., 2009; Rooney et al., 2004). Due to losses of old-growth forests and a rise in tree-planting schemes, an increasing proportion of temperate forests are recently established (Hopkins and Kirby, 2007). These newer forests tend to have more nutrient-rich soils as a result of past land use, and lack the diversity of mycorrhizal associations found in old-growth forests (Rackham, 2006). Furthermore, without active management, these forests tend to have more even-aged structures and uniformly closed canopies. Where canopy gaps are created, high levels of soil nutrients will often mean that generalist light-demanding species out-compete specialist woodland ground flora (Read and Frater, 1999).

Remaining old-growth forests have also experienced large-scale changes. Loss of traditional management practices, such as coppicing and thinning for wood products, has led to an increase in structurally homogenous 'high forests' with closed canopies. The proportion of high forest in the UK increased from 51% to 97% between 1947 to 2002, due to the loss of coppice, scrub and pasture woodland (Hopkins and Kirby, 2007). As a result, studies have revealed rapid shifts in woodland ground flora, with an increasing dominance of shade-tolerant species (Keith et al., 2009; Verstraeten et al., 2013). The loss of glades and open spaces in woodland has been cited as the primary cause for the sharp decline in many woodland butterfly species (Fartmann et al., 2013). In addition to shading, old-growth forests have also been exposed to nutrient enrichment. Atmospheric deposition of nitrogen is one contributing factor, but the increased prevalence of high forests with dense stands has also led to higher inputs of nutrients from leaf litter (Verheyen et al., 2012). Studies comparing present ground flora composition to that 70–80 years ago, have identified shifts towards more shade-tolerant and nitrophilic species, and a resulting loss of diversity at the landscape-scale (Keith et al., 2009; Rooney et al., 2004).

New threats to temperate forest biodiversity have also emerged in recent decades. The increasing global movement of plants has led to a rise in invasive species (Medvecka et al., 2018; Seebens et al., 2017), and more frequent outbreaks of introduced plant pests and pathogens (Boyd et al., 2013). Interacting environmental pressures leave forest ecosystems increasingly vulnerable to perturbations. It is not well understood how climate change will interact with these pressures, but it is likely that in many cases it will exacerbate them

(Dukes et al., 2009; Sturrock et al., 2011). Understanding how different forests will respond to climate change, will be of key importance for mitigating biodiversity loss.

1.2 Impacts of climate change

Climate change has been identified as one of the greatest threats to biodiversity, and is already affecting biological processes and ecosystems on a global-scale (Parmesan, 2006; Rosenzweig et al., 2007). Increasing global mean surface temperatures, changing rainfall patterns and elevated CO_2 concentrations will have wide-reaching impacts on ecosystem composition and function. While rising temperatures and CO_2 levels are often predicted to extend growing seasons and enhance net primary productivity (NPP) (Buitenwerf et al., 2015), this could be offset by stress and mortality induced by drought and the increasing frequency of other extreme weather events (Boisvenue and Running, 2006). The ability of the phenology and physiology of individual plants and species to adapt will determine competition dynamics and trophic asynchronies, leading to compositional change and species extinctions (Thackeray et al., 2010). A meta-analysis including 131 published predictions recently estimated a global extinction rate of 1 in 6 species under a 'business as usual' emissions scenario (Urban, 2015). Changes in plant community composition may be so fundamental that the resilience of entire ecosystems or biomes are threatened (Bellard et al., 2012). Temperate broadleaf forests are an important resource in terms of biodiversity and ecosystem services provided on a local, regional, and even global scale (Richardson et al., 2013; Thom et al., 2017b). Therefore, understanding how climate change is likely to impact on temperate forest ecosystem dynamics is of critical importance to conservation. A conceptual model of key impacts of climate change on temperate forests, and factors that will influence individual forest response, is presented in Fig. 1.2.

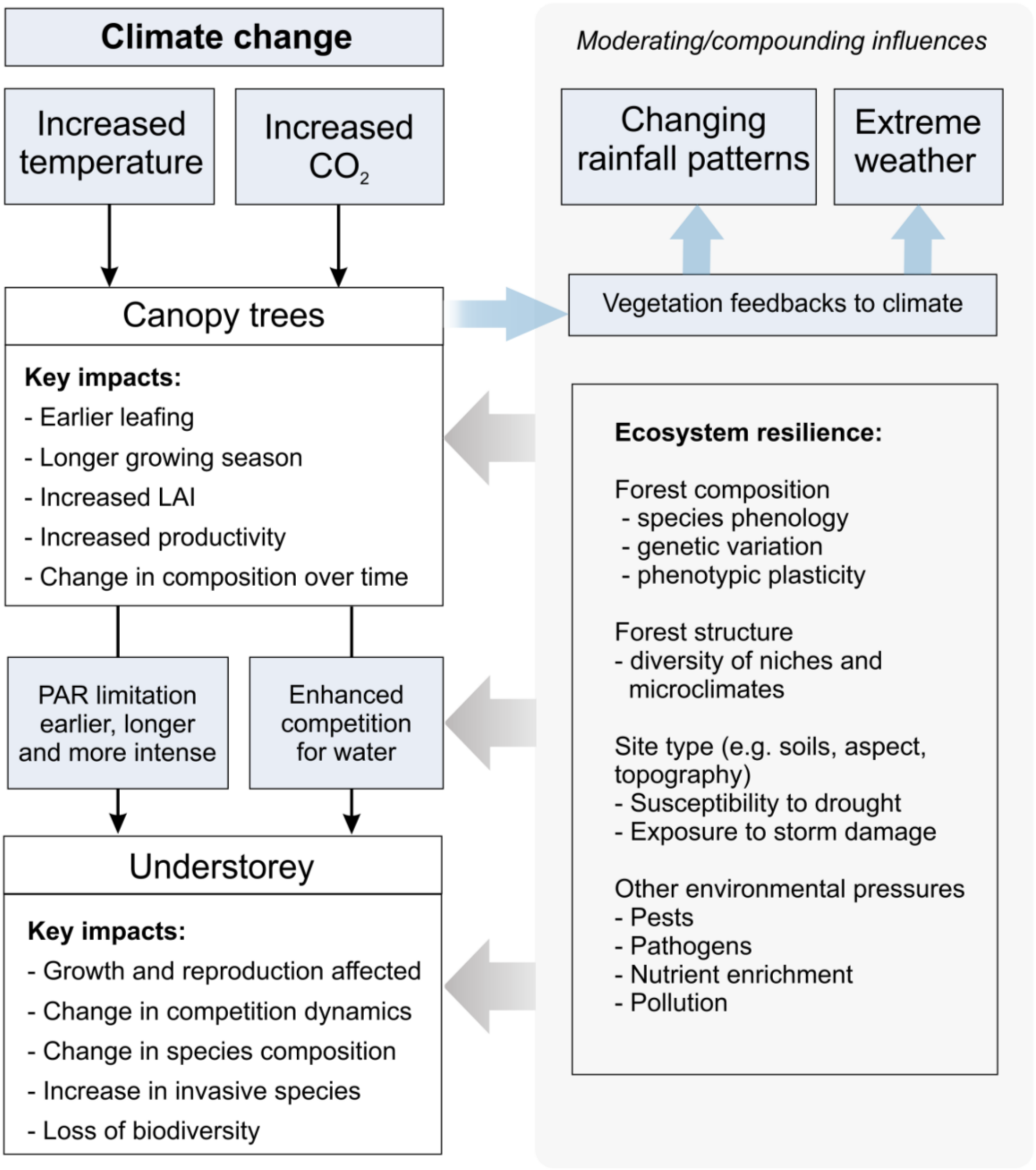
Phenology is the study of the seasonal timing of recurring biological events, and is a critical aspect of global change research that has gained increasing attention in recent years (Donnelly and Yu, 2017; Richardson et al., 2013). Phenological changes in response to climate warming have been identified across biomes and taxa (Gordo and Sanz, 2010; Parmesan, 2007), with temperate regions identified as an area experiencing rapid change (Buitenwerf et al., 2015). The availability of historic data-sets, combined with new evidence—obtained from remote sensing and ground-based observations—has enabled analyses of phenological patterns through space and time (Cleland et al., 2007b; Polgar and

Primack, 2011; Sparks et al., 2009). Studies have demonstrated trends towards longer growing seasons caused by both earlier spring leaf-out and delayed autumn senescence. Menzel and Fabian (1999) reported an average growing season extension of eleven days for temperate broadleaf tree species in Europe since the 1960s. Inter-annual variability in tree leaf phenology is strongly explained by temperature (Dragoni et al., 2011; Keenan et al., 2014b; Vitasse et al., 2009b; Wang et al., 2016), with warmer temperatures both advancing and prolonging canopy leafing.

Many studies have demonstrated the link between warmer temperatures, longer growth seasons and increased productivity in temperate forests (Crabbe et al., 2016; Dragoni et al., 2011; Keenan et al., 2014b; Richardson et al., 2010). While higher rates of respiration associated with a longer growth season have been shown to reduce net gain in plant biomass in some conifer forests (Boisvenue and Running, 2006), the majority of studies in broadleaf forests have shown higher rates of carbon assimilation at the forest-scale (Richardson et al., 2010). Elevated levels of CO_2 under future climate change could further enhance productivity—in an experimental study where CO_2 concentration was increased to 700ppm, the Leaf Area Index (LAI) of oak increased by 81% (Broadmeadow and Jackson, 2000). This has important consequences for vegetation feedbacks to the climate, as enhanced net primary productivity (NPP) increases carbon sequestration (Green et al., 2017). In addition, earlier and longer canopy leafing enhances the earth's albedo, with potentially mediating impacts on the pace of climate change (Garnaud and Sushama, 2015; Richardson et al., 2013).

However, there are a number of interrelating factors that are likely to affect tree productivity in the future. Drought is likely to become more common, with earlier onset of the growth season placing a strain on soil moisture reserves in late summer (Rotzer et al., 2013) This could cause a shift in canopy tree species composition; for example in southern England, beech is expected to contract its range (Broadmeadow et al., 2005), as is sycamore (Morecroft et al., 2008). Some authors have argued that higher CO_2 concentrations will stimulate physiological adaptations that will increase plant tolerance to drought, *e.g.,* lower stomatal density and reduced stomatal conductance (Xu et al., 2016). However, this could well be offset by previously reported increases in leaf area (Broadmeadow and Jackson, 2000). Studies that have reported observed increased productivity as a consequence of warmer temperatures, have cautioned against using short-term studies at single sites or 'space-for-time' studies, to predict future responses across the temperate forest ecosystem (Dragoni et al., 2011; Richardson et al., 2010). Many factors will determine the productivity, health and resilience of individual forests under future climate change (Fig. 1.2.).

Fig. 1.2. Conceptual model showing current and predicted impacts of climate change, and the complex factors that could determinine the response of different forest ecosystems.



Although there is a strong general trend towards temperature-driven advance in leafing phenology, phenological responses vary between species and populations. In a study of leaf-out timing in over 700 woody species in temperate forests in China, Zhang et al. (2015) identified divergent responses to early spring warming . The timing of bud-burst is controlled by a combination of external environmental factors (including winter chilling requirements, spring temperature and photoperiod) and internal genetic factors (Panchen et al., 2014; Polgar and Primack, 2011). The relative importance of these cues can vary between species and populations, and this plays an important role in niche partitioning. A recent study by Roberts et al. (2015) utilised two centuries of phenological records for British tree species to model thermal sensitivity; the study predicts a substantial advance in leaf-out timing for later leafing species such as ash and oak, while early-leafing species such as birch and hawthorn are likely to be delayed. Ash and oak leaf phenology is strongly driven by spring temperatures, whereas winter chilling is more important for triggering the leafing of birch and hawthorn. With warmer winters, the chilling requirements of some species may not be met (Laube et al., 2014; Roberts et al., 2015; Wu and Liu, 2013), causing substantial delay, and resulting in increasing synchrony of leafing time between species. Leaf phenology and growth rate of temperate trees are closely related and strongly influence fitness and survival (Vitasse et al., 2009a). Therefore, the ability of tree species to adapt their phenology will influence their resilience to the wide range of pressures associated with increasing climate change.

The implications of the changes to forest canopies and overstorey trees discussed above will have important effects on understorey processes and biodiversity. The tree canopy controls light reaching tree saplings, shrubs and ground flora, and also influences the availability of water and nutrients (Hicks and Taylor, 2015; Jolly et al., 2004; Kato and Komiyama, 2002). The trend towards earlier canopy closure, and increasing synchrony of overstorey phenology, will increase light limitation and resource pressure in the understorey. Shading experiments have demonstrated how earlier canopy closure affects growth and survival in tree saplings and ground flora. In a three-year shading experiment of *Aesculus glabra* and *Acer saccharum* saplings in Illinois, USA, mortality rates were 93% and 80% respectively for shaded individuals, compared to 0% and 27% for controls (Augspurger, 2008). Similar effects on herbaceous plant fitness have also been reported, as well as reduced reproductive capacity associated with both lower carbon gain and pollinator asynchrony (Kim et al., 2015; Kudo et al., 2008; Kudo et al., 2004). Studies in temperate North America and Europe have demonstrated that many woodland specialist ground flora species are slow colonisers, so their ability to adapt to climate variation in situ could be crucial to their survival (Augspurger and Salk, 2017; De Frenne et al., 2011). Furthermore, invasive understorey plants have been shown to increase in abundance due to their greater adaptability to stress factors associated with climate change (Polgar et al., 2014; Willis et al., 2010). Vigorous growth of invasive species will further selective forces acting on native seedlings and ground flora. The interplay of canopy closure, other stress factors, and individual forest characteristics will affect the resilience of understorey forest biodiversity as climate change progresses (Canham and Murphy, 2017).

1.3 Current monitoring approaches

Given the impacts of climate change outlined above, widespread integrated monitoring of tree phenology, canopy closure timing and understorey dynamics will be key to improving our understanding of effects on forest ecosystems. There are two main types of monitoring currently being used to assess climate change impacts on forests in Europe: routine monitoring of forest plots as part of statutory conservation assessments, and remote sensing. The contributions of these approaches are discussed here, along with the role of experimental studies and citizen science projects. The temporal and spatial scales at which different approaches generate data are explored, along with their limitations. A summary is provided in Table 1.1.

1.3.1 Routine monitoring of forest plots

Growing international recognition of the rate and scale of biodiversity loss prompted a sharp rise in forest monitoring programmes during the 1980s and 1990s (Durrant, 2000; Legg and Nagy, 2006) and the inclusion of biodiversity assessments into National Forest Inventories (NFIs). This type of mandated monitoring generally involves making rapid visual assessments to quantify a range of forest characteristics (Chirici et al., 2012). In Europe, the largest-scale coordinated forest monitoring occurs as part of the ICP Forests (International Cooperative Programme on Monitoring of Air Pollution Effects on Forests). While the original aim of this programme was to monitor the effects of transboundary

Table 1.1. A summary of attributes currently assessed as part of European forest monitoring of forest canopies and understories. Ticks show attributes that are routinely monitored, 'Occ' shows attributes that are occasionally monitored. Blank cells show the attribute is not currently monitored. Shaded rows highlight attributes likely to be important in monitoring canopy-understorey dynamics in relation to climate change, which are not currently adequately assessed by existing projects.

	Monitoring attribute	National Forest Inventories	Level II Monitoring Plots	Satellite remote sensing	Near-surface remote sensing	Citizen Science projects	References
Overstorey	Tree composition, age and size class	✓	✓				Chirici et al. 2011; Bobbertin and Neumann 2010
	Tree health (crown defoliation)	✓	✓	✓	✓		Chirici et al. 2011; Eichorn et al. 2016
	Individual tree phenology		**Occ**		✓	✓	Beuker et al. 2016; Richardson et al. 2007; Denny et al. 2014
	Plot-level tree phenology (visual assessment)		✓				Beuker et al. 2016
	Canopy greening			✓	✓		Zhang et al. 2003; Brown et al. 2016
	Canopy closure timing						
	Qualitative assessment of canopy gaps (in size classes)	**Occ**					Chirici et al. 2011
	LAI—measured directly with litterfall traps		**Occ**				Ukonmaanaho et al. 2016
	LAI—measured indirectly with photos/sensors		✓	✓	✓		Fleck et al. 2016; Verger et al. 2015; Wingate et al. 2015
Understorey	Counts of sapling numbers	✓	✓				Chirici et al. 2011
	% cover by life-form group	✓					Chirici et al. 2011
	% cover by species	**Occ**	✓				Chirici et al. 2011; Canullo et al. 2016
	Phenology					**Occ**	Denny et al, 2014

atmospheric pollution, this programme is now being seen as the principal strategy for nations to assess impacts of climate change on forests (Bussotti and Pollastrini, 2017a).

A key limitation of this type of monitoring is that frequent monitoring methods rely heavily on coarse visual assessments, while more detailed monitoring occurs too infrequently to monitor seasonal and inter-annual changes. At ICP Level II plots—which are the most intensively monitored—phenology monitoring is only compulsory at the plot-level, and involves a 'cursory assessment'. No formal sampling design is provided, as observations are intended to act only as an 'early warning system', rather than forming part of a structured study (Beuker et al., 2016). Assessments of individual tree phenology involve more detailed observations and are recommended to be carried out daily, but currently this is an optional monitoring attribute, and it is not clear how frequently individual tree phenology is actually assessed (Beuker et al., 2016). LAI is assessed, annually using litterfall traps (Ukonmaanaho et al., 2016), and every 5–10 years using hemispherical photography (Fleck et al., 2016), but no monitoring of canopy closure timing is included. Ground vegetation assessments are carried out, but it is only compulsory to do so once every five years, and the phenology of ground vegetation is not considered (Canullo et al., 2016).

Although Level II plots and NFIs are cited by government agencies as mechanisms for monitoring climate change impacts on forests (Bussotti and Pollastrini, 2017a; Forest Research, No date), the methods employed are not suitable for assessing climate change impacts on ecosystem dynamics. Temporal resolution and clear sampling designs are lacking to link observed changes to causal factors. Furthermore, the spatial resolution is inadequate for understanding the range of effects of climate change across different forest and site types. For example, there are only 22 Level II monitoring plots, covering seven different forest types, across the whole of the UK (Forest Research, No date). Higher levels of spatial and temporal replication, and more a focussed research design, is required.

1.3.2 Remote sensing

Satellite remote sensing has enabled the characterisation of large-scale trends in forest phenology, and played an important role in linking observed changes to temperature (Hamunyela et al., 2013; Wang et al., 2016; White et al., 2009; Wu and Liu, 2013). Moderate Resolution Imaging Spectroradiometer (MODIS) products are now the most widely used in phenology studies. Normalised Difference Vegetation Index (NDVI) and Enhanced

Vegetation Index (EVI) from MODIS imagery provide measures of surface reflectance of visible and near-infra-red radiation, and are used to assess canopy greening (Cleland et al., 2007b; Peng et al., 2017a). MODIS offers global coverage at a spatial resolution of around 1 km, capturing near-daily land surface phenology data (Zhang et al., 2003). However, a considerable degree of temporal resolution is lost due to atmospheric interference and cloud cover. For example, four out of every five days were lost due to cloud cover in one study (Ahl et al., 2006). As cloudy conditions are common in temperate regions, this can limit the ability to detect canopy phenology accurately. Differences of 10–15 days between ground-based estimates and satellite estimates of phenological transition dates are typical, depending on atmospheric conditions and the degree of landscape heterogeneity (Peng et al., 2017b; White et al., 2014). This can reduce the ability of satellite data to detect annual and spatial variation in phenology (Peng et al., 2017a). As such, ground data remain essential for validating satellite data and providing more detailed observations for understanding phenological changes at the forest-level.

Near-surface remote sensing techniques *e.g.*, using digital repeat photography from canopy platforms or unmanned aerial vehicles (Klosterman et al., 2018; Richardson et al., 2009) are new developments that offer higher spatial and temporal resolution. Through image analysis, indices of canopy greening and LAI can be derived (Klosterman et al., 2018; Wingate et al., 2015). While these methods can provide good resolution and reliable data, considerable cost and/or infrastructure is required. Ground-based methods can extend the coverage of data collection to many forests where near-surface remote-sensing is not feasible.

1.3.3 Experimental studies

Experimental research has provided important insights into potential impacts of warming (De Frenne et al., 2011; Rollinson and Kaye, 2012; Sherry et al., 2007), elevated CO_2 (Broadmeadow and Jackson, 2000; Xu et al., 2016) and canopy shading (Augspurger, 2008; Ida and Kudo, 2008) on forest biodiversity and processes. Experimental data provides a mechanistic understanding of how plants are affected by different scenarios brought about by climate change. However, experimental designs usually investigate single effects at a time, on specific species in specific locations (Baeten et al., 2010; Cleland et al., 2007b). In order to understand how interactive effects of climate change affect different species in different forests, and how communities of organisms interact in response to climate change, ongoing monitoring covering a large range of forests, with high levels of replication, is essential.

1.3.4. Citizen science

Citizen science is the involvement of non-professional researchers in scientific research (Dickinson et al., 2010). In the last decade interest in citizen science has expanded, with an increase in peer-reviewed publications on research design and data quality preceding a rise in publications using citizen science data (Follett and Strezov, 2015). It is now recognised that citizen science can contribute valuable information and is an important tool for increasing coverage in data sets through space and time (Dickinson et al., 2012; Tregidgo et al., 2013; Worthington et al., 2012). In particular, the contributions of citizen science to biodiversity monitoring in temperate regions has been recognised (Chandler et al., 2017).

Currently a number of citizen science projects involve participants in recording tree and herbaceous plant phenology. Much of this recording involves citizen scientists in submitting *ad hoc* records of first leafing, flowering and fruiting events (Nature's Calendar, 2017; Project Budburst, 2017) though some schemes encourage citizen scientists to visit the same areas to report on the development of plants through different phenophases (Beaubien and Hamann, 2011; Denny et al., 2014). Studies have demonstrated high levels of public interest and good retention rates in citizen science projects that address large-scale environmental issues and that involve considerable time commitment (Beaubien and Hamann, 2011; Frensley et al., 2017). Therefore, there is good potential to achieve more widespread ground-based monitoring of forest ecosystem dynamics through citizen science. There are many additional benefits to engaging citizen scientists in ecological research, including improved scientific literacy, and attitudinal and behavioural changes, which could play a role in influencing conservation policy (Dickinson et al., 2012; Stepemick and Green, 2015; Toomey and Domroese, 2013). Furthermore, due to funding restrictions and lack of researcher time, citizen science is the only realistic way to achieve monitoring over large geographic areas with high replication (Silvertown, 2009).

Although there is considerable momentum for engaging citizen scientists, in order to be effective, suitable research and method design is essential (Cooper et al., 2014; McKinley et al., 2017; Sunde and Jessen, 2013). Methods must be low-cost and have low requirements for technology, unless they utilise technology that is readily available to many people. Analysis methods must also be cost-effective, and require minimal specialist expertise or software. The methods used must be rigorously tested to ensure they provide useful data, comparably to more sophisticated methods used in professional research. Therefore, before engaging large-scale involvement of citizen scientists, careful development and testing of methods is needed to ensure outcomes are useful.

1.4 Aims of the thesis

The research presented in this thesis develops methods for monitoring the impacts of climate change on temperate forests that could be widely applied through citizen science. Research focuses on identifying cost-effective and practical methods, capable of detecting seasonal and inter-annual changes, across a range of forest types. Given the impacts of climate change on canopy phenology, and the lack of suitable methods for widespread monitoring of canopy phenology and herb-layer interactions, these areas are the principal focus for method development. The research presented in this thesis has been conducted in UK forests, but it is intended that the methods trialled would have broader application across temperate forests.

1.5 Outline of the thesis

The thesis consists of six chapters, including this introductory chapter. Next I present four chapters of novel research, and a final chapter that develops a synthesis and discusses future prospects for monitoring forest ecosystem dynamics in relation to climate change, using a citizen science approach. In brief, the basic outline is as follows:

- **Chapter 2: Seasonal dynamics of the herb-layer in relation to canopy closure in four Devon woodlands and the implications for monitoring impacts of climate change**
  This chapter explores the seasonal dynamics of forest understories in relation to canopy closure, based on a year of fieldwork in 2014 when four Devon woodlands were intensively monitored at monthly intervals. I explore the suitability of

different methods for monitoring overstorey canopy dynamics and understorey herb-layer dynamics in different forest types. This research highlights the importance of the spring period for herb-layer development and shows that forests within close proximity can vary considerably in their herb-layer composition and dynamics. The work demonstrates the importance of high levels of replication to monitor forest ecosystem dynamics in relation to climate change, and provides recommendations for monitoring approaches.

- **Chapter 3: A comparison of ground-based methods for obtaining large-scale, high resolution data on the spring leaf phenology of temperate tree species**
  In this chapter, I compare the phenological patterns detected by first event dates vs. time series data on individual tree canopy development of four tree species in a Devon woodland during spring 2015. Three methods of obtaining time-series data are compared: percentage estimates of leaf expansion, counts of leaf expansion within crown sections, and ground-based digital photography. Logistic growth models are used to derive estimates of leaf expansion timing and rate from time-series data, and to examine the effects of reduced temporal grain on phenological parameters. The work demonstrates the importance of methods that provide accurate information on the timing and rate of canopy development. Based on this, I provide recommendations for methods that could be widely applied through citizen science to provide more biologically meaningful data sets to investigate inter- and intra-species variation in spring leaf phenology.
- **Chapter 4: A comparison of ground-based methods for estimating canopy closure for use in phenology research**
  This chapter compares a range of cost effective and rapid assessment techniques—including smartphone photography and visual estimates—with digital hemispherical photography, to identify methods that are suitable for estimating canopy closure at large scales across different forest types. Data were collected in winter, spring, summer and autumn, across four different Devon woodlands in 2014. I compare professional image analysis software with free open-access software for analysing hemispherical and smartphone fisheye photographs. I also explore whether canopy closure estimates from smartphone photography are affected by smartphone model and camera user, and provide suggestions on how to

monitor canopy closure dynamics on a large scale. This chapter has been published in *Agricultural and Forest Meteorology*.

- **Chapter 5: Using smartphone photography with a fisheye lens to monitor canopy closure phenology**
  Building on the research in chapter 4, I test whether smartphone fisheye photography can be used to track the progress of canopy closure from winter to summer, using canopy photographs taken every other day in a Cornwall woodland during 2017. Phenological parameters derived from logistic growth models of smartphone fisheye photography data are compared with those from hemispherical photography and visual observations of leaf expansion. I also explore the effect of temporal grain, to assess whether less frequent data collection would still enable accurate predictions of canopy closure timing and rate.
- **Chapter 6: Monitoring impacts of climate change on forest ecosystem dynamics using citizen science**
  This chapter completes the thesis with a synthesis of key findings, and discusses how these can be used to inform a citizen science monitoring approach to enable widespread monitoring of forest ecosystem dynamics in relation to climate change. I discuss my progress in taking this project forwards with a trial currently underway. Areas for further research are highlighted.

2

Seasonal dynamics of the herb-layer in relation to canopy closure in four Devon woodlands and the implications for monitoring impacts of climate change

2.1 Introduction

The herb-layer in temperate forests is a key component of overall forest biodiversity, playing an important role in trophic interactions for many species (Gilliam, 2007). Herb-layer dynamics influence seedling recruitment and survival, and ultimately play a role in forest structure, composition and function (Gilliam, 2007; Thrippleton et al., 2016). However, the herb-layer has undergone substantial ecological change over the past century, leading to a loss of diversity and decline in woodland specialists (Augspurger and Buck, 2017; Keith et al., 2009; Mihok et al., 2009; Rooney et al., 2004). Light has been identified as the most important factor influencing growth and reproduction in the herb-layer (Whigham, 2004), but widespread structural homogenisation has resulted from changing management practices, leading to dramatic shifts towards more closed canopy forests (Hopkins and Kirby, 2007) with higher stand densities (Gold et al., 2006). A number of studies have attributed long-term changes in forest understorey composition to nutrient enrichment and increased shading, documenting shifts towards more nitrophilic and shade-tolerant species (Keith et al., 2009; Verheyen et al., 2012; Verstraeten et al., 2013). Other factors such as over-grazing and the increase in invasive species (Rooney et al., 2004) have also been cited as important contributing factors.

Against this background of complex change, the impacts of climate change are set to accelerate (Thom et al., 2017b). Climate change is already affecting temperate broadleaved forests, most notably with changes to tree leaf phenology resulting in earlier and more prolonged canopy leafing (Menzel and Fabian, 1999; Thompson and Clark, 2008; Vitasse et al., 2011). The phenology of overstorey trees controls the onset of light limitation in the understorey (Kato and Komiyama, 2002), and has been shown to profoundly influence understorey structure, composition and function (Hicks and Taylor, 2015; Kudo et al., 2008; Routhier and Lapointe, 2002). Givnish (1987) defined six guilds of herbaceous forest plants based on their vegetative phenology, the most significant groups being spring ephemerals, early summer, late summer and evergreen species. Spring ephemerals operate in a brief window when conditions are favourable for growth and reproduction, once temperatures have begun to rise and before the overstorey canopy closes. Early canopy closure has been found to affect their growth rates and reproductive success (Augspurger and Salk, 2017; Ida and Kudo, 2008; Kim et al., 2015). Exposure to high light levels prior to overstorey canopy closure has also been shown to be important for the growth and survival of early summer species as well as late-summer and evergreen species (Routhier et al. 2002; Rothstein and Zak 2001). In fact, some species typically considered 'shade-tolerant', may only be able to persist in deeply shaded understories because of the carbon gained prior to canopy closure (Lopez et al., 2008; Rothstein and Zak, 2001). As many forest herbs are slow colonisers with limited scope to adjust their ranges (Augspurger and Salk, 2017; De Frenne et al., 2011), their ability to adapt their phenology in line with overstorey trees is likely to affect survival.

The mechanisms controlling plant phenology vary between species and populations. A number of studies have investigated effects of warming on the phenology, growth and survival of specific herbaceous species. In warming experiments, temperature has been found to advance the phenology of some forest herbs, though different responses have been identified between species, and within species from different populations (De Frenne et al., 2011; Jacques et al., 2015). A community-scale experimental study found that at the level of functional groups, trees and tall forbs tended to advance leafing in response to warming, while short forbs and small trees did not (Rollinson and Kaye, 2012). This may have been due to greater reliance on photoperiod cues for the suite of small forb species included in the study, or it could have been that early season warming prevented herbaceous species from meeting winter chilling requirements (Rollinson and Kaye, 2012). Winter chilling is an important adaptation in many herb-layer species to avoid premature spring development and susceptibility to unpredictable early season temperatures due to risk of frost damage (Laube et al., 2014). Such evolutionary mechanisms could limit the ability of some herbaceous species to adjust their phenology (Augspurger and Salk 2017).

Aside from phenological shifts, climate change is driving changes in vegetation composition, with a trend towards cold-tolerant species being replaced by warmth-preferring species, in a process known as thermophilization. While higher canopy openness has been associated with higher levels of herb-layer diversity (Duguid et al., 2013), there is evidence that forests with open canopies could be more vulnerable to some effects of climate change. De Frenne et al. (2015) conducted a large-scale study of forest herb-layer communities across Europe and North America, and found that the thermophilization effect was offset in forests with more densely closed canopies. By contrast, under more open canopies, tall, competitive plants with preference for warmer temperatures had expanded their dominance (De Frenne et al., 2013). The thermophilzation effect could accelerate where canopies are opened up through climate change-induced drought or pest and pathogen outbreaks. This could have implications for seedling dynamics, as dense herb-layer vegetation can severely limit light, inhibiting tree regeneration altogether, or favouring more shade-tolerant tree seedlings, ultimately affecting overstorey composition (Thrippleton et al., 2016). However, at present our ability to predict longer term impacts of climate change on the herb-layer and regeneration is severely limited by the lack of spatial and temporal breadth in studies investigating understorey-overstorey interactions (Thrippleton et al., 2016)

Given the importance of the herb-layer for forest function and biodiversity, obtaining a better understanding of the likely impacts of climate change is imperative for conservation. However, relatively few studies have investigated herb-layer dynamics in relation to climate change, compared to the number of studies on trees (Rollinson and Kaye, 2012). Studies that have been conducted have generally focussed on a small number of species or woodlands. However, marked differences in herb-layer response to environmental change have been observed between and within forests. Murphy and McCarthy (2014) found different magnitudes of phenological change on north and south-facing slopes within a single forest complex. In a long-term study of herb-layer dynamics, Verstraeten et al. (2013) found stronger declines in herb-layer diversity, associated with shading and nutrient enrichment, on neutral sites compared to acidic sites. The way in which the herb-layer responds to early canopy closure and warming will relate to overstorey structure, composition and phenology (Dion et al., 2017; Routhier and Lapointe, 2002; Vanhellemont et al., 2014), competition dynamics in the understorey (Duguid et al., 2013), and a range of site factors including soil type (Dahlgren et al., 2007; Small and McCarthy, 2005), microclimate (Chen et al., 1999; von Arx et al., 2013), and interacting environmental pressures (Baeten et al., 2010; Jackson et al., 2013). Therefore, there is a need to monitor the response of herb-layer species in relation to their ecological context, at a range of spatial scales.

As well as studying herb-layer dynamics at a range of spatial scales, there is a need to monitor dynamics at different temporal scales. Many studies have been published in recent years that look at long-term changes in the herb-layer, comparing historic data with contemporary surveys (Keith et al., 2009; Rooney et al., 2004; Vanhellemont et al., 2014; Verheyen et al., 2012; Verstraeten et al., 2013). However, these surveys tend to provide snapshots in time, often ignoring seasonal variation altogether. There is a surprising lack of monitoring to investigate how herb-layer dynamics vary seasonally across successive years. In fact, I could find only one study that considered the interaction of long-term, annual and seasonal changes on the herb-layer (Murphy and McCarthy, 2014). This study involved resurveying plots in spring, summer and autumn, over two consecutive years, thirteen years after initial surveys. The study identified a loss of phenological niche separation between species across the growing season, over the thirteen years. This loss of complementarity between species phenologies has also been observed in trees (Roberts et al., 2015), and is likely to result in increasing competition and reduction in biodiversity over time. However, the authors noted that more frequent inter- and intra-annual sampling would be needed to understand linkages between overstorey-understorey phenology, and annual variation in climate.

While there is growing recognition of the need for more detailed and widespread monitoring of herb-layer dynamics, the time-consuming nature of such monitoring is likely the reason such studies are rare (Inghe and Tamm, 1985). In order to achieve widespread data collection, with high levels of spatial and temporal replication, effective monitoring approaches that are cost effective and efficient are needed, ideally using a citizen science approach. Citizen science is the involvement of non-professional scientists in scientific research (Dickinson et al., 2012), and this definition includes many people involved in day-to-day forest management, such as forest rangers and wardens, as well as volunteers. Tree phenology data collection has been bolstered in recent years through the rise in citizen science (Elmore et al., 2016; Jeong et al., 2013; Mayer, 2010), enabling data collection at a much larger scale than would otherwise be achievable. A similar approach to studying the seasonal and annual changes in forest plant dynamics could enable new insights that are not possible with current methods. Citizen science projects in Canada and the UK already involve the public in recording first flowering events in woodland flora (Beaubien and Hamann, 2011; Collinson and Sparks, 2008). The USA National Phenology Network involves people recording forb phenophase status and intensity through time, providing more detailed information on leaf emergence timing across a population (Denny et al., 2014). A community-scale approach, where citizen scientists record the dynamics of the herb-layer community in relation to light levels and overstorey dynamics, with spatial replication within and between forests, would provide valuable information to help understand interactions at the forest-level, and across forested landscapes.

Given the importance of light for understorey plant dynamics, and the relevance of canopy closure to forest microclimates, monitoring the understorey in relation to light levels and overstorey canopies is essential. Direct measurement of understorey light is practically difficult and resource intensive, requiring access to highly expensive specialist equipment (Keeling and Phillips, 2007). Furthermore, accurate characterisation requires long-term measurement, which negates the value of this method for measuring changes over short periods. As an alternative, hemispherical photography is commonly used to infer understorey light from the canopy structure (Frazer et al., 1997; Gonsamo et al., 2013; Whitmore et al., 1993). Photographs can be analysed to obtain solar radiation indices, such as global site factor (GSF), and more straightforward indices based purely on canopy geometry, such as canopy openness (Rich et al., 1999). GSF is the proportion of solar radiation penetrating the canopy, relative to that in the open (Anderson, 1964). Specialist analysis software is required to compute GSF, which calculates canopy gap position in relation to the solar path, using inputted information on site latitude, longitude and directional alignment of the photograph (Rich et al., 1999). By contrast, canopy openness represents the proportion of visible sky that is unobstructed by the canopy, when viewed from a single point on the ground. When analysed with specialist software, the position of canopy gaps in relation to zenith angle is computed to correct for lens distortion, but gap position in relation to the solar path is not considered (Rich et al., 1999). If canopy openness provides comparable estimates to GSF under a range of canopy conditions, it may provide options for more rapid assessment as part of widespread monitoring efforts.

In addition to light and canopy conditions above the herb-layer, light reaching the ground-layer is also important for seedling dynamics (Gilliam, 2007). Where herb-layer cover is high and structurally dense, ground-level light can be severely limited, reducing the potential for seedling recruitment and survival (Aubin et al., 2000; Jefferson, 2008; Royo and Carson, 2006). Despite the importance of ground-level light, few studies consider ground-level light conditions separately to light reaching the herb-layer (Thrippleton et al., 2016). The extent to which GSF/canopy openness below the herb-layer can be characterised as a function of GSF/canopy openness above the herb-layer, will be important to consider.

In terms of monitoring the herb-layer, it is important to understand what attributes will provide meaningful data, given the need for relatively low-tech, rapid and cost effective methods. In experimental studies investigating impacts of early canopy closure and warming on plant performance, gas exchange, chlorophyll fluorescence and leaf biochemistry are frequently analysed to measure photosynthetic efficiency and stress (Ida and Kudo, 2008; Jacques et al., 2015; Rothstein and Zak, 2001), but are unsuitable for widespread monitoring programmes. Similarly, biomass and specific leaf area are often used to assess growth (De Frenne et al., 2011; Ida and Kudo, 2008; Kim et al., 2015; Routhier and Lapointe, 2002), but are unsuitable for widespread monitoring as they are labour intensive and require destructive sampling. Long-term monitoring of herb-layer dynamics usually relies on assessment of species composition and abundance, species richness and species diversity (Murphy and McCarthy, 2014; Scheller and Mladenoff, 2002; Vanhellemont et al., 2014; Verheyen et al., 2012; Verstraeten et al., 2013). It will be important to assess to what extent these attributes capture seasonal variation in the herb-layer. Bare ground cover could be a useful attribute to assess, as it can show both seasonal and inter-annual variation (Hicks and Taylor, 2015; Murphy and McCarthy, 2014). In addition, information about the structure of herb-layer vegetation obtained from point frequency and height estimates could be useful for monitoring changes in herb-layer productivity and biomass (Axmanova et al., 2012; Brathen and Hagberg, 2004). It is important to assess the extent to which these different attributes characterise seasonal variation in herb-layer dynamics across different woodlands.

In this study I carried out detailed monitoring of canopy and understorey dynamics in four Devon woodlands, over the course of one growing season. This study did not seek to explain spatial patterns of understorey composition in terms of environmental variables, which are highly site specific (Burton et al., 2011; Chudomelova et al., 2017). Instead, I aimed to: a) identify seasonal patterns of canopy openness and understorey light (GSF), above and below the herb-layer, and interrogate how these patterns varied between and within woodlands; b) identify seasonal patterns of herb-layer dynamics and the extent to which these varied between and within woodlands; and c) identify which methods are most suitable for widespread monitoring of forest canopies and understories in relation to climate change.

2.2 Methods

2.2.1 Study woodlands and data collection

The woodlands included in this study were all broadleaved ancient semi-natural woodlands (ASNW), but differed in terms of site history, compositional and topographical features (Table 2.1). Woodland communities were assigned using the National Vegetation Classification (NVC) (Hall et al. 2004), and classification was based on species composition across the whole woodland site (see Appendix 2.1: Table A2.1, for additional detail on woodland composition and how NVC communities were assigned). Although all woodlands were in relatively close proximity, they differed in their National Vegetation Classification (NVC) classes, and in their dominant species (Table 2.1). These differences capture some of the diversity found in UK woodlands, in order to identify monitoring approaches applicable across a range of forests types.

In each woodland, a 0.3 ha area was randomly selected, and six 3 x 3 m plots were established to represent a range of canopy conditions. This was done by visual assessment in the summer of 2013. Two plots were chosen to represent ‘dense’, ‘intermediate’ and ‘open’ canopies. These categories were chosen to be relative to conditions within a woodland, and did not necessarily correspond absolutely between woodlands. Fixed point 5-m transects were also established through each plot. Plots were monitored on a monthly basis from February to December 2014. Hunshaw and Newton Mill were monitored a week prior to Hardwick and Whitleigh each month.

Table 2.1. Location, size, NVC class and soil type information for four Devon woodlands. NVC class is for the whole woodland and based on Hall et al. (2004). Soil type obtained from Cranfield University (2018).

Woodland	**Size (ha)**	**Aspect**	**Site history and management**	**NVC class based on whole woodland composition**	**Dominant tree species in 0.3 ha area where plots were selected**	**Dominant herb-layer species in 0.3 ha area where plots selected**	**Soil type**
Hardwick Wood (50°22'N, 4°4'W)	22	Flat	Urban fringe ASNW, owned by Woodland Trust. Extensive wind-blow in 1990 storms: some replanting and extensive regeneration has occurred.	W8e *Fraxinus excelsior - Acer campestre - Mercurialis perennis* (*Geranium robertianum* sub-community)	*Fraxinus excelsior, Acer pseudoplatanus*	*Hyacinthoides non-scripta, Urtica dioica, Mercurialis perennis, Galium aparine*	Free-draining slightly acid but base-rich
Hunshaw Wood (50°55'N, 4°7'W)	18	S	ASNW upland oak wood SSSI in favourable condition. Owned by Clinton Devon Estates. Small-scale management to reduce sycamore and plant oak saplings.	W16b *Quercus spp. - Betula spp. - Deschampsia flexuosa* (*Vaccinium myrtillus - Dryopteris dilatata* sub-community)	*Quercus robur, Fagus sylvatica, Sorbus aucuparia, Corylus avellana*	*Vaccinium myrtillus, Dryopteris dilatata, Blechnum spicant*	Free-draining acid loam over rock
Newton Mill (50°52'N, 4°15'W)	25	NE	Privately owned, former oak coppice. Coppicing being restored in parts of the site. Some deer browsing evident.	W11a *Quercus petraea - Betula pubescens - Oxalis acetosella* (*Dryopteris dilatata* sub-community)	*Quercus robur, Corylus avellana, Fagus sylvatica*	*Hyacinthoides non-scripta, Milium effusum, Dryopteris dilatata*	Free-draining slightly acid loam
Whitleigh Wood (50°25'N, 4°8'W)	20	N	Urban ASNW, owned by Woodland Trust. Removal of *Prunus laurocerasus* and *Rhododendron* from understorey in the last 20 years.	W10a *Quercus robur - Pteridium aquilinum - Rubus fruticosus* (typical sub-community)	*Quercus robur, Betula pendula, Corylus avellana*	*Dryopteris dilatata, Rubus fruticosus, Pteridium aquilinum, Lonicera periclymenum*	Free-draining acid loam over rock

Overstorey dynamics and understorey light

In order to monitor seasonal changes in the overstorey canopy and understorey light regime, hemispherical photographs were taken every month, using a Nikon Coolpix 990 3.34 MP camera with Nikon Fisheye Converter FC-E8 lens (Nikon Corporation, Tokyo, Japan). One photograph was taken in the plot centre to assess light levels reaching the herb-layer, with the camera mounted and levelled on a tripod at 1.2 m above the ground, to eliminate any shading influence of the herb-layer vegetation. In addition, five photographs were taken at ground-level, at 1 m intervals along the plot transect, to assess how ground-level light dynamics varied through the year. A circular bubble level was used to level the camera, and a small beanbag was placed underneath the camera to achieve a flat orientation. The camera timer function was used to enable the photographer to move out of view of the image before each photograph was taken. For all photographs, a small, bright coloured marker was placed just inside the camera's field of view, to mark north. To reduce risk of over-exposure and to obtain even lighting across the image, photographs were taken under overcast skies where possible, or early/late in the day to avoid direct sunlight entering the lens (Rich, 1990). The automatic aperture and shutter settings were used, and the camera's histogram function was reviewed after image capture to manually check for overexposure (Beckschafer et al., 2013). When required, the exposure settings were manually lowered to -2.0 EV, the minimum limit on this camera model.

All images were analysed in HemiView Canopy Analysis Software v.2.1 (Delta-T Devices, Cambridge, UK) to derive global site factor (GSF) and canopy openness values for each plot, in each month of the year. For both GSF and canopy openness estimation, HemiView calculates the canopy gap fraction—defined as the proportion of unobstructed sky in a given region of the projected image plane (Frazer et al., 1997). In order to calculate gap fractions, HemiView separates black pixels (canopy) and white pixels (sky), according to given threshold values. Thresholds must be manually set using this software package. This was done individually for each photograph to achieve the best contrast. This was important as photos had to be taken under a range of sky conditions on days when monitoring was scheduled, and therefore applying a universal threshold would likely result in considerable error. In cases where tree trunks or herb-layer vegetation appeared brighter than background sky, photos were edited in ImageJ (Rueden, 2016) prior to analysis in

HemiView. This editing involved blacking out the trunks or herb-layer, so they could be correctly differentiated from the sky during image analysis.

Canopy openness is a straightforward measure of canopy structure, representing the sum of all gap fraction values in the hemispherical image. In HemiView, gap fraction values are weighted according to zenith angle, to account for the distortion of the hemispherical lens (Frazer et al., 1997). To correct for lens distortion during image analysis, lens settings were set to the Coolpix 900 setting, which is pre-programmed in HemiView, and is appropriate for analysing images from the Coolpix 990 (Hale and Edwards, 2002). GSF—the proportion of solar radiation penetrating the canopy, relative to that in the open (Anderson, 1964)—is a more complex index of solar radiation, which requires knowledge of site latitude and longitude, and correct alignment of the photograph with compass bearings. This enables the estimation of direct and diffuse radiation based on the position of canopy gaps in relation to the solar path (Rich et al., 1999). In order for GSF to be calculated, site coordinates were inputted into HemiView, and photos were aligned to north using the north marker placed in the photos during image capture. Each image was then analysed to give GSF and canopy openness values, which were multiplied by 100 to convert them to percentages.

Understorey plant dynamics

Plant composition in each plot was recorded every month by estimating percent cover of vascular plant species. Percent bare ground cover was also recorded. In addition, 50 point frequency measurements were made along each transect (at 0.1 m intervals). Vegetation height was measured at 1 m intervals along the transect, using a metre ruler and estimating by eye the height below which 80% of the vegetation was growing (Stewart et al., 2001). An average was then derived from the five estimates along the transect. At the same intervals, soil temperature readings were taken at a depth of 15 cm using a temperature probe (Fisherbrand, ISO 17025, A2LA, NIST, Fisherbrand Scientific UK), and averaged across the transect.

2.2.2 Statistical analyses

Comparison of GSF and canopy openness

GSF and canopy openness, obtained from both above and below herb-layer photographs, were compared. Linear regression was used to assess relatedness of GSF and canopy openness values across all woodlands, and at each individual woodland. Analysis of Covariance (ANCOVA) was used to find out whether the relationships between GSF and canopy openness were the same across the four woodlands. The same statistical methods were used to investigate relationships between above and below herb-layer measurements. I also assessed whether GSF and canopy openness were similarly consistent measurements. I did this by comparing the coefficients of variation derived for each plot over the June–August period when very little change in overstorey canopies is expected.

Temporal and spatial variation in canopy openness

To assess heterogeneity in the understorey light environment of each woodland, I computed standard deviations of canopy openness values for each month. These were plotted, to visualise absolute variation in canopy openness between months. Coefficients of variation were then calculated to assess relative variation in canopy openness in different months. In order to test whether plots within a woodland were similar in terms of their above herb-layer canopy openness, I carried out a two-factor analysis of variance without replication, followed by pairwise comparisons of plots. This was done using data from all months initially, and then using data from summer months only (May–September). In each woodland, plots were then grouped based on statistical similarity between their summer canopy openness values, as these were deemed to be most important in terms of influencing light availability for herb-layer growth. These canopy openness groups were used throughout the rest of the analysis to compare trends through time in relation to relative within-woodland canopy openness levels. Two-way ANOVA without replication, followed by pairwise comparisons, were also used to compare plots at each woodland in terms of their canopy openness below the herb-layer, between May–September.

Understorey plant dynamics

Mean Ellenberg values for light, nutrients, moisture and pH were derived for each woodland based on species presence using the corrected Ellenberg values for British flora (Hill et al., 2004). In addition, species composition was summarised by growth-form category, using the criteria from Hill et al. (2004).

Plant composition data were analysed using PRIMER 6 v.1.13 and PERMANOVA+ (Clarke and Gorley, 2006). All data were transformed using the square-root transformation. I first compared overall species composition across all woodlands, by deriving the Bray-Curtis Similarity and conducting a one-way repeated measures PERMANOVA with 999 permutations, followed by pairwise comparisons of sites for each month of the year. Multi-dimensional Scaling (MDS) was used to visualise relationships between woodlands. This method was repeated in order to compare woodlands in terms of growth-form composition. I then assessed the spatial and temporal variation in species composition at each woodland separately. Bray-Curtis Similarity was derived for each woodland, and MDS plots were used to visualise patterns of change over time and relationships between plots according to canopy openness categories. To compare seasonal changes in composition I conducted one-way repeated measures PERMANOVAs for each woodland, followed by pairwise comparisons of months. Due to lack of replication at the level of plot canopy openness categories, I could not test for differences between plots, within the repeated measures design. Therefore, a separate one-way PERMANOVA was carried out for each woodland to investigate differences between plots, followed by pairwise comparisons. To better understand species-level changes through time, in relation to plot canopy openness, I also plotted seasonal change in cover for the dominant species at each woodland, for each canopy openness category.

Species richness and Shannon diversity were calculated for each plot, in each month of the year. To investigate changes through time in richness and diversity, I conducted one-way repeated measures ANOVAs, followed by pairwise comparisons. To investigate differences between plots, I carried out two-way ANOVAs without replication. This analysis was repeated for soil temperature and all vegetation structural parameters: point frequency, vegetation height and bare ground cover.

All statistical analyses were carried out in R 3.4.3 (R Core Team, 2017), except where I have specified that PRIMER was used. Mauchly's sphericity test was carried out for repeated-measures ANOVAs, and where data did not meet assumptions for sphericity, the Greenhouse-Geisser corrected *p*-value was used. Where data residuals did not meet the assumptions for normality, I used the Aligned Rank Transform (ART) procedure in the R package ARTool (Kay and Wobbrock, 2016), followed by repeated-measures ANOVAs. The ART procedure is an appropriate way to analyse datasets with non-normal distributions, and is described in more detail by Wobbrock et al. (2011). I then performed *post hoc* contrasts between months using estimated marginal means with the emmeans package (Lenth, 2017), which can be used with the ART procedure. For comparisons of plots where residuals were not normally distributed, I used a Kruskal-Wallis test, as a two-way ANOVA without replication cannot be conducted using the ART procedure.

2.3 Results

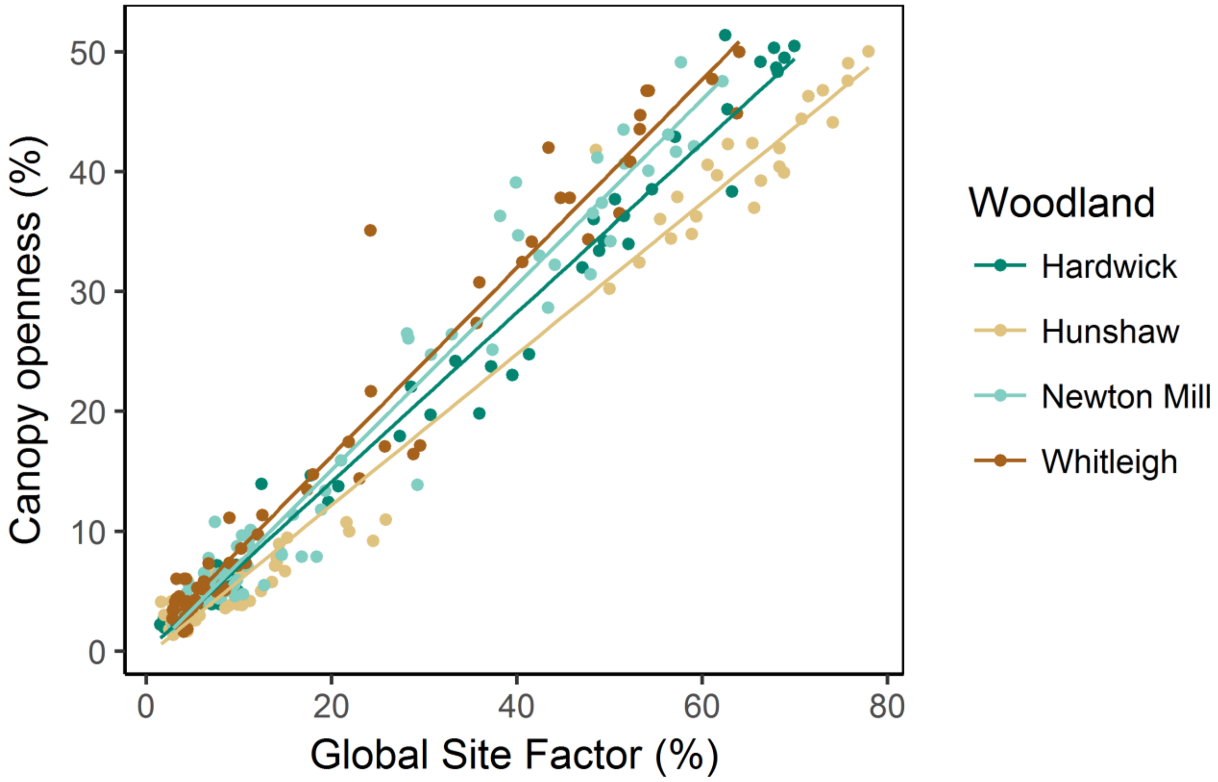
2.3.1 Canopy openness and understorey light

Global site factor (GSF) and canopy openness were highly related (Table 2.2) for both above and below herb-layer comparisons at all woodlands ($R^2 > 0.96$, $p < 0.001$). The slope of this relationship varied between woodlands, with significant differences found between all woodlands except Newton Mill and Whitleigh (Fig. 2.1). Hunshaw, which had a south-facing aspect, had the highest GSF values relative to canopy openness, and Newton Mill and Whitleigh (with a northeast and north-facing aspect respectively) had the lowest GSF values relative to canopy openness. Canopy openness was a more consistent measure than GSF, as it remained more constant from June–August when very little change in the tree canopy would be expected. The average among-plot coefficient of variation for canopy openness across all woodlands in this period was 7.31 %. By contrast, GSF was much more variable, with an average among-plot coefficient of variation of 21.46 % across the woodlands. For this reason, I used canopy openness to characterise the understorey light environments of the sampled plots.

Table 2.2. Proportion of variation explained (R^2) and statistical significance (p) for relationships between global site factor (GSF) and canopy openness (CO), above and below the herb-layer, for all woodlands combined, and for individual woodlands.

Comparison	All sites		Hardwick		Hunshaw		Newton Mill		Whitleigh	
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
Above herb-layer: GSF v CO	0.95	<0.001	0.98	<0.001	0.98	<0.001	0.96	<0.001	0.98	<0.001
Below herb-layer: GSF v CO	0.97	<0.001	0.99	<0.001	0.99	<0.001	0.98	<0.001	0.98	<0.001
Above GSF v Below GSF	0.95	<0.001	0.94	<0.001	0.96	<0.001	0.96	<0.001	0.98	<0.001
Above CO v Below CO	0.94	<0.001	0.95	<0.001	0.98	<0.001	0.97	<0.001	0.99	<0.001

Fig. 2.1. Relationship between global site factor (%) and canopy openness (%) across the four woodlands. Analysis of covariance showed similar slope relationships between Newton Mill and Whitleigh ($F_{1,128} = 0.18$, $p = 0.67$). Different slope relationships were found between other woodlands: Hardwick and Hunshaw ($F_{1,128} = 23.04$, $p < 0.001$), Hardwick and Newton Mill/Whitleigh ($F_{2,192} = 7.15$, $p < 0.001$) and Hunshaw and Newton Mill/Whitleigh ($F_{2,192} = 32.83$, $p < 0.001$).



Canopy openness above the herb-layer showed similar broad seasonal trends across all woodlands and plots (Fig. 2.2). In absolute terms, heterogeneity in canopy openness within woodlands was highest during winter, and patterns of within woodland heterogeneity varied between woodlands in spring and late autumn. Hardwick Wood showed high variation in canopy openness in April, and Newton Mill showed high variation in canopy openness in May. By contrast, Hunshaw and Whitleigh showed relatively low-levels of between-plot variation in canopy openness in April and May. Hardwick also showed much higher variation in canopy openness in November than other woodlands. All woodlands showed low between-plot variation in canopy openness during summer and early autumn months (June–October). However, relative variation in canopy openness between plots was highest between May–September when average between-plot coefficient of variation ranged between 31.81–35.52 % across the woodlands, compared to 5.20–19.23% across the woodlands in other months of the year.

When canopy openness between plots in each woodland were compared across the whole year, I only identified significant differences in canopy openness values between plots at Hardwick Wood (ANOVA: $F_{10,5} = 11.312$, $p < 0.001$). Plots that were the most open in summer, were not necessarily the most open at other times of the year (Fig 2.3). When plots were compared using summer values only (May–September), significant differences were identified between plots within all woodlands (Fig. 2.3). These differences were more subtle than I had predicted from my *a priori* judgements based on visual assessment of the summer canopy. This meant that there were not always clear differences between plots originally classed as 'dense' and 'intermediate', or 'intermediate' and 'open'. In most cases, rank order was still the same as initially predicted. I grouped plots according to whether they were statistically similar in their summer canopy openness (Fig. 2.3), and visualised this with colour coding. Due to the higher than expected similarities between some plots, I did not have replicates for all canopy openness levels, meaning that I could not statistically test for interaction effects between month of the year and plot-level canopy openness on herb-layer dynamics.

There was a strong relationship between above and below herb-layer canopy openness at all woodlands (Table 1). However, I did detect that the herb-layer effect on ground-level light availability varied between woodlands. The slope of the relationship varied by a small but statistically significant amount, showing that herb-layer shading had a stronger effect at Hardwick and Whitleigh, than at Hunshaw and Newton Mill (Fig. 2.4). At Hardwick, the effect of herb-layer shading in more open canopy plots was particularly apparent, as open plots and dense plots had similar below herb-layer canopy openness in summer (Fig 2.3).

Fig. 2.2. Temporal dynamics of canopy openness heterogeneity above the herb-layer, across each woodland. Error bars represent standard deviation of canopy openness across the six plots in each woodland in each month.

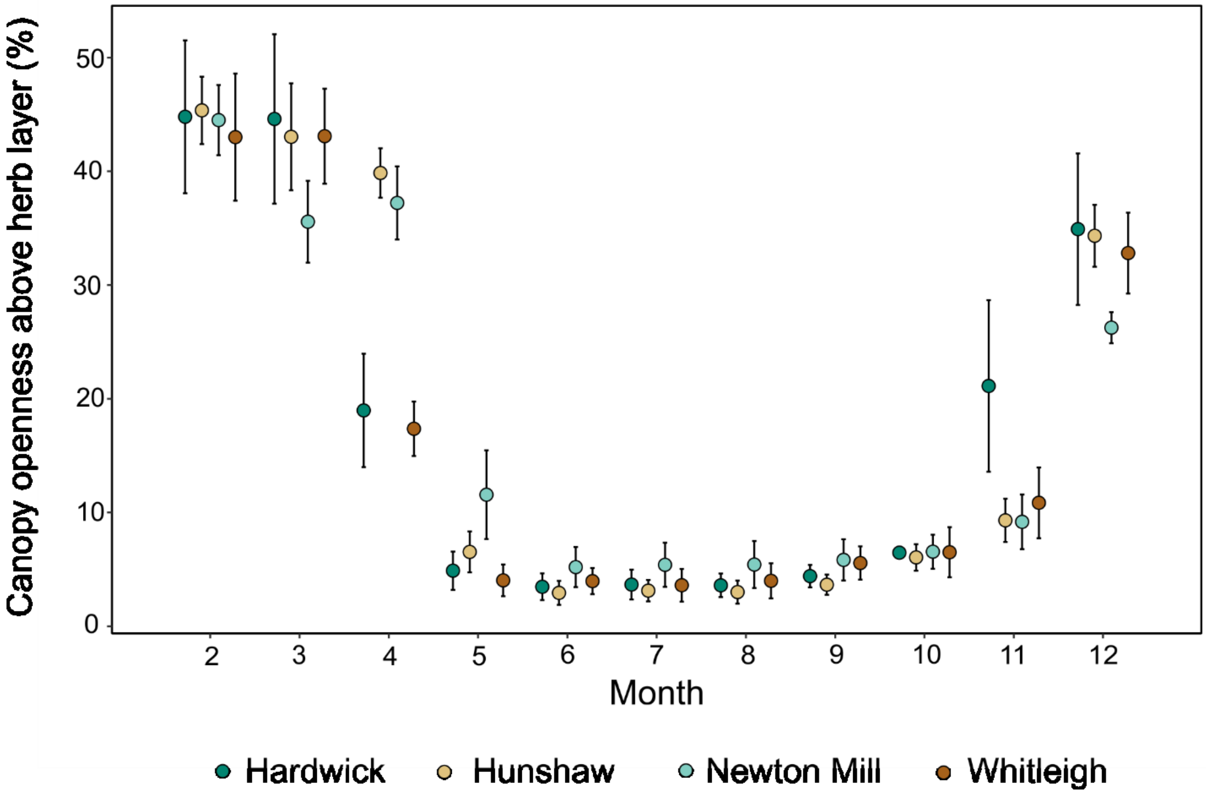


Fig. 2.3. Change in canopy openness (%) through months of the year at each woodland. Statistical relationships between plots based on May-September canopy openness values are shown by the hexagonal diagrams: the numbers 1–6 represent the six plots in each woodland, and connecting lines show which plots were statistically similar. Colours correspond to above herb-layer canopy openness, with darker colours representing plots with lower canopy openness.

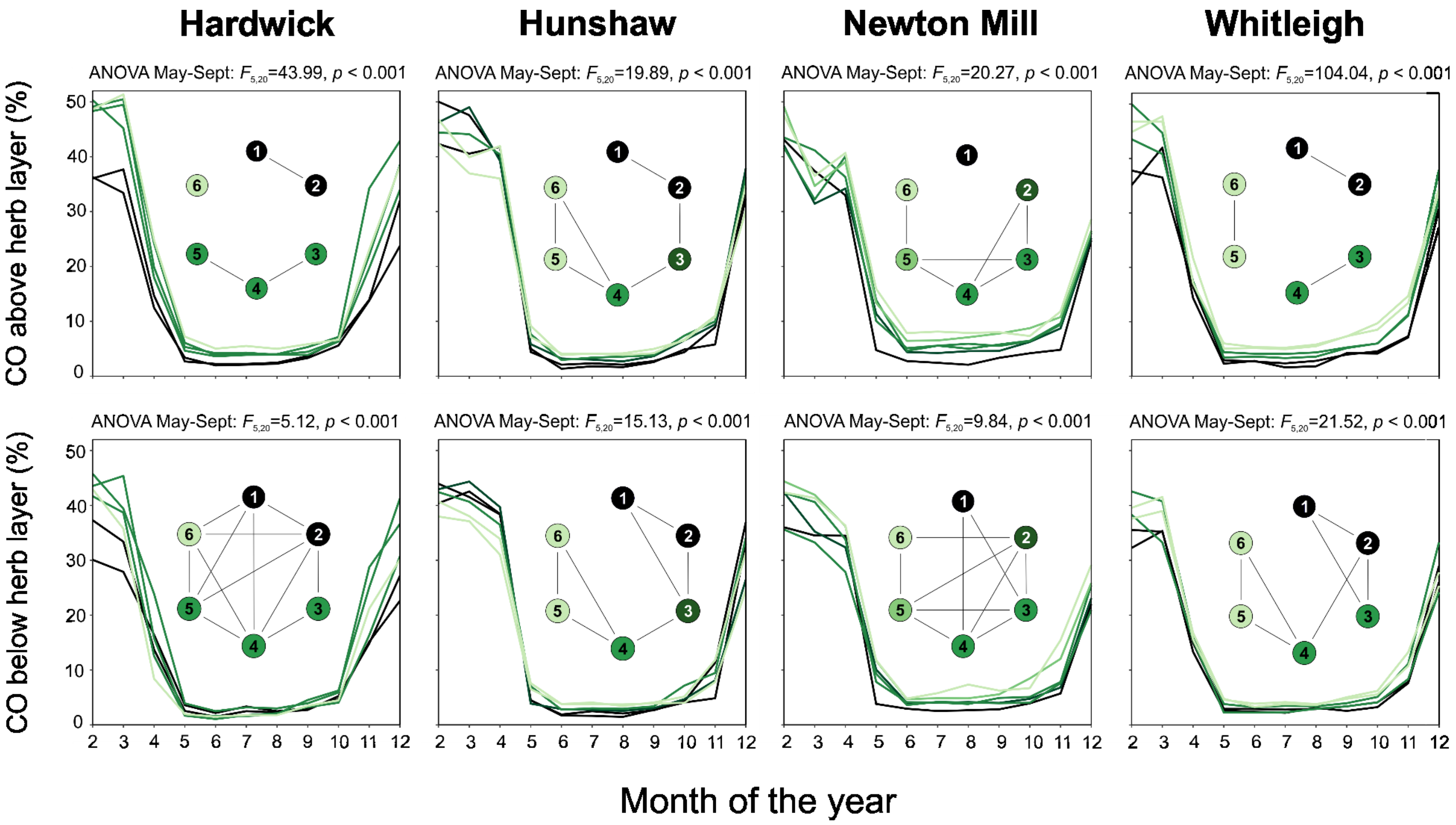
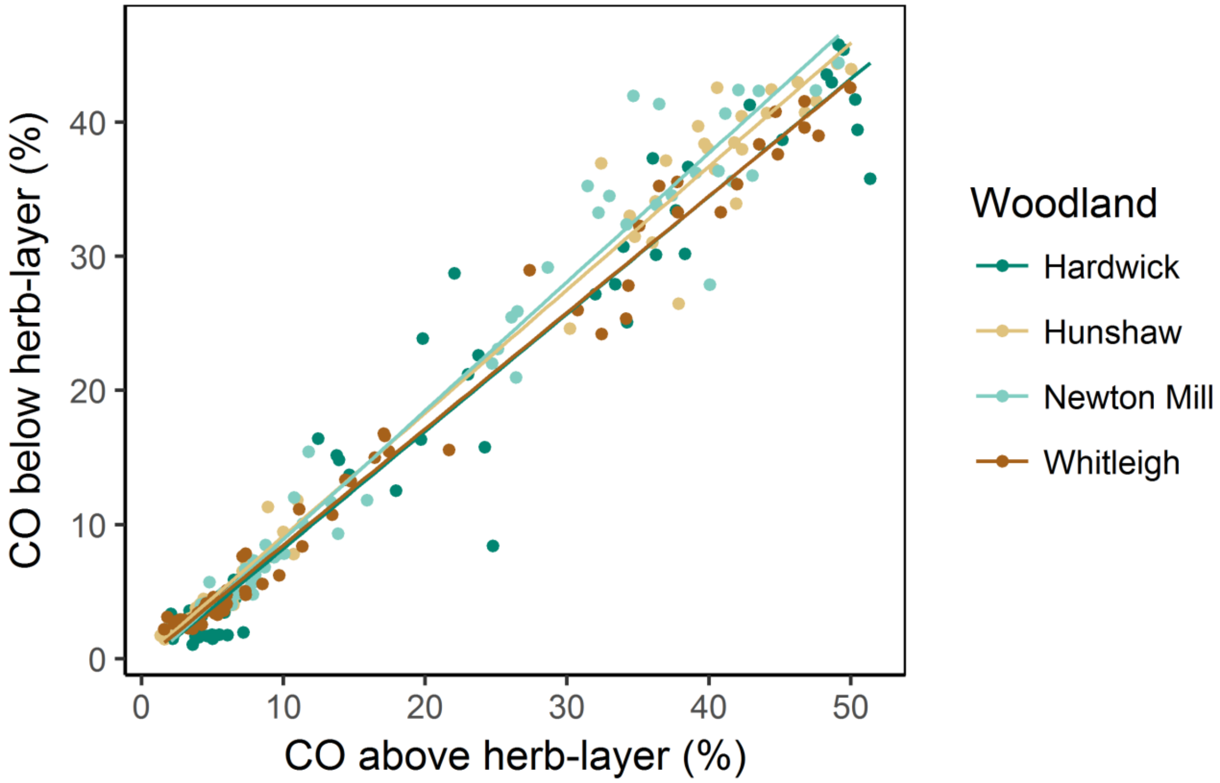


Fig. 2.4. Relationship between canopy openness (CO) above the herb-layer and CO below the herb-layer, for the four woodlands. There were similar slope relationships between Newton Mill and Hunshaw (ANCOVA: $F_{1,128}$ = 2.51, p = 0.12), and between Hardwick and Whitleigh (ANCOVA: $F_{1,128}$ = 0.09, p = 0.77). Different slope relationships were found between the other woodlands: Hardwick and Hunshaw/Newton Mill (ANCOVA: $F_{2,192}$ = 3.89, p = 0.022) and Whitleigh and Hunshaw/Newton Mill (ANCOVA: $F_{2,192}$ = 7.08, p = 0.001).



2.3.2 Understorey plant dynamics

Average monthly temperatures for Devon in the year of study were below average for winter, spring and autumn (Fig. 2.5). Soil temperature patterns were fairly consistent between plots at each woodland (Fig. 2.6). No differences were found in soil temperature between plots at Hunshaw (ANOVA: $F_{10,50}$ = 2.33, p =0.06) or Whitleigh (ANOVA: $F_{10,50}$ = 2.13, p =0.08). Significant differences were identified at Hardwick (ANOVA: $F_{10,50}$ = 7.53, $p <$ 0.001), with plots 4 and 6 different to plots 1 and 2 ($p < 0.005$), but all other plots were similar ($p > 0.05$). Significant differences were also found between plots at Newton Mill (ANOVA: $F_{10,50}$ = 4.68, p =0.001), with differences between plot 1 and 6 ($p < 0.001$) and plot 5 and 6 ($p = 0.03$), but all other plots were similar ($p > 0.05$). However, these differences were fairly small in absolute terms; the maximum difference in soil temperature in any one month was less than 2° C, and on average the difference between plots was less than 0.8° C.

Woodlands varied in terms of plot mean Ellenberg values for soil nutrients and pH, though showed little difference for light and moisture (Table 2.3). Plots at Hardwick showed a comparatively eutrophic and base-rich signal, while plots at Hunshaw showed a nutrient-poor and acidic signal. All woodlands differed in terms of species composition (Fig. 2.7. Repeated-measures PERMANOVA: Pseudo-$F_{33,220}$ = 11.06, p = 0.001; pairwise comparisons revealed all woodlands differed in all months: $p < 0.05$). There were also significant differences between woodlands based on growth-form composition (Table 2.4, repeated-measures PERMANOVA: Pseudo-$F_{33,220}$ = 6.72, p = 0.001, Appendix 2.1: Table A2.2), though Hunshaw and Whitleigh were similar (pairwise comparisons between Whitleigh and Hunshaw: $p > 0.05$ for all months). All other woodlands were different in terms of growth-form composition, across all months of the year, with the exception of Hunshaw and Newton Mill, which were similar in November only (p = 0.124). Hunshaw and Whitleigh, both lacked spring ephemerals, and Whitleigh also lacked early summer species, which contributed strongly to composition and seasonal variation at Hardwick and Newton Mill (Table 2.5). Hardwick and Newton Mill exhibited strong seasonal changes in composition (Fig. 2.8 and 2.9), with spring being the most dynamic season. By contrast, Hunshaw and Whitleigh showed much less seasonal distinction in terms of compositional change (Fig. 2.10 and 2.11). Due to the differences between woodlands, their seasonal vegetation dynamics are considered separately.

Table 2.3. Structural and compositional features of four Devon woodlands. NVC class was based on an assessment of the composition of the whole woodland, using Hall et al. (2004). Stand density was estimated from the 0.3 ha area from which the six survey plots were selected. Mean Ellenberg values based on Hill et al. (2004), were calculated based on species composition in the six 3 x 3 m plots at each woodland.

Woodland	**Size (ha)**	**NVC class (based on whole woodland)**	**Soil type**	**Stand density (trees/ha)**	**Aspect**	**Mean growing season GSF (%)**	**Mean Ellenberg values (averaged across the six surveyed plots)**			
							Light	**Nutrients**	**Moisture**	**pH**
Hardwick Wood (50°22'N, 4°4'W)	22	W8e *Fraxinus excelsior - Acer campestre - Mercurialis perennis* (*Geranium robertianum* sub-community)	Free-draining slightly acid but base-rich	1360	Flat	5.6	4.6	6.5	5.6	6.6
Hunshaw Wood (50°55'N, 4°7'W)	18	W16b *Quercus spp. - Betula spp. - Deschampsia flexuosa* (*Vaccinium myrtillus - Dryopteris dilatata* sub-community)	Free-draining acid loam over rock	556	S	6.8	5.2	4.0	5.5	4.2
Newton Mill (50°52'N, 4°15'W)	25	W11a *Quercus petraea - Betula pubescens - Oxalis acetosella* (*Dryopteris dilatata* sub-community)	Free-draining slightly acid loam	456	NE	10.5	4.8	5.2	5.5	5.3
Whitleigh Wood (50°25'N, 4°8'W)	20	W10a *Quercus robur - Pteridium aquilinum - Rubus fruticosus* (typical sub-community)	Free-draining acid loam over rock	1111	N	5.1	5.1	5.1	5.6	5.2

Table 2.4. Plot composition at each woodland by plant growth form. Numbers represent the percentage contribution of each growth form to the total composition, averaged across plots and the year. Ph = Phanerophyte, Pn = Nanophanerophyte, Ch = Chamaephyte, hc = Hemicryptophyte, Gn = Non-bulbous geophyte, Gb = Bulbous geophyte, Th = Therophyte. Classifications based on Hill et al. (2004). Additionally, hemicryptophytes and non-bulbous geophytes have been classified into sub-categories: pteridophytes (pt) and flowering herbs (hb).

Woodland	**Ph**	**Pn**	**Ch**	**hc (pt)**	**hc (hb)**	**Gn (pt)**	**Gn (hb)**	**Gb**	**Th**
Hardwick	35	11	1	8	13	0	2	17	13
Newton Mill	2	7	7	28	18	1	3	34	0
Hunshaw	8	43	0	34	0	11	0	0	3
Whitleigh	13	38	0	37	0	12	0	0	0

Table 2.5. Plot composition at each woodland by phenological guild. Numbers represent the percentage contribution of each guild to the total composition, averaged across plots and the year. Classifications based on Givinish (1987). Spring ephemerals are species that leaf in early spring and senesce prior to/during canopy closure; early summer species are those that leaf during spring and remain after canopy closure, but reach peak cover before midsummer; late summer species leaf in mid- or late-spring and reach peak cover after midsummer; evergreen species retain leaves year-round.

Woodland	**Spring ephemerals**	**Early summer**	**Late summer**	**Evergreen**
Hardwick	28	28	5	39
Newton Mill	37	29	28	6
Hunshaw	0	3	69	28
Whitleigh	0	0	53	47

At Hardwick Wood, there were marked seasonal changes in composition through spring and early summer, with compositional changes slowing from June/July (Fig. 2.8). Differences in composition were found between plots (PERMANOVA: $Pseudo\text{-}F_{5,65} = 18.10$, $p = 0.001$), with only the most closed canopy plots (1 and 2) being statistically similar ($p = 0.10$) and all other plots being significantly different ($p < 0.05$). It should be noted that while I was unable to test statistically whether plots showed similar patterns of seasonal change, due to lack of replication of plots with similar canopy openness, similar seasonal patterns between plots are apparent from the MDS (Fig. 2.8). A more detailed look at the seasonal patterns for dominant species supports this (Fig. 2.12). The majority of dominant species reached peak abundance in spring (March-May), prior to or just after canopy closure, across all plots. Trends in vegetation structure also showed spring to be the most productive period, with low bare ground cover and a rapid increase in point frequency prior to canopy closure (Fig. 2.13). Significant differences in vegetation structure were found between plots ($\text{ANOVA}_{\textit{BARE GROUND}}$: $F_{5,50} = 6.24$, $p < 0.001$; $\text{ANOVA}_{\textit{POINT FREQUENCY}}$: $F_{5,50} = 8.87$, $p < 0.001$; $\text{ANOVA}_{\textit{VEG HEIGHT}}$: $F_{5,50} = 13.41$, $p < 0.001$; full pairwise comparisons in Appendix 2.2: Table A2.3). The most open plot (plot 6) was different to all other plots in terms of bare ground cover and point frequency ($p < 0.05$), except for plot 5 ($p > 0.10$). The most open plot maintained high vegetation cover all-year, with very little dieback occurring among ferns or *Rubus fruticosus*. By contrast, the most densely shaded plots (plots 1 and 2) had low point frequency and vegetation height during the main growing season. This corresponds to patterns of cover for dominant species in these plots, with the exception of *Hyacinthoides non-scripta*, which disappears prior to canopy closure, and *Hedera helix,* which retains cover all year.

Newton Mill also showed strong seasonal change in composition, with spring and early summer being the most dynamic period (Fig. 2.9). There were significant differences in composition between the plots (PERMANOVA $\textit{Pseudo-}F_{5,65} = 12.77$, $p = 0.001$). Plots 4 and 5 had similar composition ($p = 0.06$), but all other plots were significantly different ($p < 0.03$). However, as with Hardwick, there were comparable seasonal trends across plots, with a clear spring development and late summer senescence, which was most evident from the dynamics of dominant species (Fig. 2.14). Again, the majority of species reached peak abundance in spring, and late season cover was largely maintained by *Dryopteris dilatata* in the more open canopy plots. Vegetation structure showed strong seasonal change, with a clear peak in productivity in spring (Fig. 2.13). There were also clear differences between the plots ($\text{ANOVA}_{\textit{BARE GROUND}}$: $F_{5,50} = 27.23$, $p < 0.001$; $\text{ANOVA}_{\textit{POINT FREQUENCY}}$: $F_{5,50} = 20.30$, $p < 0.001$; $\text{ANOVA}_{\textit{VEG HEIGHT}}$: $F_{5,50} = 25.36$, $p < 0.001$; full pairwise comparisons in Appendix 2.2: Table A2.4). Although the two most closed canopy plots (1 and 2) were not similar in composition ($p < 0.001$), both were highly similar in terms of bare ground and point frequency ($p = 1.00$) and different from all other plots ($p < 0.05$). All other plots were similar in terms of bare ground and point frequency ($p > 0.20$), with the exception of plot 5 and 6 being different in point frequency ($p = 0.005$). Height trends showed differences between plot 5 and all other plots ($p < 0.001$), and between plot 2 and all other plots (p <0.001), with the exception of plot 1 (p = 0.08). All other plots were similar in terms of vegetation height (p >0.10).

No significant compositional changes were identified at Hunshaw over the year (Fig. 2.10) (repeated-measures PERMANOVA: $Pseudo\text{-}F_{10,65} = 0.76$ $p = 0.81$). All plots were significantly different in their composition (PERMANOVA: $Pseudo\text{-}F_{5,65} = 53.55$, $p = 0.001$; pairwise comparisons: $p = 0.001$). Although no overall seasonal change in composition was apparent across all plots, within plots it was apparent that changes do occur through the months, and these were most pronounced in spring, though the nature of these changes are plot-specific. For example, in plots 4, 5 and 6 there was considerable change between February and March (Fig. 2.10). If we look at changes in the woodland's dominant species (Fig. 2.15), this change appears to have been the influence of *Vaccinium myrtillus* coming into leaf. Emergence of *Pteridium aquilinum* between April-June, and new frond growth on *Dryopteris dilatata*, also contributed change during spring. After May, very little compositional change was observed in the more open plots, until dieback occurred in autumn. Structural parameters showed that there were highly significant differences between the plots (ANOVA$_{BARE\ GROUND}$: $F_{5,50} = 77.28$, p <0.001; ANOVA$_{POINT\ FREQUENCY}$: $F_{5,50}$ = 50.83, p <0.001; Kruskal-Wallis$_{VEG\ HEIGHT}$: $H_5 = 42.59$, p <0.001; full pairwise comparisons in Appendix 2.2: Table A2.5). The most closed canopy plots (1 and 2) and plot 4 were statistically similar in terms of their low bare ground cover and low vegetation height (all p >0.35), and as such seasonal trends were weak (Fig.2.13). Bare ground cover, point frequency and vegetation height in the most open plots (5 and 6), and plot 3, were significantly different to plots 1, 2 and 4 (p <0.001). These plots showed much higher levels of vegetation growth, particularly in spring, with height and point frequency increasing to peaks in May and June (Fig. 2.13).

Similarly to Hunshaw, no significant temporal changes in composition were identified at Whitleigh (repeated-measures PERMANOVA: $Pseudo\text{-}F_{10,65} = 0.25$ $p = 1.00$), and all plots were significantly different (PERMANOVA: $Pseudo\text{-}F_{5,65} = 176.32$ $p = 0.001$). The MDS shows that there were subtle seasonal changes within the open and intermediate canopy plots (Fig. 2.11). Spring was identifiable as the most dynamic period, with summer composition being stable and detectable dieback occurring in autumn, though it is apparent from looking at seasonal trends for dominant species that some species did not exhibit winter dieback (Fig. 2.16). Very little compositional change occurred in the most closed canopy plots (1 and 2). There were clear differences between plots in terms of vegetation structure (Fig. 2.13; $\text{ANOVA}_{\mathit{BARE\ GROUND}}$: $F_{5,50} = 118.16$, $p < 0.001$; $\text{ANOVA}_{\mathit{POINT\ FREQUENCY}}$: $F_{5,50} = 49.28$, $p < 0.001$; $\text{ANOVA}_{\mathit{VEG\ HEIGHT}}$: $F_{5,50} = 49.28$, $p < 0.001$, full pairwise comparisons in Appendix 2.2: Table A2.6). The two most closed canopy plots (1 and 2) were similar ($p = 1.00$) and different to all other plots ($p < 0.01$), for all structural parameters. Very few plants were growing in these plots, and therefore seasonal change was minimal. For other plots, the spring to early summer period was the most dynamic in terms of plant growth, with vegetation cover increasing from April-June (Fig. 2.13).

For all woodlands, there were highly idiosyncratic responses of species richness and diversity to seasonal change across the plots (Fig. 2.17). Significant differences in species richness were identified at all woodlands between months of the year (repeated-measures ANOVAs: Hardwick, $F_{1,10} = 29.57$, $p < 0.001$; Hunshaw, $F_{1,10} = 8.98$, $p < 0.001$; Newton Mill, $F_{1,10} = 6.36$, $p < 0.001$; Whitleigh, $F_{1,10} = 5.84$, $p < 0.001$) and between plots (ANOVAs: Hardwick, $F_{5,50} = 61.68$, $p < 0.001$; Hunshaw, $F_{5,50} = 42.95$, $p < 0.001$; Newton Mill, $F_{5,50} = 44.20$, $p < 0.001$; Whitleigh, $F_{5,50} = 31.62$, $p < 0.001$), but there were no clear patterns. Significant differences in species diversity were identified between months at Hardwick, Hunshaw and Whitleigh (repeated-measures ANOVAs: Hardwick, $F_{1,10} = 5.90$, $p < 0.001$; Hunshaw, $F_{1,10} = 5.26$, $p < 0.001$; Whitleigh, $F_{1,10} = 6.15$, $p < 0.001$), but not Newton Mill ($F_{1,10} = 1.70$, $p = 0.106$). Differences in diversity were also found between plots in all woodlands (ANOVAs: Hardwick, $F_{5,50} = 28.12$, $p < 0.001$; Hunshaw, $F_{5,50} = 27.90$, $p < 0.001$; Newton Mill, $F_{5,50} = 12.27$, $p < 0.001$; Whitleigh, $F_{5,50} = 54.78$, $p < 0.001$), but again there were no clear patterns. The interaction between time of year, and species richness and diversity, appears to have been plot and woodland-specific.

Fig. 2.5. Monthly average temperatures for 2014 in mid-Devon, set against monthly averages for the period 2004–2017. Data source: Haytor weather station (50.57° N, 3.94° W).

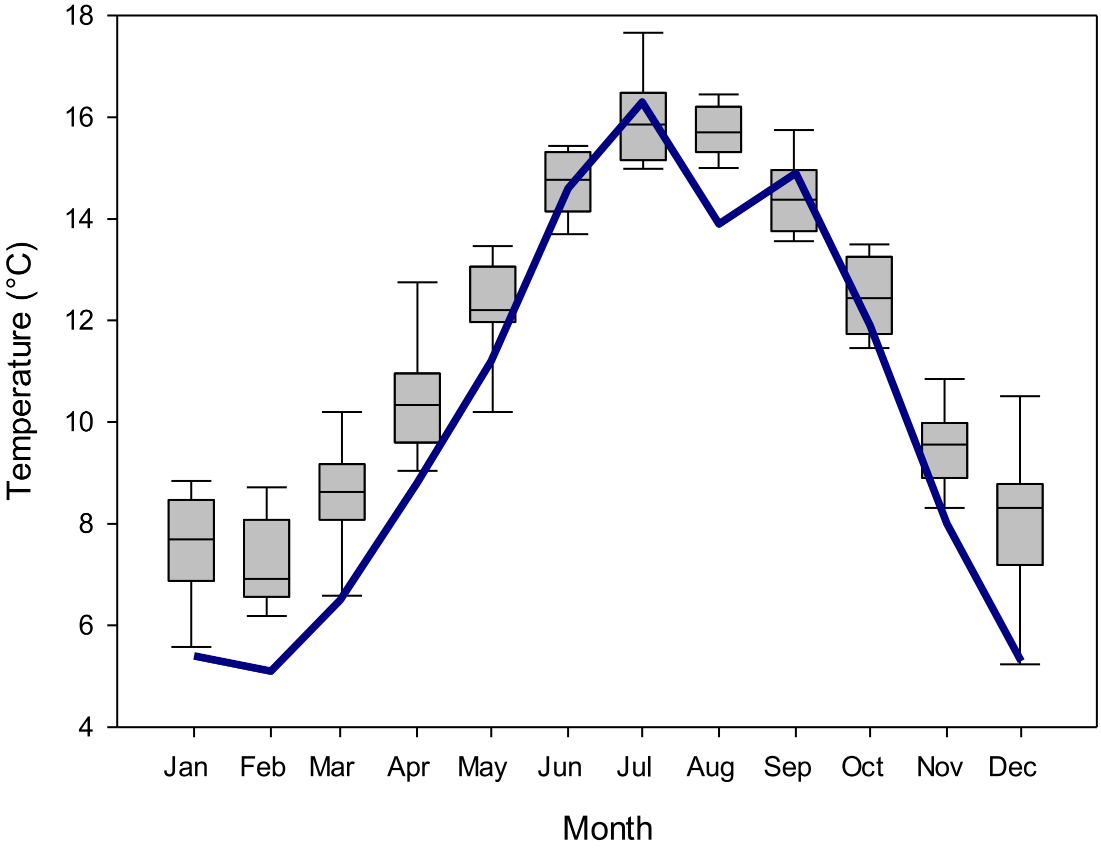


Fig. 2.6. Soil temperature patterns for all woodlands over 11 months. Colours reflect the canopy openness levels, with darker colours representing more closed canopy plots.

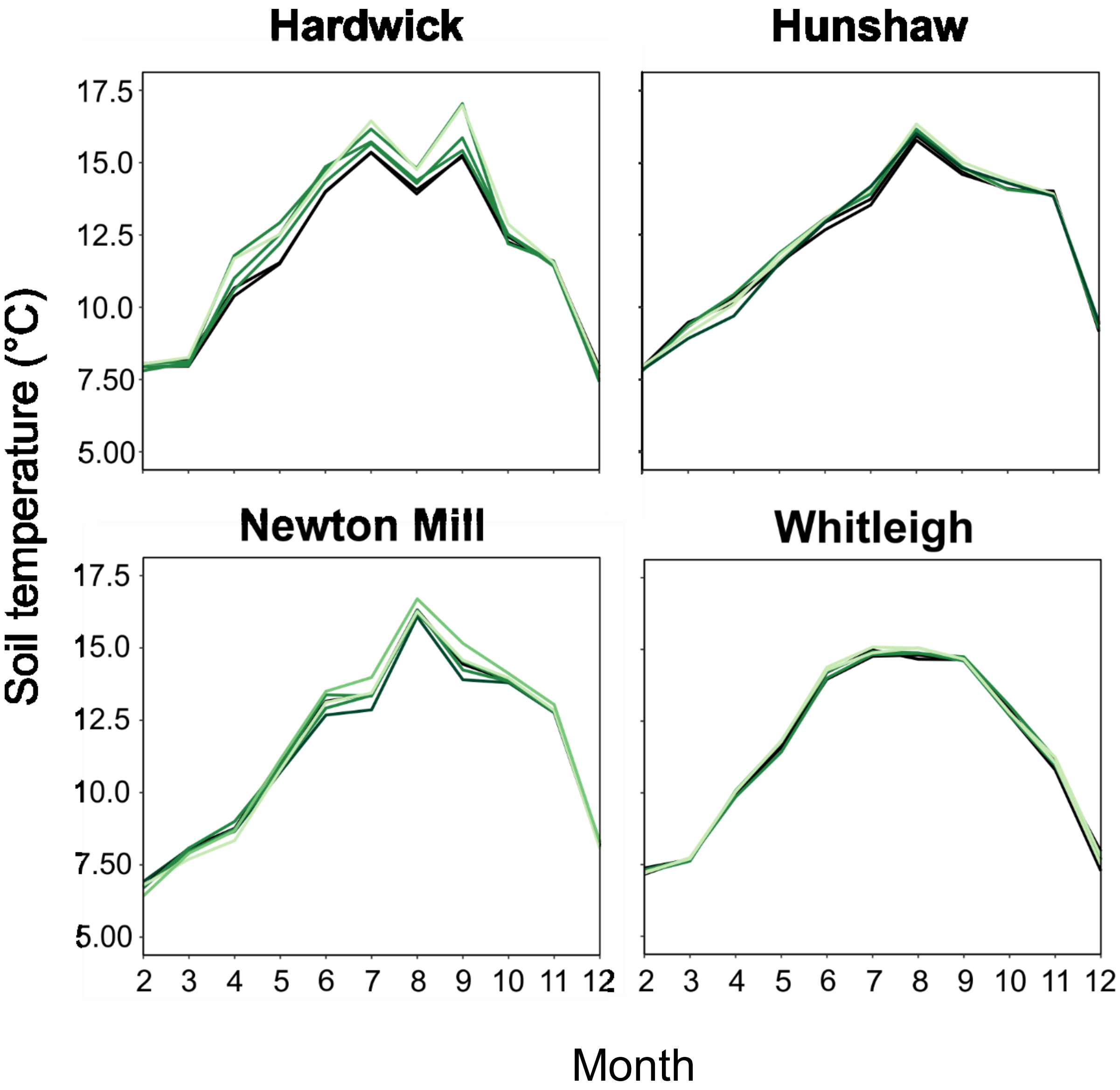


Fig. 2.7. MDS plot of vascular plant species composition across the year in four Devon woodlands. Points represent monthly observations made in each of six plots within each woodland. 2D stress: 0.18.

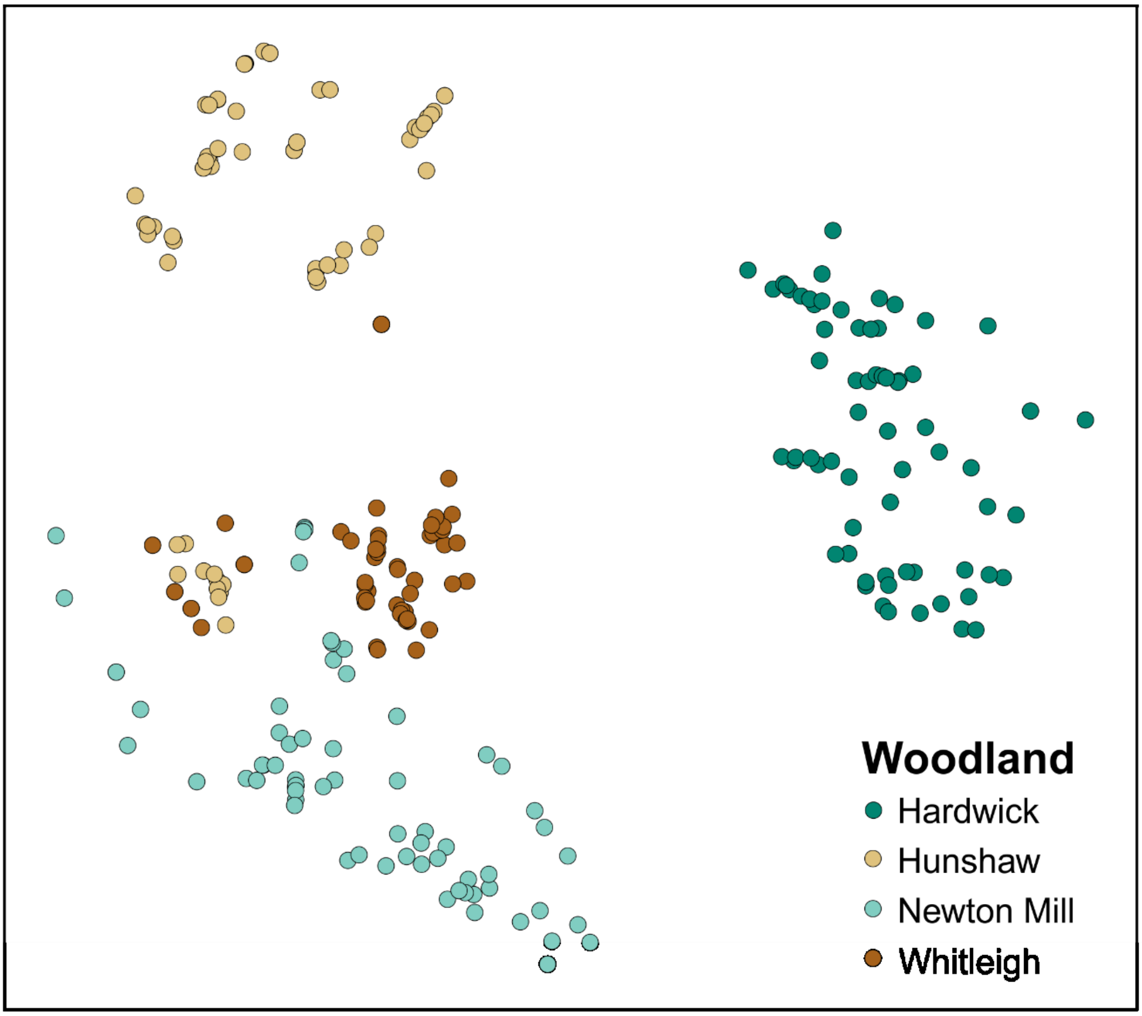


Fig. 2.8. MDS plot of vascular plant species composition at Hardwick, for six plots in each month of the year (February-December). Each symbol represents a different plot (see legend). Labels next to the symbols identify the month of the year (*i.e.,* 2 = February, 3 = March *etc.*). Colours reflect the canopy openness levels, with darker colours representing more closed canopy plots. 2D stress: 0.19. Repeated-measures PERMANOVA revealed significant changes in composition between months ($Pseudo\text{-}F_{10,65}$ = 18.10, p = 0.001). Pairwise comparisons of months are shown below the MDS. Months with similar composition are joined by a line (p > 0.10). Dashed lines represent borderline significant relationships (p = 0.05–0.10).

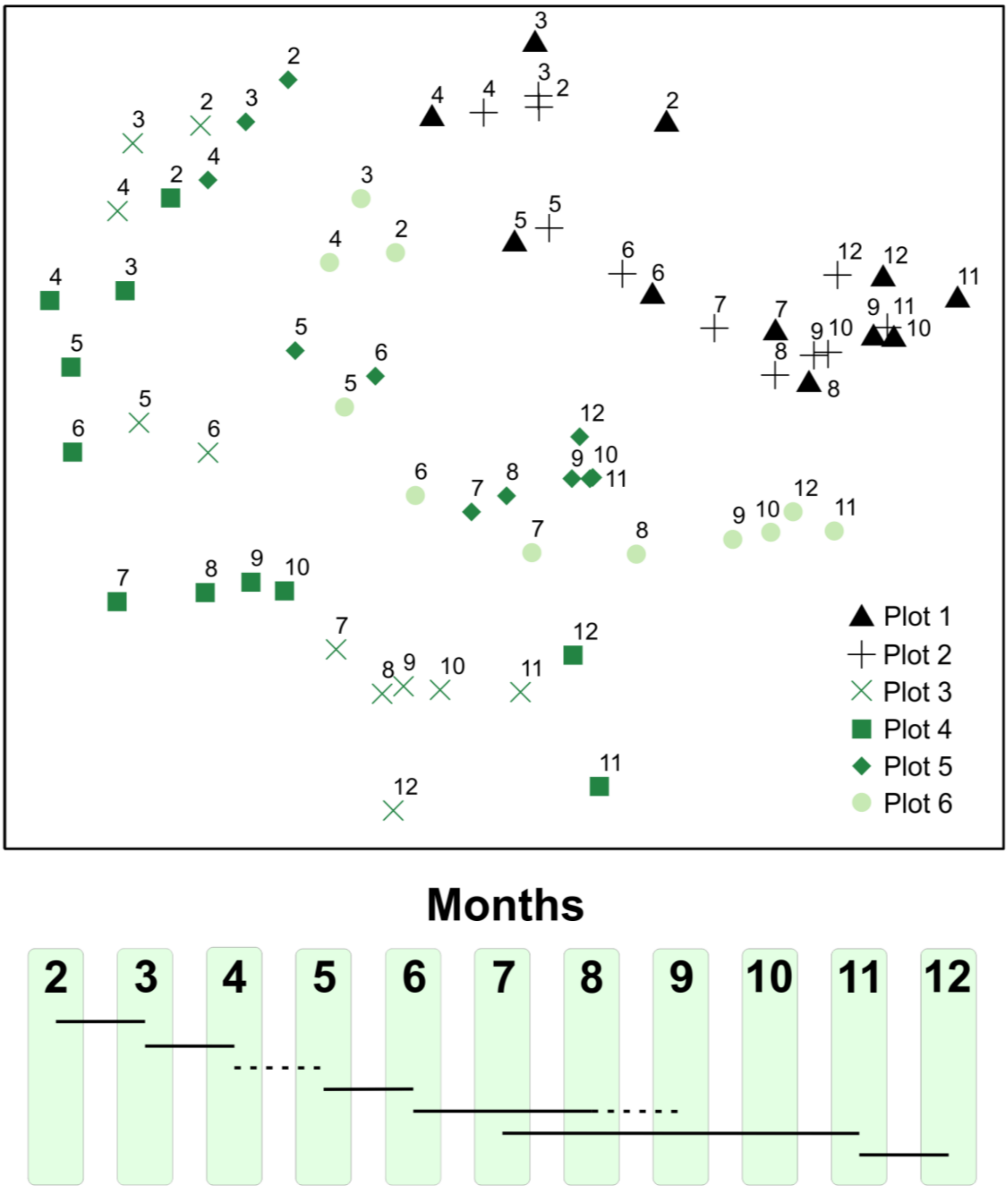


Fig. 2.9. MDS plot of vascular plant species composition at Newton Mill, for six plots in each month of the year (February-December). Each symbol represents a different plot (see legend). Labels next to the symbols identify the month of the year (*i.e.,* 2 = February, 3 = March *etc.*). Colours reflect the canopy openness levels, with darker colours representing more closed canopy plots. 2D stress: 0.17. Repeated-measures PERMANOVA revealed significant changes in composition between months in the year ($\mathit{Pseudo}\text{-}F_{10,65} = 4.86$, $p = 0.001$). Pairwise comparisons of months are shown below the MDS. Months with similar composition are joined by a line ($p > 0.10$). Dashed lines represent borderline significant relationships ($p = 0.05–0.10$). Filled circles are used to denote significant relationships between non-contiguous months.

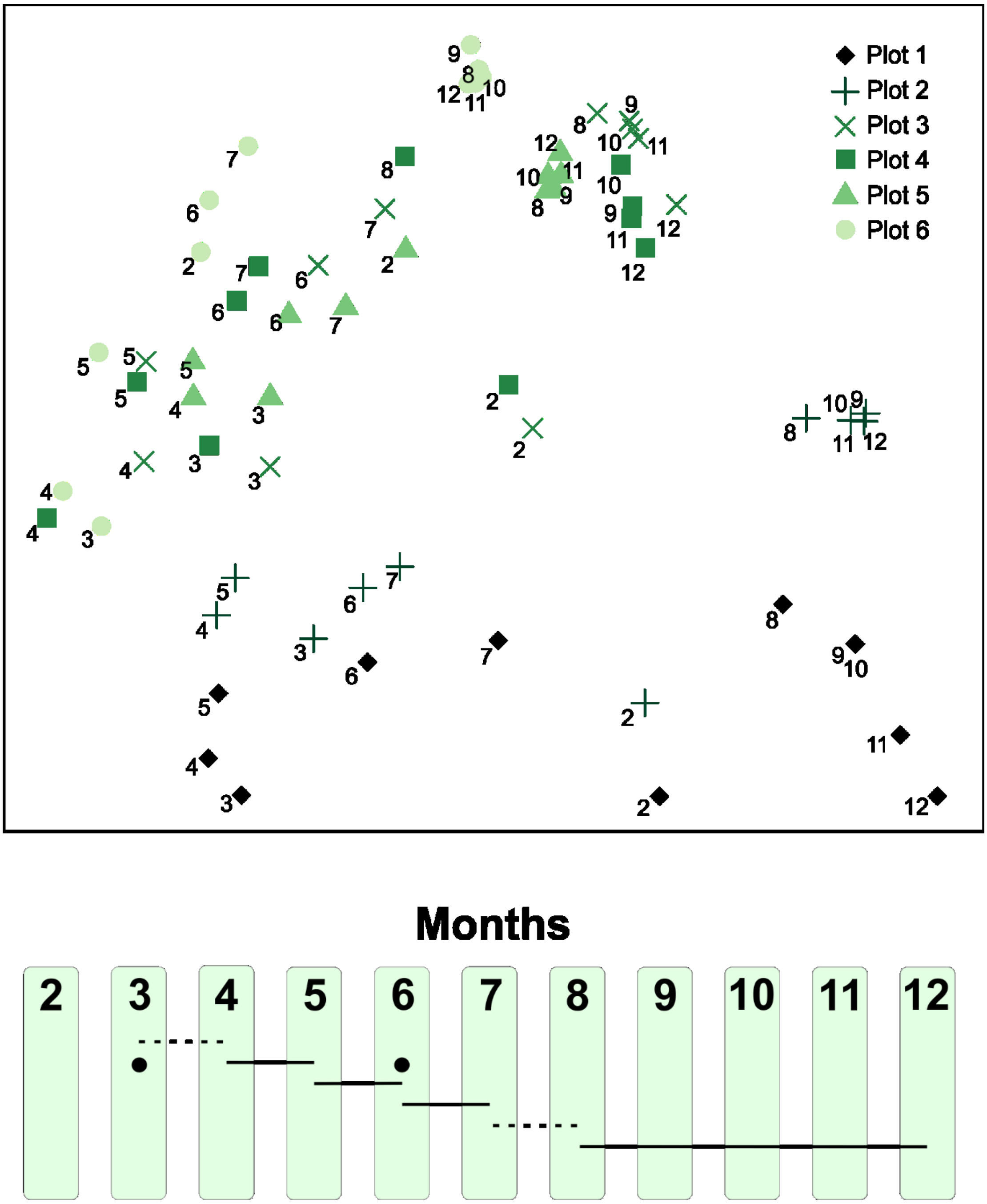


Fig. 2.10. MDS plot of vascular plant species composition at Hunshaw, for six plots in each month of the year (February-December). Each symbol represents a different plot (see legend). Labels next to the symbols identify the month of the year (*i.e.,* 2 = February, 3 = March *etc.*). Colours reflect the canopy openness levels, with darker colours representing more closed canopy plots. 2D stress: 0.09. Repeated-measures PERMANOVA showed no significant change in composition through months (Pseudo-F10,65 = 0.76, p =0.81).

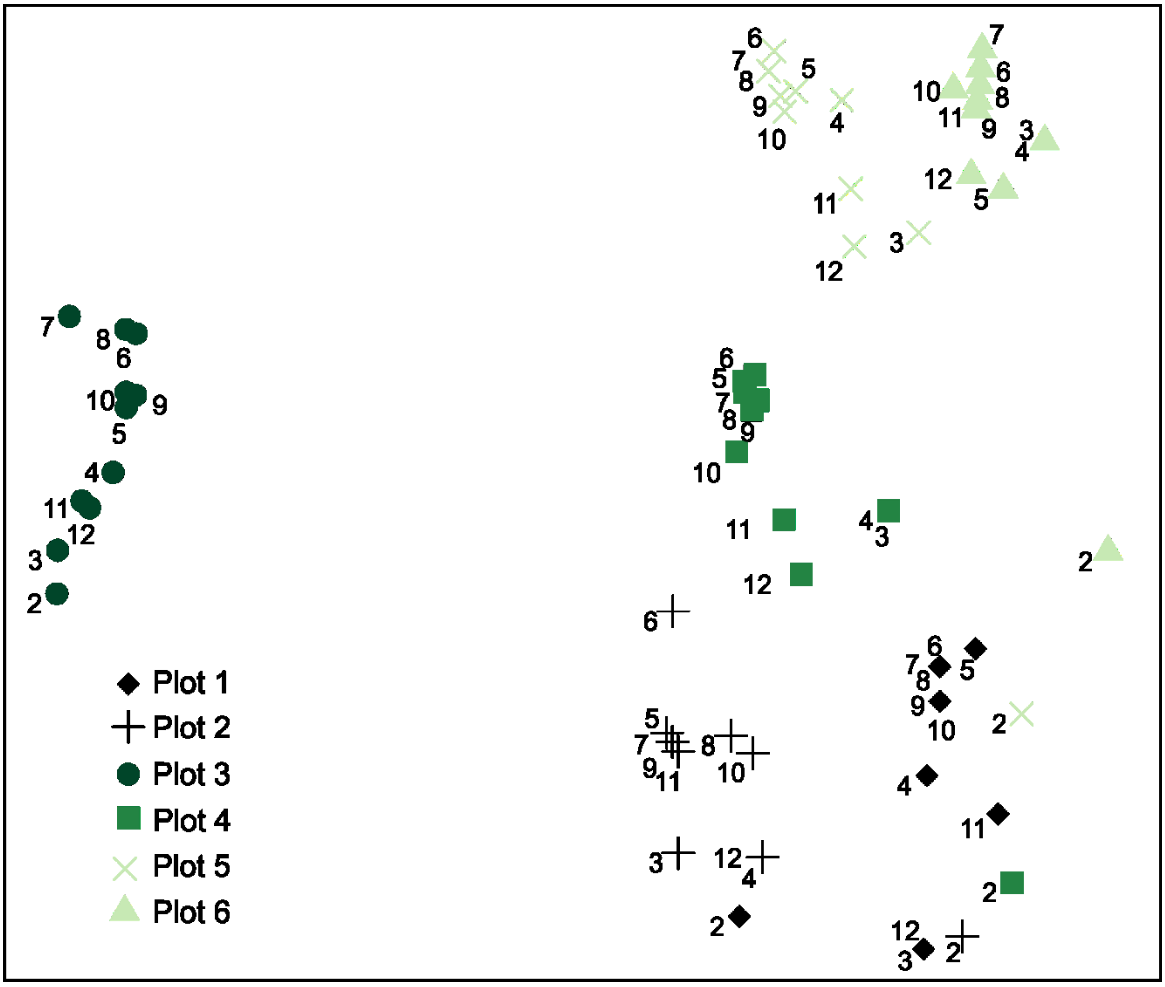


Fig. 2.11. MDS plot of vascular plant species composition at Whitleigh, for six plots in each month of the year (February-December). Each symbol represents a different plot (see legend). Labels next to the symbols identify the month of the year (*i.e.,* 2 = February, 3 = March *etc.*). Colours reflect the canopy openness levels, with darker colours representing more closed canopy plots. 2D stress: 0.09. Repeated-measures PERMANOVA showed no significant change in composition through months (*Pseudo-*$F_{10,65}$ = 0.25, p =1.00).

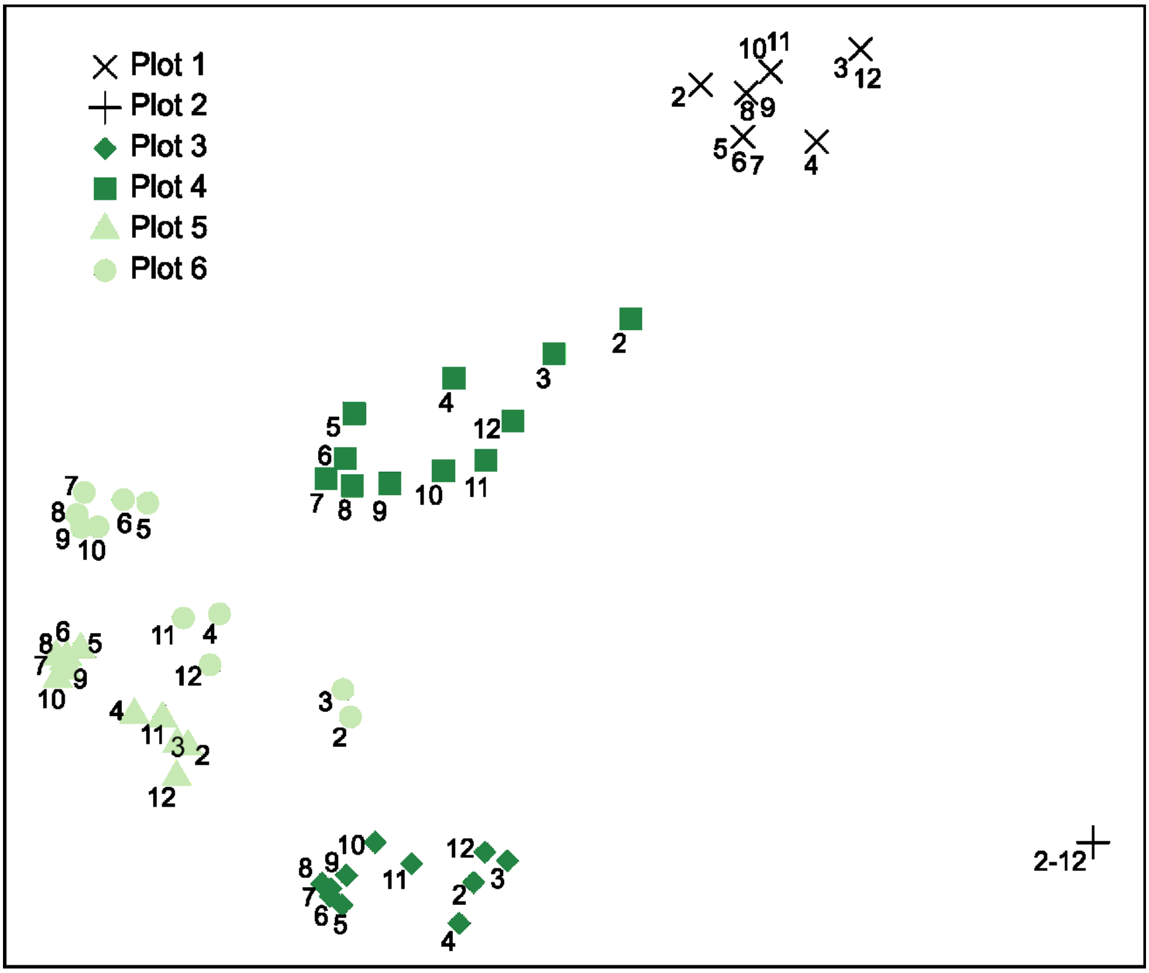


Fig. 2.12. Seasonal variation in cover (%) for dominant species at Hardwick. Dominant species were those that were most abundant when cover was averaged across plots and months. Dotted lines indicate onset and completion of overstorey canopy closure.

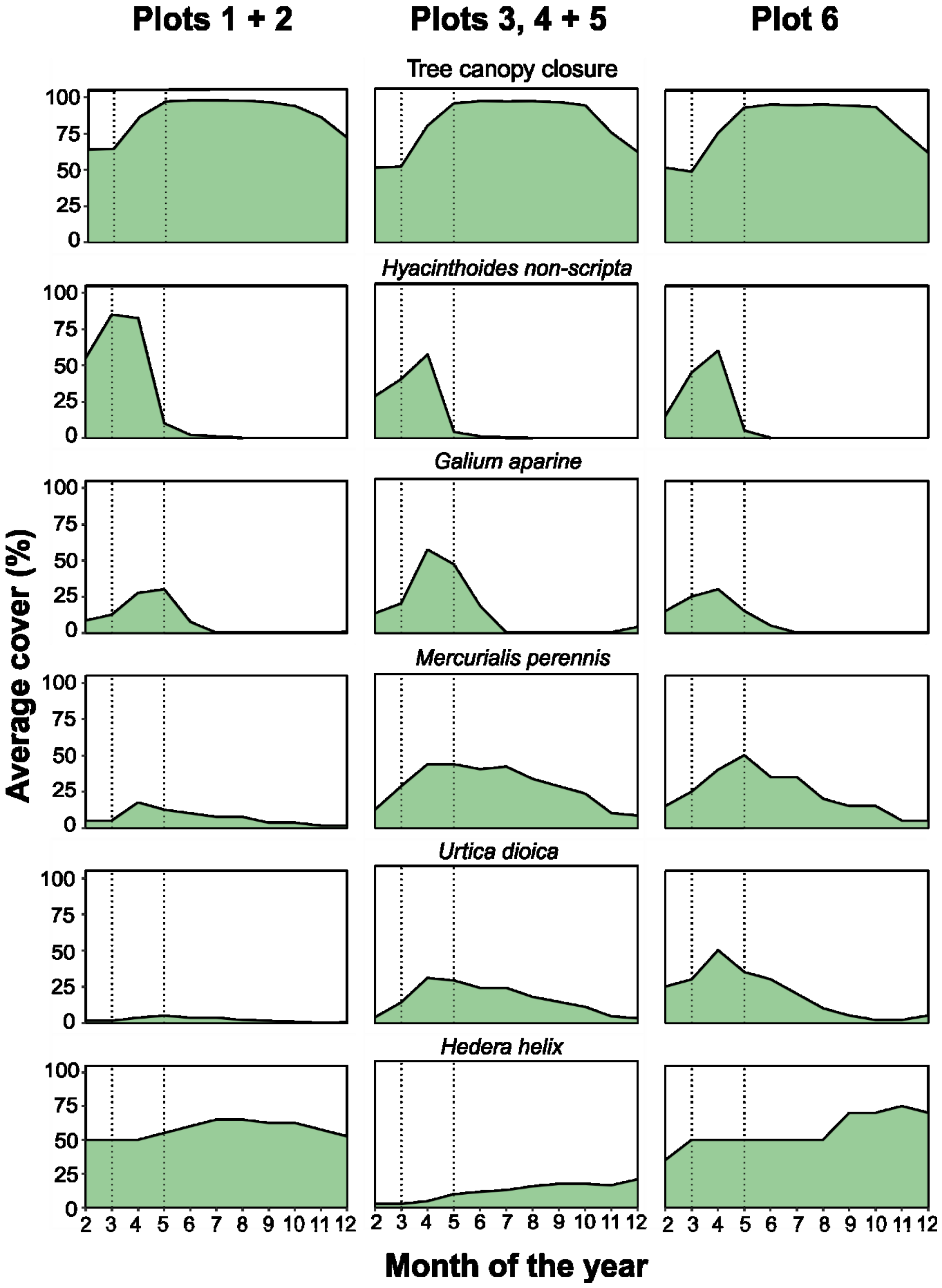


Fig. 2.13. Vegetation structural dynamics over 11 months, for six plots in each woodland. Coloured lines reflect the canopy openness levels, with darker colours representing more closed canopy plots. For full statistical comparisons of months and plots, refer to Appendix 2.2: Tables A2.7, A2.8, A2.9 and A2.10.

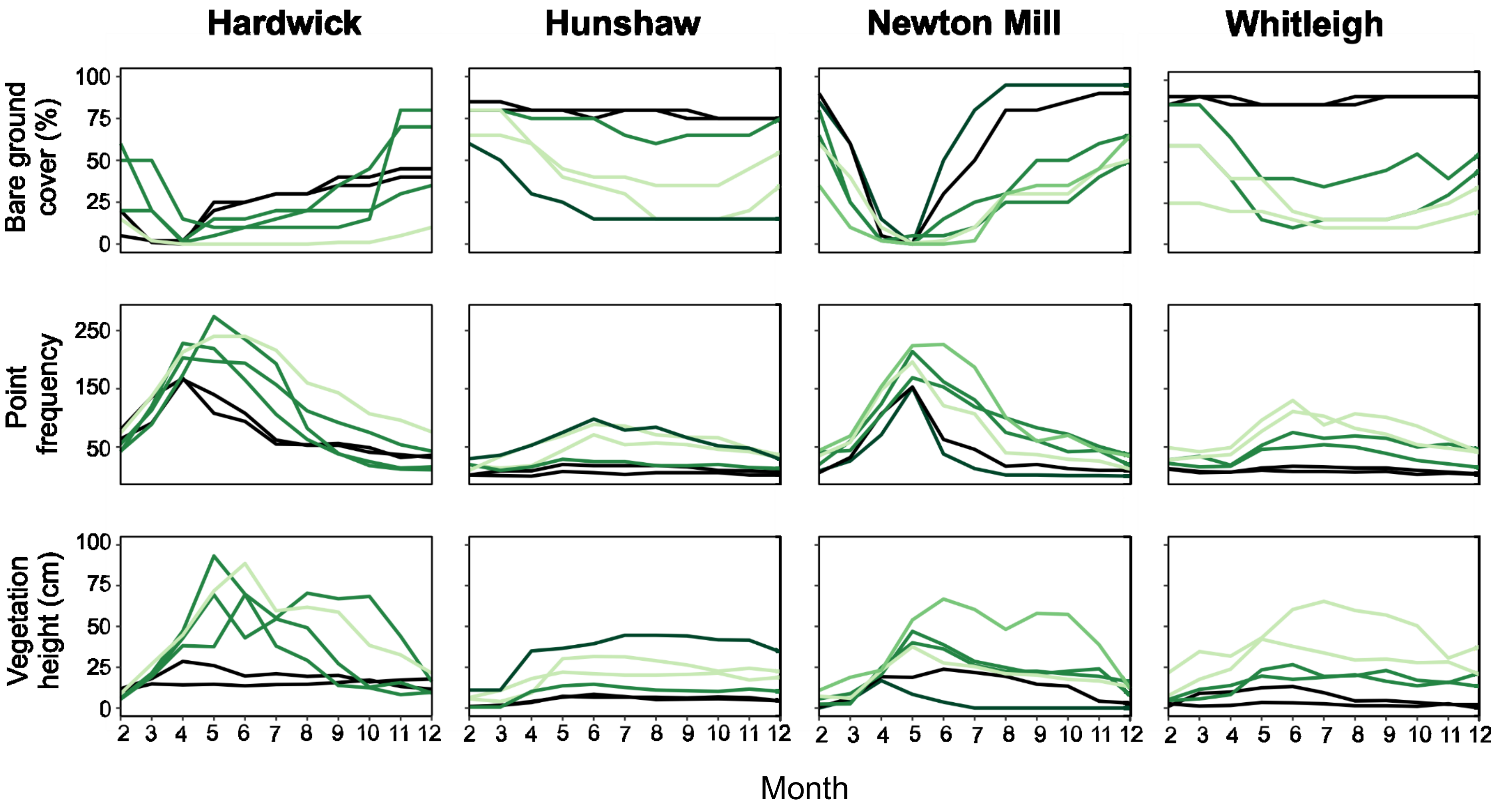


Fig. 2.14. Seasonal variation in cover (%) for dominant species at Newton Mill. Dominant species were those that were most abundant when cover was averaged across plots and months. Dotted lines indicate onset and completion of overstorey canopy closure.

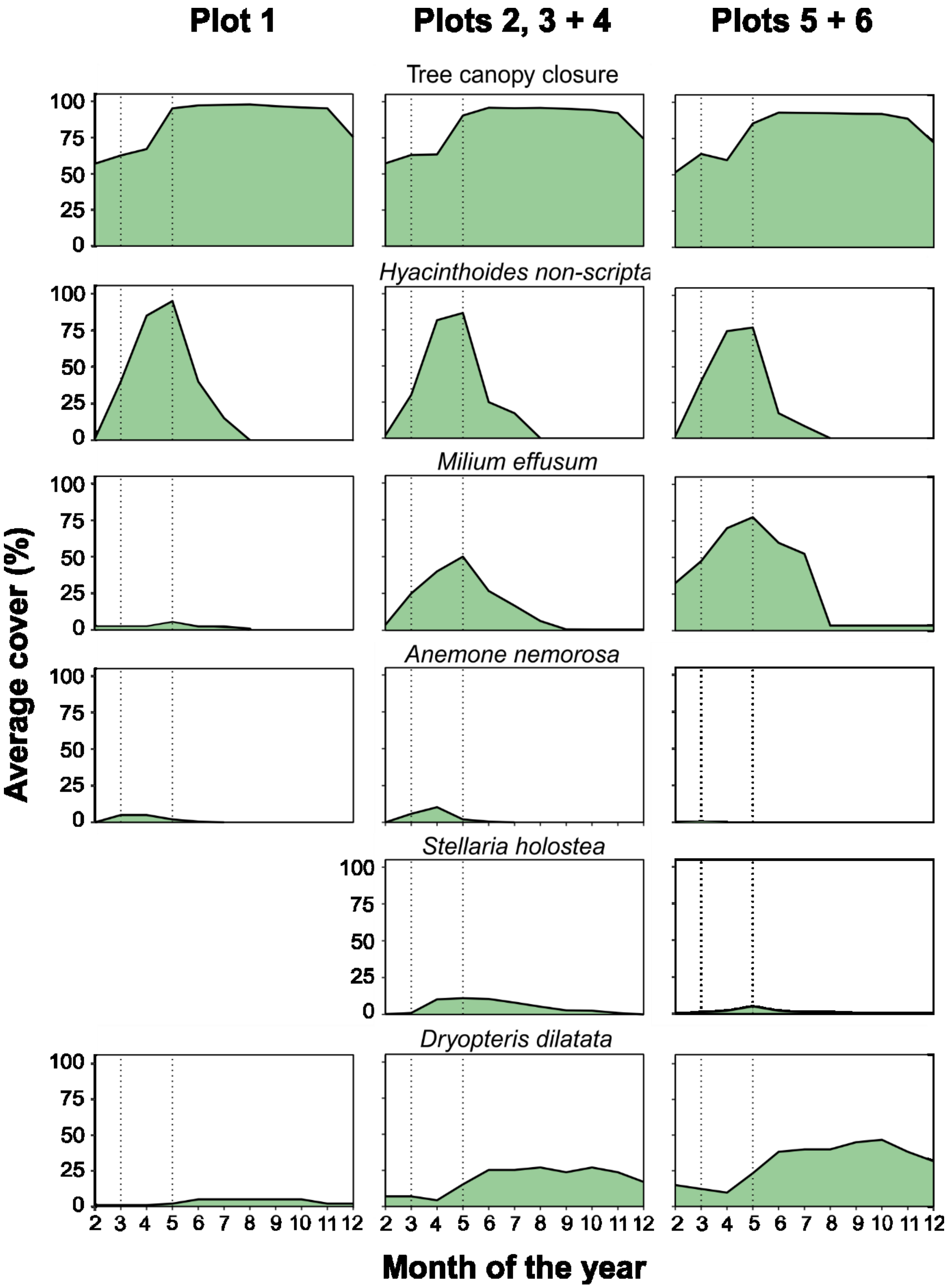


Fig. 2.15. Seasonal variation in cover (%) for dominant species at Hunshaw. Dominant species were those that were most abundant when cover was averaged across plots and months. Dotted lines indicate onset and completion of overstorey canopy closure.

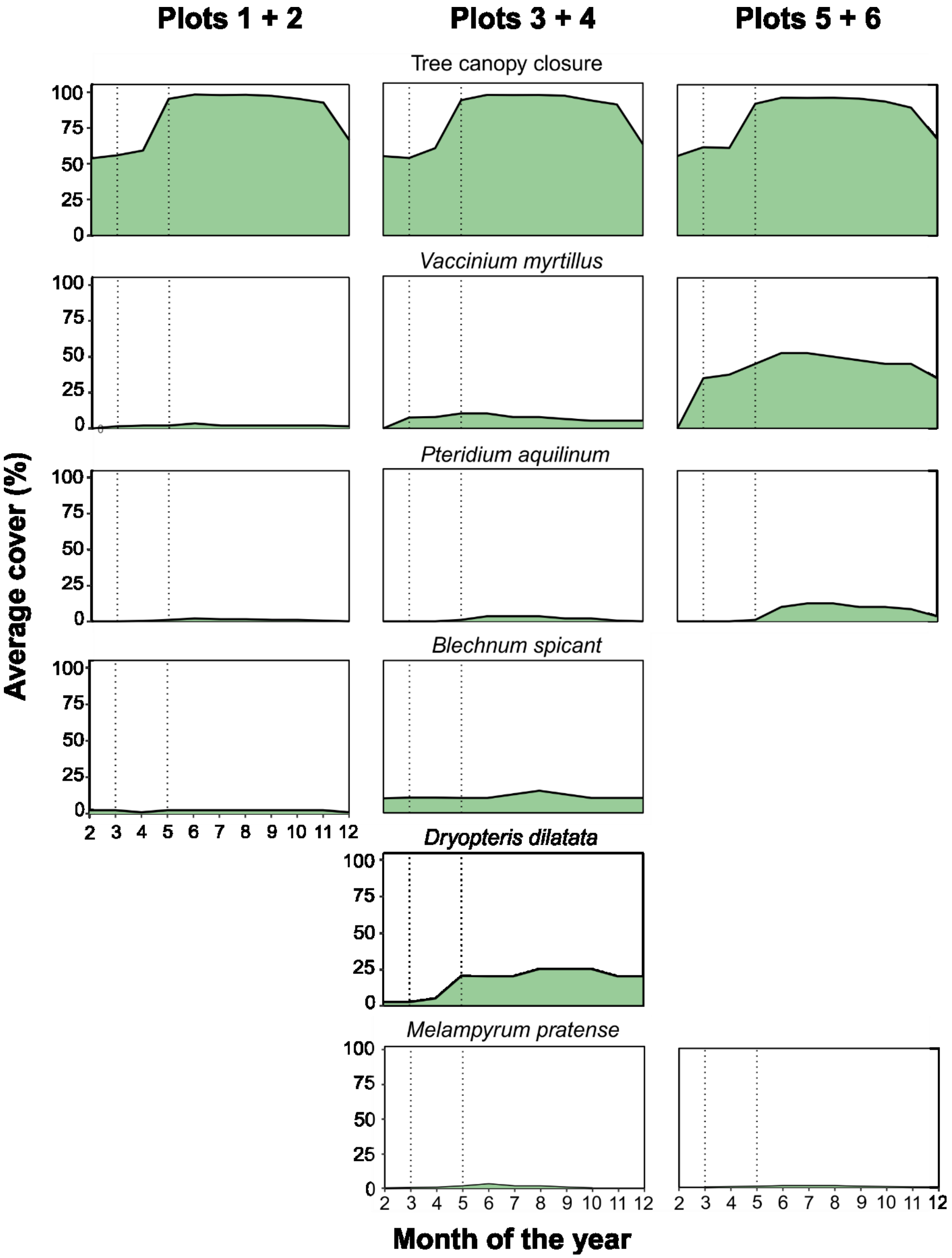


Fig. 2.16. Seasonal variation in cover (%) for dominant species at Whitleigh. Dominant species were those that were most abundant when cover was averaged across plots and months. Dotted lines indicate onset and completion of overstorey canopy closure.

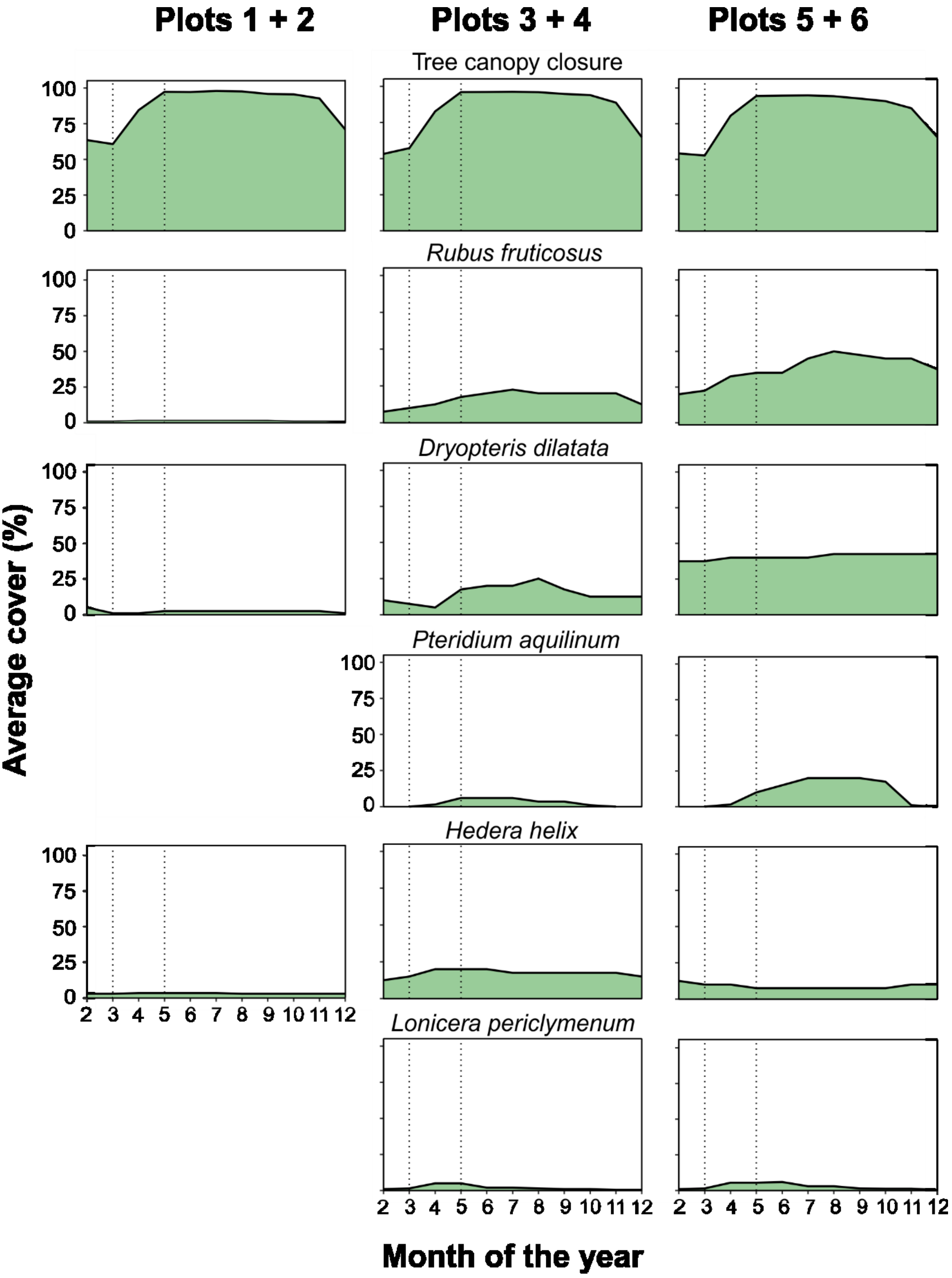
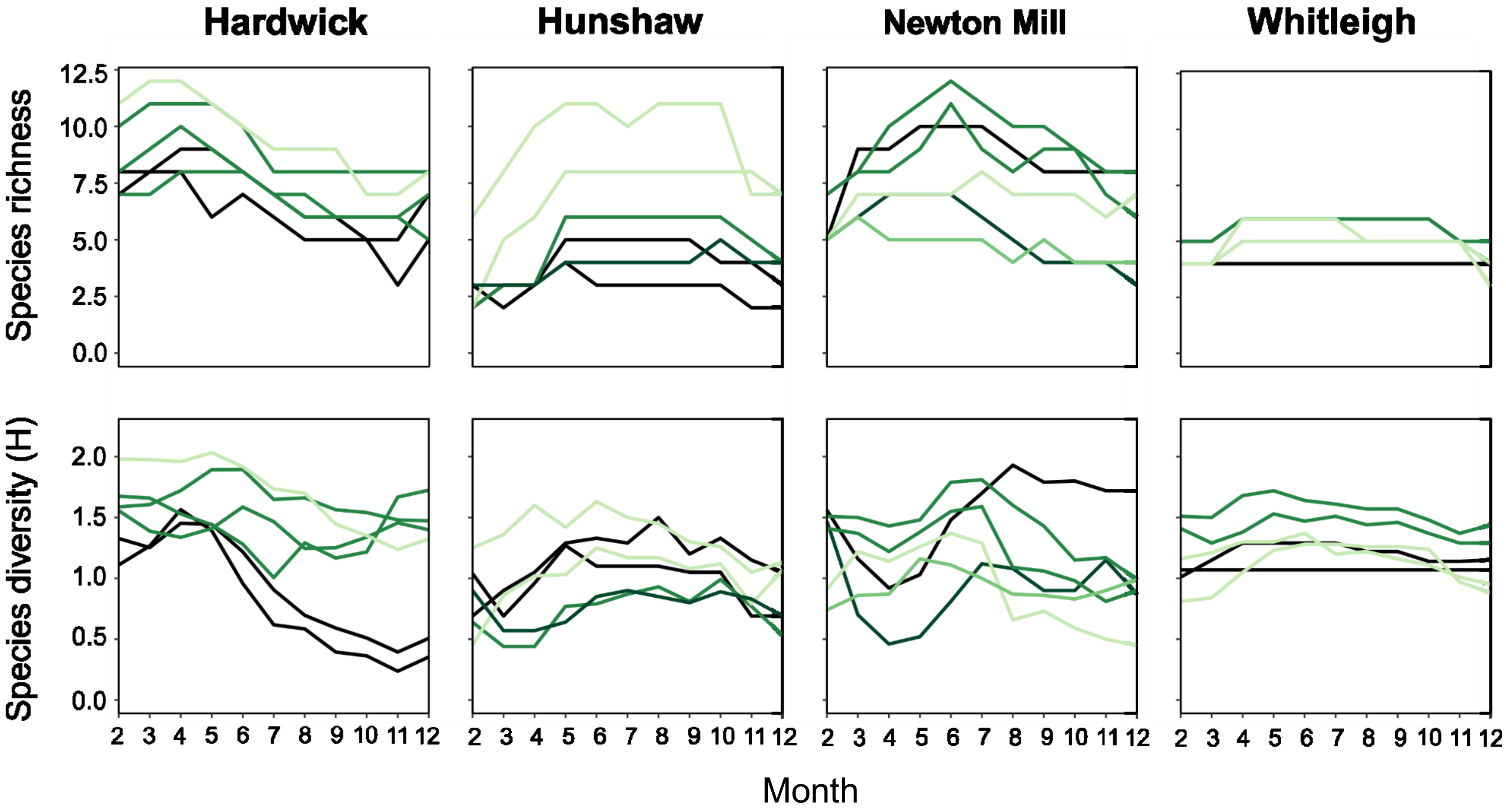


Fig. 2.17. Patterns of species richness and diversity over 11 months, for six plots in each woodland. Coloured lines reflect the canopy openness levels, with darker colours representing more closed canopy plots.



2.4 Discussion

With more studies focussing on the impacts of climate change on phenology (Cleland et al., 2007a; Kramer et al., 2000; Tang et al., 2016), and an increase in studies investigating long-term trends in forest understories, it is interesting to note the dearth of research on intra- and inter-annual changes in herb-layer dynamics. The majority of coordinated climate change monitoring in forests focuses on tree health (Anderson-Teixeira et al., 2015; Bussotti and Pollastrini, 2017a; Bussotti and Pollastrini, 2017b) and tree phenology (Brown et al., 2016; Jeong et al., 2011; Zhang et al., 2003), without considering the effects on understorey dynamics (Routhier and Lapointe, 2002). Studies that have focussed on the understorey, have tended to look at a small number of species or woodlands, and have not integrated monitoring of the forest canopy with monitoring herb-layer response (Murphy and McCarthy, 2014). Despite improved understanding of the complex biotic and abiotic interactions influencing forest ecosystem dynamics, there remains an implicit assumption that it is reasonable to extrapolate from a small number of studies to predict how temperate forests will respond to climate change. In this study of four Devon woodlands, I demonstrate that even across a small geographic area, forests can vary considerably in terms of composition and seasonal dynamics in the herb-layer. This study emphasises that high levels of spatial replication are needed to predict how different forests will respond to climate change. These results are based on one year of data collection, when temperatures were below average for winter, spring and autumn. Long-term data collection is necessary to study seasonal dynamics in relation to annual variation in climate. Citizen science, with its potential to provide data simultaneously across large geographical areas, and year after year, is the only realistic way to achieve the levels of replication required (Silvertown, 2009). The findings of this study provide insight into attributes that would be useful to monitor, and the methods that would be suitable for widespread use in different forests.

As well as differences between woods, I found considerable variation in herb-layer dynamics within woodlands, demonstrating the need for spatial replication of monitoring within forests. Spatial replication should reflect the breadth of canopy openness conditions in the forest. Although subtle in absolute terms, within each woodland there were differences in canopy openness between plots, and this coincided with substantial differences in the herb-layer. Summer canopy openness variation in each woodland was similar, with coefficients of variation ranging between 31–36 %. This is comparable to the variation found in secondary forests in North America, where coefficients of variation averaged 32%, compared to old-growth forests with coefficients of variation averaging 65% (Scheller and Mladenoff, 2002). Although all of the study woodlands were classed as Ancient Semi-Natural Woodland, this lower degree of canopy openness heterogeneity reflects the trend towards increasingly closed canopy and structurally homogenous forests (Hopkins and Kirby, 2007).

Light levels were likely to be the main factor limiting herb-layer growth in the most dense canopy plots. Where canopy openness was less than 3% (in all of the most dense canopy plots), the only notable change in composition and structure occurred prior to canopy closure, when spring ephemerals were active. Cover of summer-green species was severely limited at these low light levels, as has been noted in other studies (Hicks and Taylor, 2015). At the woodlands where spring species were absent, very little activity occurred in these plots all year. Earlier onset of canopy closure could lead to reduction in spring ephemerals and early-summer species (Rothstein and Zak, 2001), resulting in sparse herb-layers where canopy closure is particularly high.

Differences in herb-layer vegetation between more open and intermediate canopy plots were less clear, demonstrating that other factors are likely influencing the fine-scale spatial patterning of the herb-layer where light is less limiting. Burton et al. (2011) found that understorey light levels explained little of the fine-scale spatial variation in herb-layer composition in a study of 215 plots in a second-growth forest in North America. They proposed that this finding could have been related to the low degree of variation in the light environment in their study. Chudomelova et al. (2017) did identify canopy openness as having a significant effect on fine-scale spatial variation in herb-layer composition, though it was a weaker explanatory variable than soil pH, where canopy openness exceeded 5%. In the intermediate and open canopy plots, where light levels were less limiting, the spatial arrangement of species is likely a combination of abiotic factors, disturbance history and patterns of dispersal (Ehrlen and Eriksson, 2000; Fraterrigo et al., 2006; Gazol and Ibanez, 2010). Soil temperature was fairly consistent between plots, so this was unlikely to be a factor influencing within-woodland variation in this study. At Hunshaw, where soil nutrients were likely a limiting factor, pockets of more nutrient rich soils may well have influenced the richer herb-layer found in a more closed canopy plot towards the base of the surveyed slope. Hardwick Wood had an abundance of pits and mounds as a result of high levels of historic storm damage, and these micro-topographical features may have contributed to compositional variability among the intermediate and open canopy plots at that woodland (Beatty, 1984). These factors demonstrate problems associated with low-levels of replication in forests, where high levels of heterogeneity between plots can reduce statistical power to detect treatment effects (Royo and Carson, 2008). This further emphasises the importance of a monitoring approach that facilitates high spatial replication through the use of citizen science.

A focus on detailed monitoring of spring phenology will be important for understanding impacts of climate change on the herb-layer. Despite differences between the woodlands in this study, the spring season was clearly important in terms of herb-layer productivity at all woodlands. This was most evident at the two woodlands with spring ephemerals and early summer species. Considerable compositional change was evident at these woodlands as plants developed and then senesced prior to or shortly after canopy closure. By contrast, compositional change was much less apparent at Hunshaw and Whitleigh. These woodlands were dominated by summer-green and semi-evergreen species, particularly hemi-cryptophytic ferns and nanophanaerophytes, so there was no pronounced turnover in species composition during spring to early summer. Nevertheless, the spring period was still important, evident from structural changes—the increase in point frequency and vegetation height that occurred at this time—and the increases in cover of dominant species and decline in bare ground cover.

Ida and Kudo (2008) highlighted the importance of the early spring period for summer-green plants, as high carbon gain during this time is allocated to increasing leaf area, helping maximise photosynthetic activity after canopy closure. Furthermore, they found early canopy closure reduced available carbon for fruit production, affecting reproductive success. Currently, coordinated national schemes for monitoring forest herb-layer phenology focus on a small number of spring ephemerals *e.g.,* Nature's Calendar (2017). I recommend that species included in monitoring should be chosen according to the composition at each monitored woodland, and should include species from different phenological guilds, in order to capture trends for dominant herb-layer species in different forests. Phenology monitoring should be frequent enough to capture change in timing of herb-layer development in relation to the timing of canopy closure. In this study, the monthly frequency was clearly too coarse for this, but more frequent monitoring was not practical. This further demonstrates the necessity for a citizen science approach to enable widespread data collection at high temporal frequency.

Given the importance of the spring period prior to canopy closure, monitoring changes in the timing of canopy closure alongside herb-layer dynamics is essential. Given the very strong relationship between GSF and canopy openness at all woodlands, it can be concluded that canopy openness provides a good estimate of GSF in different forests. The relationship between GSF and canopy openness did vary to a small degree depending on forest aspect. This is likely to be due to a link between woodland aspect and canopy gap position. Hunshaw Wood was on a fairly steep south-facing slope, so the canopy to the north was dense with few gaps. The opposite was true for Newton Mill and Whitleigh on north-facing slopes. For very detailed studies where absolute measures of understorey light are required, GSF or a direct measurement using quantum sensors may be required (Tobin and Reich, 2009). However, for widespread monitoring where the purpose is to assess relative change through time, canopy openness is an appropriate surrogate. It is also likely to be more reliable, as I obtained much more consistent measurements than for GSF. The high degree of variation in GSF values between June-August, when low within-plot variation would be expected, was related to minor differences in camera orientation of a few degrees. While the precision of camera orientation could be improved with changes to the data collection methodology, this would increase time spent in the field. Given the need for high replication, and efficient methods that can be easily and reliably repeated by multiple surveyors, canopy openness is a better option.

A variety of more cost effective methods that provide estimates of canopy openness are also available (Jennings et al., 1999). The canopy scope has been widely used in forestry for coarse-scale assessments of openness (Brown et al., 2000; Hale and Brown, 2005), but may be suitable for monitoring seasonal change. In addition, the arrival of new technology such as smartphone cameras with fisheye lens attachments, present opportunities for cost effective alternatives to canopy openness assessment with hemispherical photography. There is a need to test these methods against hemispherical photography, and assess the temporal frequency required to track changes in canopy closure timing. Another alternative is to use visual observation of budburst and leaf expansion timing as a proxy for canopy closure. In this study, while canopy openness data were collected too infrequently to identify differences in canopy closure timing between woodlands, I did detect higher spatial variation in spring canopy openness between plots at Hardwick and Newton Mill, than at Hunshaw and Whiteigh. The former two woodlands had more diverse overstories, containing both early-leafing species such as sycamore/birch respectively, as well as oak, and late-leafing ash. By contrast Hunshaw and Whitleigh were dominated by beech and oak. Observational recording of tree phenology has been widely used to assess the onset of the growing season in overstorey trees (Elmendorf et al., 2016; Schaber and Badeck, 2005; Sparks et al., 2009; Vitasse et al., 2009b), and the method has the advantage of being cost effective. A recent UK citizen science initiative sought to relate flowering phenology of spring ephemerals to timing of dominant tree leaf expansion (Track a Tree, 2017). However, the extent to which tree species vary in their phenology across a woodland, and the relationship between leaf expansion of individual trees and whole canopy closure, needs to be considered if effects on the herb-layer are to be inferred from the phenology of a subset of overstorey trees.

The herb-layer can also affect light-levels reaching the ground, with dense cover excluding almost all light from the ground-layer, inhibiting seedling regeneration of trees and herbaceous species (Jefferson, 2008; Royo and Carson, 2006). Despite the highly significant relationship between above and below herb-layer canopy openness in this study, it is important to note the more extensive herb-layer shading at Hardwick and Whitleigh and possible explanations for this. The most open plots at Whitleigh had high cover of *Rubus fruticosus* all year, and the most open plot at Hardwick had the densest cover of understorey vegetation of all surveyed plots. It is likely that overstorey disturbance from past storm damage combined with nutrient-rich soils has led to the establishment of the dense understorey cover here. The development of recalcitrant understories, with the formation of dense cover of native woodland species such as *Rubus fruiticosus*, has been observed in response to overstorey disturbance elsewhere (Royo and Carson, 2006) and has been shown to severely impede seedling development. Climate change is likely to bring about increasing overstorey disturbance, with defoliation/mortality events in trees as a result of drought, severe storms, pests and diseases (Thom et al., 2017a). Combined with the effect of warming, such events could lead to more widespread dominance of vigorous species, especially in more eutrophic woodlands. Another interesting point to note is that high vegetation cover in open plots at Hardwick and Whitleigh was maintained all year. These woodlands were more oceanic and lower in altitude than Hunshaw and Newton Mill, so it is possible that warmer winters reduced vegetation dieback. Milder winters as a result of climate change could affect seedling germination where herb-layer cover is maintained through winter.

In addition to detailed monitoring of herb-layer development in spring in relation to canopy closure, I recommend monitoring changes in vegetation cover at repeated intervals in summer, autumn and winter, each year. As the results of this study demonstrated lower levels of within-season change during these periods, monitoring the herb-layer once in each season should be adequate to capture annual variation. Monitoring at these intervals will be important for understanding later season effects of canopy closure timing on summer-green and evergreen species. In addition, it will enable the combined effects of temperature and gap dynamics to be assessed. While I detected little seasonal variation in cover of *Dryopteris dilatata*, this species was an important component in three of the study woodlands, and is predicted to disappear from southern Britain by 2050 (Bakkenes et al., 2002). Therefore there could be dramatic changes in cover between survey years, as has been documented for different species elsewhere (Murphy and McCarthy, 2014). As with spring monitoring, species selected should include woodland dominants, as well as those species with potential to develop dense cover in response to disturbance, such as *Rubus fruticosus* and *Pteridium aquilinum*. Non-native invasive species should also be included where present. Although not present in the survey plots in this study, non-native invasive species are becoming increasingly prevalent, and are likely to gain competitive advantage due to more plastic responses to shade and temperature extremes (Willis et al., 2008). Since species richness and diversity showed no clear seasonal patterns, and as species inventories can be problematic in widespread monitoring using citizen science (Crall et al., 2011; McDonough MacKenzie et al.), I recommend that focussing on key species is a better approach to full species inventories. Additionally monitoring bare ground cover would capture wider changes in the herb-layer community, and help identify the deterioration of understorey cover or its proliferation, in response to contrasting pressures brought about by climate change.

2.5 Conclusions

Even over small geographic ranges forests vary considerably in their composition and seasonal dynamics. Therefore, to predict impacts of climate change, widespread monitoring that gathers data on seasonal and inter-annual changes across a wide range of forests is critical. The spring period is particularly important for herb-layer development, and small variation in canopy openness can have considerable effects on herb-layer cover and composition. Citizen scientists could help to collect data by monitoring herb-layer cover and changes in the abundance of key species, alongside monitoring of the overstorey canopy. Research is needed to identify methods that could be used to monitor tree canopy development and canopy openness on a large-scale.

3

A comparison of ground-based methods for obtaining large-scale, high resolution data on the spring leaf phenology of temperate tree species

3.1 Introduction

Changes in the leaf phenology of temperate trees are one of the best studied and most recognisable impacts of climate change, with a large body of research demonstrating trends towards earlier leafing with warmer spring temperatures (Menzel and Fabian, 1999; Menzel et al., 2006; Polgar and Primack, 2011). The majority of data is now obtained from remote-sensing, which captures phenological trends at regional and global scales, but at coarse temporal and spatial resolutions (Buitenwerf et al., 2015; Crabbe et al., 2016; Hamunyela et al., 2013; Wang et al., 2016; White et al., 2014; Wu and Liu, 2013). By contrast, ground-based observations gather species and site-specific information, but tend to lack geographic coverage and vary considerably in their approaches to characterising phenology (Denny et al., 2014). While many studies have focussed on identifying large-scale phenological patterns, comparatively few have investigated how changes in phenology affect local-level forest ecosystem dynamics (Cole and Sheldon, 2017). Leaf phenology is fundamental to tree growth, fitness and survival (Chuine, 2010; Vitasse et al., 2009a), and the timing of canopy development has widespread implications for competition dynamics and trophic interactions (Cole and Sheldon, 2017; Roberts et al., 2015; Thackeray et al., 2010). Therefore, understanding subtle changes in the timing and order of leaf expansion in a forest ecosystem is important. As forests are highly heterogeneous, there is a need for widespread monitoring of forests at a high resolution. Phenology at the local level will vary according to species composition, genetic and epigenetic diversity (Basler, 2016; Cleland et al., 2007b; Polgar and Primack, 2011). In addition, environmental factors such as topography (Fisher et al., 2006) and soils (Arend et al., 2016; Lapenis et al., 2017) can vary markedly over small spatial gradients, and influence phenology at scales missed by remote-sensing. Therefore, harmonised methods that enable large-scale data collection on the phenology of individual trees are needed to understand impacts on ecosystem dynamics and biodiversity.

Temperate tree leafing is controlled by a combination of winter chilling requirements, spring forcing temperatures and photoperiod controls (Polgar and Primack, 2011). The relative importance of the environmental cues varies between species, and represents a compromise between maximising photosynthetic potential and minimising risk of frost and herbivory damage (Augspurger, 2009; Chuine, 2010). Evolutionary history, physiology and ecology all influence the phenological expression of a species (Cole and Sheldon, 2017; Panchen et al., 2014). Some early-leafing species lack photoperiod control altogether, enabling them to take advantage of high light periods prior to neighbouring dominant or co-dominant trees coming into leaf and limiting direct radiation (Richardson and O'Keefe, 2009). Similarly, low or no requirements for winter chilling can enable a more plastic response to warm spring temperatures, as observed in non-native invasive species (Polgar et al., 2014; Willis et al., 2010). At present, the winter chilling requirements of different species are not well known, but this could strongly influence ecosystem dynamics. As winters become warmer, species with chilling requirements may have significantly delayed leafing, while others continue to advance their leafing with warmer springs (Laube et al., 2014; Polgar et al., 2014; Roberts et al., 2015; Vitasse et al., 2011). A recent study by Roberts et al. (2015) predicts increasing synchrony of leaf-out times in temperate forests, as oak and ash continue to advance their leaf expansion, and birch and hawthorn are delayed. This shift away from phenological complementarity will increase competition for light and soil moisture, and drive changes in forest composition over time. Monitoring methods that detect subtle changes in the order of leaf expansion among different tree species will be important to predict future changes in forest composition.

As well as detecting variation in leaf-out phenology between species, methods also need to detect within-species variability. It is well-established that variation within species occurs between populations as a result of genetic adaptation to environmental conditions, particularly in relation to latitude, longitude and altitude (Chmura and Rozkowski, 2002; Vitasse et al., 2009a). A recent study showed high levels of variation within populations. Delpierre et al. (2017) found within-population variability in budburst dates for oak and beech were comparable to the variability between populations spanning an altitudinal gradient of over 500 m. In that study, genetic and phenotypic variation were found to be responsible for the observed within-species variation, over and above the influence of local environmental factors, though this is likely to vary according to the heterogeneity of the forest site. The fact that individuals within a species can vary so starkly, even within close proximity, demonstrates the need for high levels of replication within and between sites. The extent of genetic and/or phenotypic variation within a population could determine its competitive position and ability to persist in a given forest ecosystem. This variation could also determine the survival of insect species with synchronised life-cycles, and in turn the species that depend on them for food (Cole and Sheldon, 2017). To understand such impacts, information on when tree populations reach peak foliar development would be required, across forested landscapes, at a range of spatial scales. The recent rise in citizen science has led to the establishment of continental-scale phenology networks, and opened up the potential for much greater coverage of monitoring (Gerst et al., 2017; Jeong et al., 2013), but there is a need to ensure harmonised and efficient methods to maximise potential.

At present the approaches used to characterise leaf phenology vary considerably between observational studies. Key historical phenological records are based on first event dates (Primack and Miller-Rushing, 2012; Sparks and Carey, 1995) and many subsequent studies have characterised tree leaf phenology based on first budburst or first leaf expansion (Collinson and Sparks, 2008; Fu et al., 2015; Menzel and Fabian, 1999; Polgar et al., 2014; Roberts et al., 2015; Schaber and Badeck, 2005). Both international and national phenology monitoring programmes use first event metrics (Chmielewski, No date; Nature's Calendar, 2017; NatureWatch Canada, 2017; Project Budburst, 2017) due to their advantages in terms of lower survey effort and ease of identification (Miller-Rushing et al., 2008). However, studies looking at the reliability of metrics in avian and flowering phenology have found that first event dates produce biased estimates, identifying extreme responses at one end of the phenological period (Miller-Rushing et al., 2008; Moussus et al., 2010). There appears to be surprisingly little information on time taken from first budburst to canopy development, in individual trees, and how this varies between and within species. Richardson and O'Keefe (2009) reported that in a study of sixteen canopy species, there was a maximum difference of eighteen days in the time taken to progress from 50% budburst to 50% leaf expansion. They also noted that some species changed rank order between phenophases, *i.e.,* species with earliest budburst were not necessarily earliest to achieve leaf expansion. This suggests that relying on budburst dates alone could lead to inaccuracies in predicting leaf development.

As an alternative to simply recording first budburst or first leaf expansion dates, some studies have recorded multiple dates to identify transitions between phenophase growth stages, using standardised scales such as the BBCH system (Finn et al., 2007) or bespoke indices (Capdevielle-Vargas et al., 2015; Cole and Sheldon, 2017; Richardson et al., 2006; Vitasse et al., 2009b). Recently the USA National Phenology Network (USA-NPN) introduced status and intensity monitoring into their citizen science programme (Denny et al., 2014; Elmendorf et al., 2016). Observers are encouraged to record both the phenophase growth stage and the intensity, for example by estimating the percentage budburst or leaf expansion, in order to track the entire progress of canopy development for individual trees. The major advantage of collecting time-series for individual trees is it enables the rate of canopy development to be established, and peak leaf development timing to be identified. However, as observations increase in complexity, data quality challenges arise. Lower levels of accuracy have been reported when citizen scientists have to identify emerging leaves, as opposed to expanding leaves, as the former is a finer detail that is harder to identify, particularly when the canopy is very high (Fuccillo et al., 2015). Subjectivity associated with visual estimates can also be a problem leading to between-observer bias (Morrison, 2016), particularly where a large and variable tree canopy is being considered. Studies comparing estimates of vegetation cover have demonstrated lowest accuracy for estimates over large areas (> 4 m^2) because it is difficult to consider the whole area at once (Vittoz and Guisan, 2007). Improved accuracy is found for cover estimates with smaller focal areas, and highest accuracy is found where objective counts are used (Vittoz et al., 2010). Therefore, a method involving counts of leaf expansion, focussing on different sections of a tree crown, may offer a more repeatable measure for quantifying leaf expansion. The extent to which counts of leaf expansion within crown sections are representative of the phenology of the whole crown needs to be tested.

In order to detect subtle variation in tree phenology between and within tree species, it is important that observations are made frequently enough to capture the timing of leaf expansion. In reviewing the literature I found observational studies that monitored trees every other day (Wesolowski and Rowinski, 2006), 2–3 times per week (Capdevielle-

Vargas et al., 2015; Cole and Sheldon, 2017), once a week (Delpierre et al., 2017; Richardson et al., 2006) and every 10 days (Vitasse et al., 2009b). In order to maximise volunteer time and increase take-up among citizen scientists, it would be useful to understand minimum frequencies required to detect inter- and intra-species variation in leaf phenology. Remote-sensing tends to obtain data sets with an 8–16 day resolution due to loss of images from cloud cover and atmospheric interference (Ahl et al., 2006; Hamunyela et al., 2013). Logistic growth models have now been widely used with remote-sensing data to characterise the phenological pattern using known data points to predict missing observations (Cleland et al., 2007b). A similar approach can be applied to observational data sets (Cole and Sheldon, 2017; Richardson et al., 2006). It would be useful to compare estimates of leaf expansion timing and rate derived from logistic growth models using observations conducted at different temporal grains, *i.e.*, every two days, four days *etc.*, to identify how often observations are needed to accurately characterise the leaf expansion of individual trees.

Recently, near-surface remote sensing techniques have emerged that offer good potential for gaining data on tree leaf phenology, with both high spatial and temporal resolution (Jeong et al, 2013; Keenan et al. 2014). Digital cameras or Normalised Difference Vegetation Index (NDVI) sensors that track canopy greening can be positioned just above the canopy, and capture data at multiple intervals per day. These methods can detect green signals that indicate leaf emergence and development with high-levels of accuracy (Inoue et al., 2014; Soudani et al., 2012). Such methods are not affected by cloud conditions like satellite imagery (Polgar and Primack, 2011), but may be affected by the influence of understorey greening (Inoue et al., 2014). Sideways-facing cameras, as employed through the Phenocams network in the United States (Richardson et al., 2007) and as part of the Phenological Eyes Network in Japan (Inoue et al., 2014), are less influenced by the understorey, though image quality can be affected by light conditions (Mizunuma et al. 2012). With both types of canopy imagery it is possible to isolate trees so that time-series of individual tree canopy development can be derived (Inoue et al., 2014; Polgar and Primack, 2011), though in dense forest stands it may be hard to separate leafing of an individual tree from leafing of other trees in the image background. Despite the lower cost associated with these techniques, in comparison to manually operated ground-based techniques such as hemispherical photography (Richardson et al., 2007; Soudani et al., 2012), the cost and logistics of installing equipment will still limit this approach to a relatively small number of sites. Given the rise in interest in citizen science and phenological monitoring, there may be potential to engage citizen scientists in photographing tree crowns and branches, reducing the need to use visual estimates that can be time-consuming and open to between-observer bias. However, the practicalities of photographing individual tree crowns and branches from the ground within a forest requires testing, as does the ability to fit the derived data to logistic models to obtain phenological metrics.

In this study I aim to assess the effectiveness of a range of methods for characterising spring leaf phenology of individual trees in a forest, to identify the best approach for obtaining large-scale data that can improve understanding of forest ecosystem dynamics under climate change. Ten individual trees across four tree species were monitored every other day, from the period prior to budburst, until all trees had fully expanded their leaves. For each tree, first budburst and first leaf expansion dates were recorded, and the progress of leaf expansion was monitored using two visual observations: an objective method involving counts of buds on three sections of the tree crown, and a percentage estimate considering the whole tree crown. In addition, photographs were taken to assess whether handheld digital photography from ground-level could be used to monitor the progress of leaf expansion using greenness signals. I then assessed whether time-series from counts, percentage estimates and photographs could be fitted to logistic growth models to characterise the rate and timing of leaf development. I compare the consistency of phenological patterns derived from first event dates versus time-series data, and from the three data collection methods: counts, percentage estimates and photographs. Finally, I test whether lower frequency observations provide comparable estimates of leaf expansion timing, and I consider the practicalities of the trialled methods for obtaining temporally rich and spatially extensive data on leaf expansion using a citizen science approach.

3.2 Methods

3.2.1 Study site and data collection

The study took place in Widey Woods, an 8 ha broadleaved woodland in Plymouth, England (50°24 N, 7°7 W), during spring 2015. The four tree species included were European ash (*Fraxinus excelsior*), European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*). These species were selected as they were dominant in the canopy of the study site, and are widespread species across European temperate forests. Ten mature trees from each species were randomly selected for inclusion in the study, fitted with a removable plastic tag for identification, and GPS marked for ease of relocation. Trees were selected within the diameter at breast height (DBH) size class of 20–60 cm. Average tree DBH was 35 cm (±10 cm) and average height was 18 m (±4 cm).

Trees were visited weekly from the middle of February 2015 to assess for signs of imminent budburst, indicated by bud-swelling. This was three weeks prior to earliest reported budburst for target species (Elmendorf et al., 2016), based on budburst records from the previous year for south-west England (Nature's Calendar, 2017). Bud-swelling was evident from the last week in March, so trees were visited every other day from then onwards, until all trees had attained full leaf expansion (2 June). During the period January-June 2015 regional temperatures were close to the 20-year average, with the exception of April which was 2°C warmer (Data source: Haytor weather station, 50.57° N, 3.94° W).

First budburst was recorded as the Julian calendar day of year (DOY) when green leaves were first visible emerging between bud scales at any location on the tree. First leaf expansion was recorded as the DOY when the first leaf with characteristic shape for its species was visible on the tree. From the date of first leaf expansion, two different methods of visual estimation were used to monitor canopy development. First, the extent of leaf expansion across the whole tree crown was estimated as a percentage. Estimates were made in increments of 5% between 5–100%, but allowed for smaller increments from 1–5% so that early activity could be captured. Secondly, counts were made of leaf expansion in three sections of the tree crown. These sections were established prior to first budburst, and reference photographs were taken to ensure the same areas were assessed on each visit. In each section, a count was made of the number of buds out of 50 that had at least one fully expanded leaf present, giving a total count out of 150 buds. Binoculars with x10 magnification were used to aid observations, and a clicker counter used to reduce risk of counting errors.

For each tree, data were converted along a proportional scale from 0 to 1, with 0 representing the crown prior to leaf expansion, and 1 representing the crown with full leaf expansion. For count data, this was achieved using equation (1):

$$a = (x - crown_{\mathrm{MIN}}) / (crown_{\mathrm{MAX}} - crown_{\mathrm{MIN}}) \tag{1}$$

Here, a represents the leaf expansion proportion for a given DOY, x is the number of leaves out of 150 buds that were expanded on that DOY, $crown_{\mathrm{MIN}}$ represents the number of leaves expanded at the start of the time series (*i.e.,* 0), and $crown_{\mathrm{MAX}}$ represents the number of buds with at least one fully expanded leaf at the end of the time series. As the estimate data were in percent increments, these were simply divided by 100 to convert them to proportions. As well as considering the time-series for each individual tree, tree observations were also combined to generate a single time-series for each species. For the time-series based on count data, counts across the ten trees in each species category were combined, to derive proportions based on the number of leaves expanded out of 1500 buds. For the estimate data, percent leaf expansion estimates were averaged from each day, across the ten trees in each species category.

In addition to visual observations, digital photographs were taken to estimate leaf development on a subset of ten of the surveyed trees (four ash, two beech, two oak and two sycamore). The same crown sections that were used for counts were photographed, with the photographer standing at a fixed distance from the tree. Photographs were taken using a Panasonic Lumix DMC-TZ35 16.1 MP camera. The camera was handheld during image capture, and automatic exposure settings were used. It is important to note that while photos were taken of the same tree sections that counts were conducted on, they captured a larger area of the branch than the 50 buds assessed using the count method. Furthermore, the size of branch area captured in a photo was not standardised across the photographs, as the method was supposed to be rapid and easily used by citizen scientists conducting a walk around a site. Photographing stopped once the count data indicated all buds had expanded leaves.

Images were stored as JPEGs (4608 x 3456) and analysed using the open access software ImageJ (Rueden, 2016). The Region of Interest (ROI) manager was used to ensure the area contained in the image for each tree section was consistent for each date, and to remove any influence of neighbouring trees in the image periphery. To estimate crown greening, red, green and blue colour channels were separated and analysed independently. The analysis was done using the multi-measure tool in the ROI manager to derive mean digital numbers (DN) representing intensity for each colour channel. The Greenness Index for each image was calculated using equation (2), after Richardson et al. (2007).

$$Greenness\ Index\ (\%) = \frac{Green\ DN}{Red\ DN + Green\ DN + Blue\ DN} \tag{2}$$

Greenness Index values were then standardised on a proportional scale using equation (1), to provide a time-series of crown greening from 0 (no leaves) to 1 (maximum green signal). In this case, a in equation (1) is the Greenness Index proportion on a given DOY, x is the absolute Greenness Index value on that DOY, $crown_{\mathrm{MIN}}$ is the minimum Greenness Index value (*i.e.,* from the first photo in the series where the crown section had no budburst), and $crown_{\mathrm{MAX}}$ represents the highest Greenness Index value in the photo series. As well as obtaining time-series for each crown section, proportions were averaged across the three crown sections to obtain a single time series of crown greening for each photographed tree.

3.2.2 Deriving phenological metrics from time-series data

A range of phenological metrics were derived from the time-series data—for crown sections, whole tree crowns and species—using data from observational and photographic methods. In addition to first budburst DOY and first leaf expansion DOY obtained from visual observation of the whole crown, leaf expansion completion was determined as the DOY when it was first observed that leaf expansion exceeded 95% (hereafter referred to as completion DOY). I then fitted each time series using a logistic growth model, to identify when leaf expansion reached the half maximum (hereafter referred to as 50% DOY) and to characterise the rate of the leaf expansion process. Time to leaf expansion was then calculated as the number of days from first budburst to 50% DOY.

Logistic growth uses non-linear regression to fit a sigmoidal curve, equation (3):

$$y = \frac{\theta_1}{1 + \exp\left[-(\theta_2 + \theta_3 x)\right]} \tag{3}$$

where y is the response variable (proportion of leaf expansion), x is the predictor variable (DOY), and θ_1, θ_2 and θ_3 are the model fitting parameters (Fox and Weisberg, 2011). θ_1 is the upper asymptote. As the data were based on proportions, θ_1 was fixed at 1, as this was the maximum possible value. Two biologically meaningful parameters are derived from the model: the rate parameter (θ_3) and the half-maximum (ψ). The rate parameter is based on the steepness of the curve at its mid-point and represents the proportional increase per day. The half-maximum is a measure of timing, and represents the DOY when leaf expansion (or greenness) reaches 50%, calculated as $\psi = \theta_2/\theta_3$, and hereafter referred to as 50% DOY. Standard error and statistical significance of model parameter estimates were assessed to provide a measure of confidence in the model fits for each data set. All logistic models were fitted using the car package and nls function in R (Fox and Weisberg, 2011).

Finally, I generated time-series to explore the effect of interval time between sampling days (temporal grain) on 50% DOY and rate values from count and percentage estimate data. The original data was collected every other day (two-day temporal grain), so temporal grains of four-days and six-days were simulated by removing data for different DOYs. Regardless of when leaf expansion began for each tree, the start date for different temporal grains was held constant at DOY 107 for all time-series (which was the DOY when leaf expansion was first observed across the monitored trees), as in practise individual trees would be monitored on the same days. Where the DOY for $crown_{\mathrm{MAX}}$ was removed as a result of altering the temporal grain, I inserted the maximum value on the next DOY when data collection would have been carried out. I then re-ran the logistic growth model for each tree.

3.2.3 Statistical analyses

Linear regression was used to explore relatedness between first budburst DOY, first leaf expansion DOY, 50% DOY and completion DOY, based on observational methods (count and percentage estimates). To explore whether these different metrics (and methods) identified similar phenological patterns between species, separate one-way analysis of variance (ANOVA) tests were carried out for each metric and method, followed by pairwise comparisons of species using Tukey Honestly Significant Difference (HSD) tests. One-way ANOVA and Tukey HSD tests were also used to identify whether the time to leaf expansion (*i.e.,* from first budburst to 50% DOY) was consistent between species.

Linear regression was then used to explore relatedness between 50% DOY and rate metrics from counts, percentage estimates and photograph data. Where relationships were identified, paired t-tests were conducted to assess whether the methods produced statistically similar values of 50% DOY and rate for individual trees. Finally, Linear regression and paired t-tests were used to compare 50% DOY and rate metrics derived from the 2-day temporal grain, with those derived from reduced temporal grains. All statistical analyses were carried out in R 3.3 (R Core Team, 2016) .

3.3 Results

3.3.1 Comparison of phenological patterns from first event dates vs. time-series data

Species were different in terms of first budburst dates (Table 3.1, Fig. 3.1 A), with pairwise comparisons showing that ash budburst was significantly later than oak ($p = 0.003$) and sycamore ($p = 0.045$), but all other species were similar ($p > 0.05$). However, considerably different results were obtained from leaf expansion data. There were significant differences between species in terms of first leaf expansion and 50% DOY (Table 3.1, Fig. 3.1 B–D), but ash was similar to all other species ($p > 0.05$). According to first leaf expansion dates, beech and oak were significantly different ($p = 0.027$) as were sycamore and oak ($p = 0.015$), with oak leaf expansion beginning later than the other two species. However, using the 50% DOY only oak and sycamore were different, with oak leafing later than sycamore ($p = 0.036$ based on visual estimate of percentage leaf expansion across the whole crown, and $p = 0.037$ based on counts of leaf expansion on three crown sections). Using the completion DOY metric, differences between species were only significant based on visual estimates of percentage leaf expansion across the whole crown (Table 3.1, Fig. 3.1 I–J), with oak being significantly later than sycamore ($p = 0.046$) but all other species were similar ($p > 0.05$).

As well as identifying differences between species, it is clear that there is considerable variation within species (Fig. 3.1). Ash is the most variable species in terms of first budburst dates, with a 30 day difference in budburst timing from the earliest to the latest individual (Fig. 3.1 A). Other species showed lower intra-species variation in budburst timing (16–19 days). Both oak and ash were highly variable in terms of first leaf expansion (varying by 22–28 days respectively, Fig. 3.1 B). However, oaks were much more consistent in terms of leaf expansion 50% DOY and completion DOY (Fig. 3.1 C–D and I–J). Ash remained highly variable throughout the whole process of leaf development, with ash individuals being both the earliest and latest trees among all species to achieve full leaf expansion (Fig. 3.1 I–J). Beech individuals were fairly consistent in their first budburst and leaf expansion dates, though variability increased as leaf expansion progressed. Sycamore individuals were consistent in first budburst and completion of leaf expansion, but varied considerably at the start of leaf expansion and in their 50% DOY.

There was a significant difference between oak and all three other species, in the time taken from first budburst to 50% DOY (Table 3.1, Fig. 3.1 E–F), with oak taking significantly longer to achieve leaf expansion than the other three species. However, no significant differences were found between species in the time taken from first leaf expansion to 50% DOY, indicated by the similar rates of leaf expansion (Table 3.1, Fig. 3.1 G–H). While the relationship between all metrics of leaf expansion timing, including first leaf expansion dates, were strongly related (all $R^2 > 0.80$, $p < 0.001$), the relationship between first budburst dates and leaf expansion appears curved, and was poorly explained by a linear model (Fig. 3.2; $R^2 = 0.40$, $p < 0.001$ based on counts, $R^2 = 0.42$, $p < 0.001$ based on percentage estimates). This result indicates that trees with later budburst tended to expand leaves more rapidly than trees with earlier budburst.

3.3.2 Comparison of methods for obtaining time-series data

All time series data from count and percentage estimate methods could be fit to the logistic model, obtaining model parameters with low standard error and high significance, indicating good model fits (Appendix 3.1: Tables A3.1 and A3.2). Count and percentage estimate methods were highly related in terms of the 50% DOY values calculated from their respective logistic model fits ($R^2 = 0.97$, $p < 0.001$) and produced statistically similar values for individual trees (Table 3.2). The overall model fits produced by the two methods for each species were almost identical (Fig. 3.3). Both methods identified very similar phenological patterns across species based on 50% DOY and completion DOY (Table 3.1, Fig. 3.1). They also identified similar rates of leaf expansion between species, though the count method showed higher variability of leaf expansion rate for beech and sycamore (Fig. 3.1, G–H). However, estimates of leaf expansion rate from the two methods were found to be statistically similar (Table 3.2).

Of the ten trees included in the photograph trial, data from two trees were excluded because they were affected by foliage expansion of neighbouring trees, such that it was impossible to separate leaves of the target tree from other tree(s) in the image frame. This left eight time series of whole individual tree crowns, with greening based on the average of three crown sections, and 24 time-series of individual crown sections. I was able to fit logistic models to all but one crown section time-series. Parameter estimates for three models based on crown section Greenness Index were not significant ($p > 0.05$), indicating poor model fits. Parameter estimates for the remaining 20 time-series of crown sections indicated good model fits ($p < 0.05$). Logistic models based on eight time-series of Greenness Index values for whole crowns produced good fits with significant parameter estimates and low standard error (Appendix 3.1: Tables A3.3 and A3.4). Statistical comparisons between counts and photographs of crown sections showed that 50% DOY values were related (Fig. 3.4, $R^2 = 0.76$, $p < 0.001$), and actual 50% DOY values were statistically similar (paired t-test: $t_{19} = 0.10$, p = 0.923). However, there was no relationship between the rate parameters from the two methods ($R^2 = 0.01$, p = 0.696).

After removing every other observation from the time-series to simulate a four-day temporal grain, logistic models could be fitted to all forty time-series based on percentage estimate data, and to thirty-seven time-series based on count data (Appendix 3.1: Tables A3.5 and A3.6). The three time-series that could not be fitted with the logistic model (one from beech and two from oak) had only three data points remaining after removal of every other observation, since leaf expansion occurred very rapidly in those individuals. Using the 4-day temporal grain, 50% DOY and rate values were highly similar to values obtained from the 2-day temporal grain, for both percentage estimate and count data (Table 3.2). A six-day temporal grain was tested, but ten logistic models based on count data failed to run due to there being only three data points remaining (Appendix 3.1: Table A3.7). Using estimate data, the six-day temporal grain still produced model fits for all but one time-series, but two further time-series had non-significant parameter estimates (Appendix 3.1: Table A3.8).

Table 3.1. Differences between tree species, according to different phenological metrics and methods of estimation, based on one-way ANOVA and Tukey HSD pairwise comparisons. BB refers to budburst and LE is leaf expansion. Time to 50% DOY is the time taken from first budburst to reach the 50% DOY (*i.e.,* 50% leaf expansion). Significant differences are in bold text.

Metric	**Method of estimation**	***df***	***F***	***p***	**Ash-Beech**	**Ash-Oak**	**Ash-Sycamore**	**Beech-Oak**	**Beech-Sycamore**	**Oak-Sycamore**
First BB	Whole crown % estimate	3	5.41	**0.004**	0.098	**0.003**	**0.019**	0.515	0.893	0.905
First LE	Whole crown % estimate	3	4.74	**0.007**	0.228	0.749	0.148	**0.027**	0.995	**0.015**
50% DOY	Count of 3 crown sections	3	2.91	**0.048**	0.814	0.737	0.292	0.244	0.798	**0.037**
50% DOY	Whole crown % estimate	3	3.04	**0.042**	0.735	0.789	0.243	0.223	0.815	**0.036**
Completion DOY	Count of 3 crown sections	3	2.78	0.055	0.819	0.631	0.433	0.182	0.913	**0.046**
Completion DOY	Whole crown % estimate	3	2.96	**0.045**	0.867	0.623	0.362	0.212	0.814	**0.033**
Rate of LE	Count of 3 crown sections	3	0.33	0.814						
Rate of LE	Whole crown % estimate *	3		0.400						
Time to 50% DOY	Count of 3 crown sections	3	45.03	**<0.001**	0.985	**<0.001**	0.168	**<0.001**	0.310	**<0.001**
Time to 50% DOY	Whole crown % estimate	3	22.79	**<0.001**	0.177	**<0.001**	0.440	**<0.001**	0.940	**<0.001**

*Kruskal-Wallis test used instead of ANOVA due to non-normal distribution of residuals

Table 3.2. Comparison of methods for deriving time-series data on tree leaf development. The relationship between methods is explored with regressions, and the proportion of variation explained (R^2) and statistical significance (p) is shown. Where relationships existed, paired t-tests were carried out to assess differences between absolute values. Methods with statistically similar values according to the paired t-test are highlighted in bold.

		Regression		**Paired t-test**		
Method comparison	**Metric**	R^2	p	*df*	*t*	p
Counts vs Whole crown percentage estimates	**50% LE**	0.97	<0.001	39	0.083	**0.935**
	Completion of LE	0.96	<0.001	39	2.811	0.008
	Rate of LE	0.55	<0.001	39	0.609	**0.546**
Counts vs Photos (Greenness Index)	**50% LE**	0.76	<0.001	19	0.098	**0.923**
	Rate of LE*	0.01	0.696			
2-day v 4-day temporal grain (Counts)	**50% LE**	0.99	<0.001	36	1.320	**0.195**
	Rate of LE	0.88	<0.001	36	-0.921	**0.363**
2-day v 4-day observation frequency (Whole crown percentage estimates)	**50% LE**	0.99	<0.001	39	0.073	**0.942**
	Rate of LE	0.89	<0.001	39	-1.787	**0.082**

*Wilcoxon signed rank test used as variances not equal

Fig 3.1. Comparison of phenological patterns for four tree species, derived from different metrics and methods: A = First budburst dates; B = First leaf expansion dates; C = 50% DOY (from percentage estimates); D = 50% DOY (from counts); E = Time from first budburst to 50% DOY (from percentage estimates); F = Time from first budburst to 50% DOY (from counts); G = Leaf expansion rate (from percentage estimates); H = Leaf expansion rate (from counts); I = Completion DOY (from percentage estimates); J = Completion DOY (from counts). On the box and whisker plots, the horizontal line shows the median, the box represents values within the 25–75% quartiles, and the error bars show the minimum and maximum values. Species with statistically similar patterns share a lower case letter. Statistics are provided in Table 3.1.

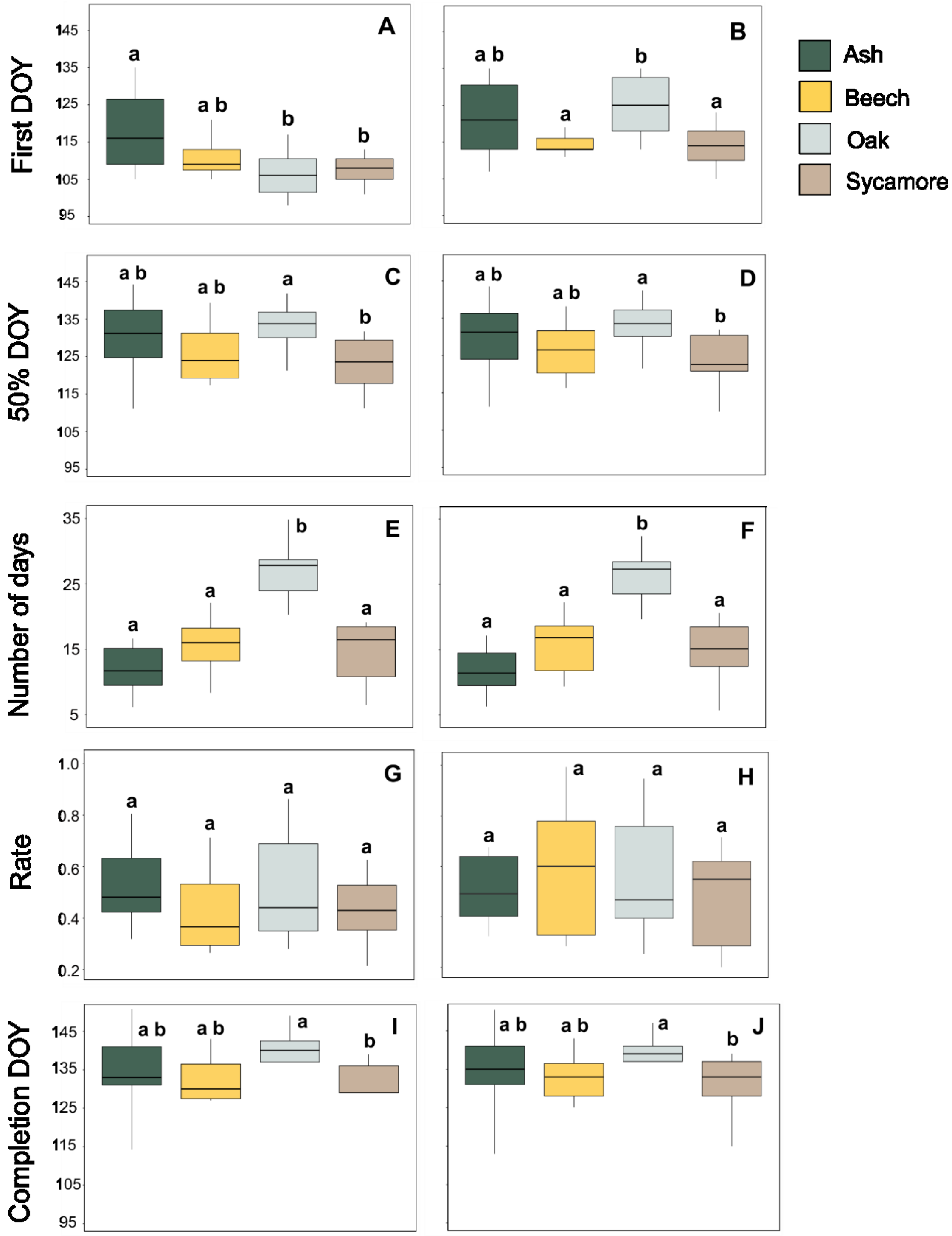


Fig. 3.2. Relationship between first budburst dates and 50% DOY for the four tree species. A = 50% DOY from percentage estimate data; B = 50% DOY from count data.

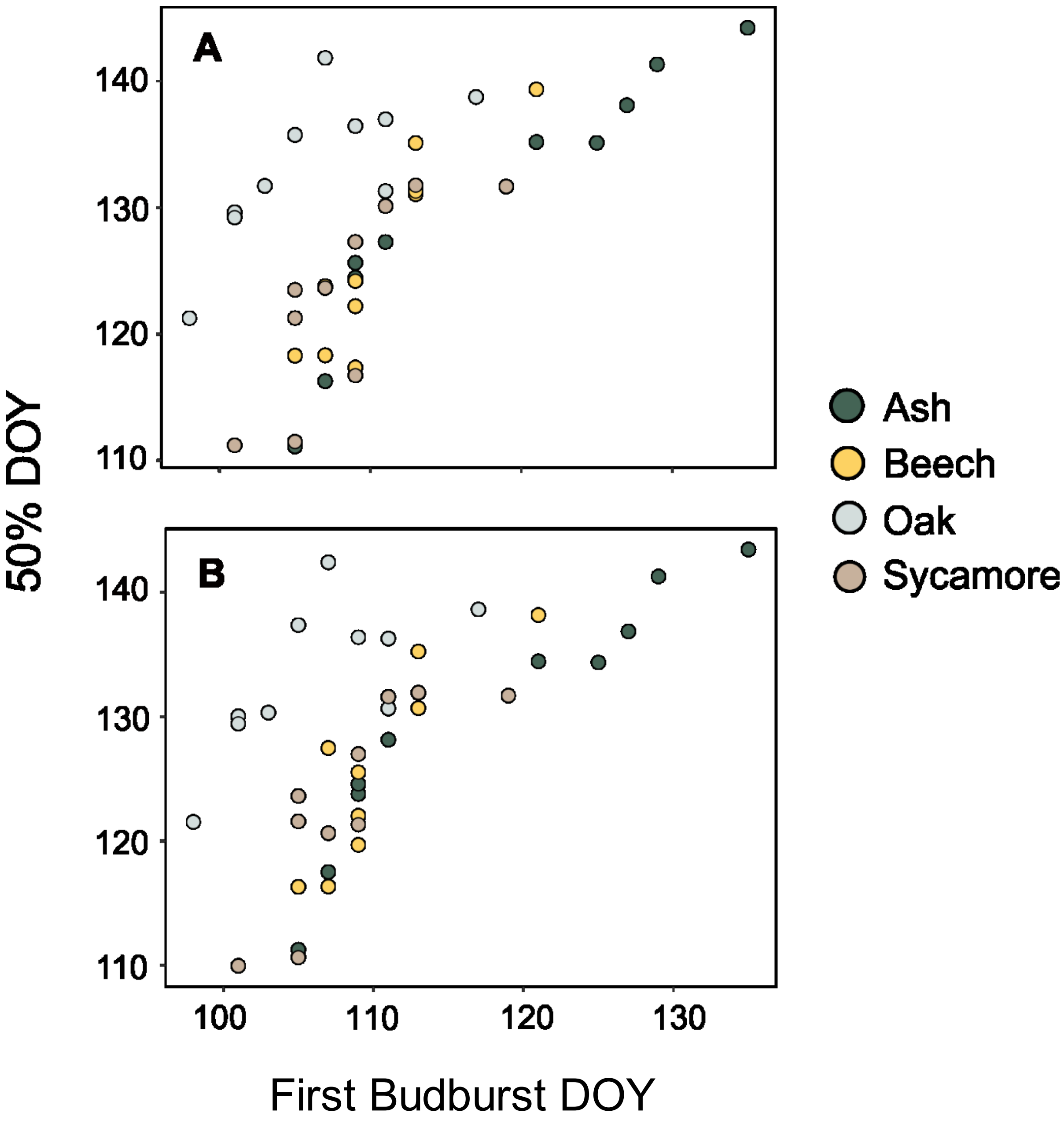
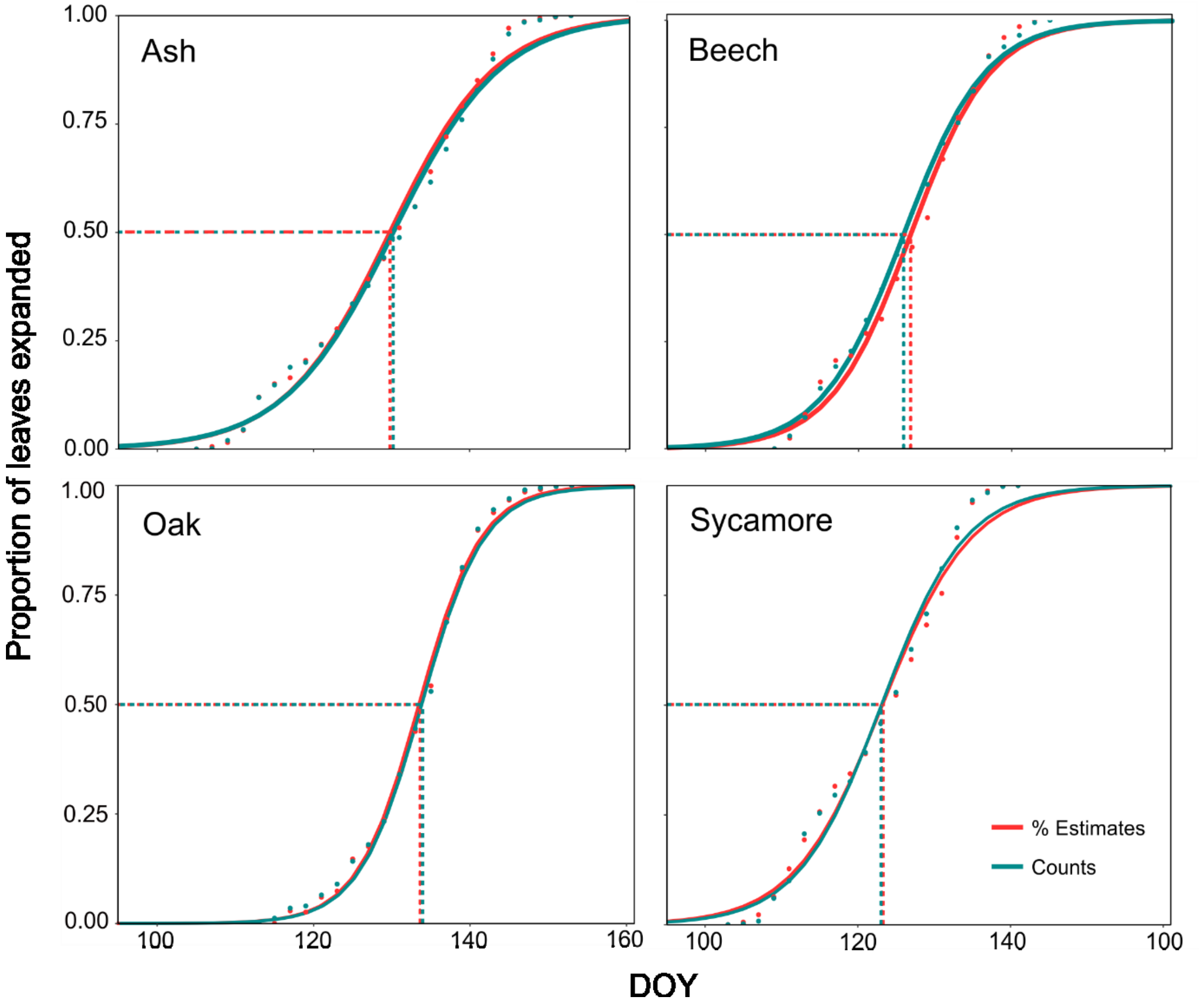
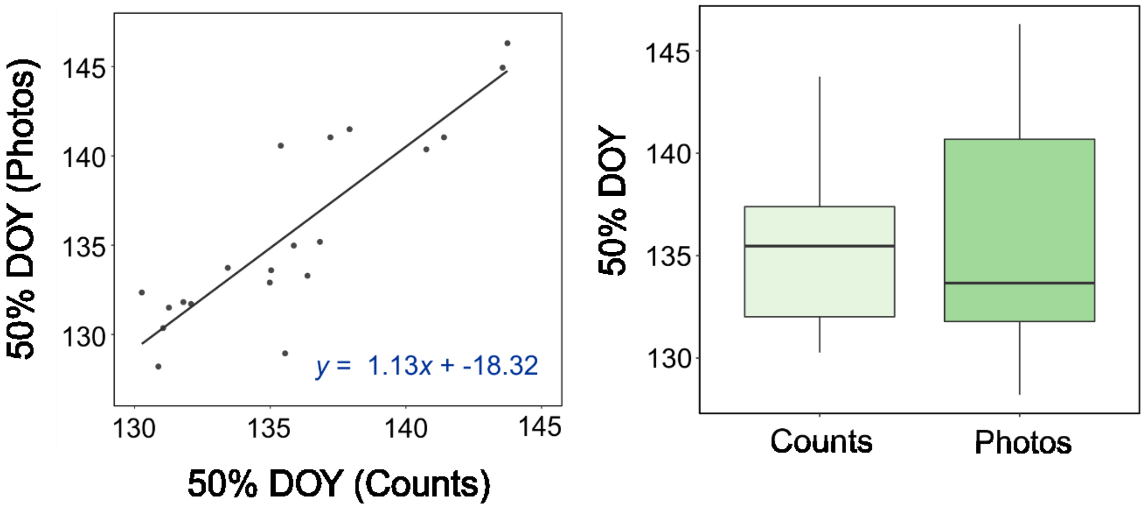


Figure 3.3. Logistic growth models showing overall model fits for each species based on count and percentage estimate data. Dashed lines show the 50% DOY. The model parameter values along with their standard error and significance are reported in the table below to give an indication of goodness of fit. For the 50% DOY parameter the model only gives the standard error.



Species	Method	ɵ2	SE	*p*	ɵ3	SE	*p*	50% DOY	SE
Ash	% estimate	-18.72	0.88	<0.001	0.14	0.007	<0.001	130.2	0.36
	Count	-19.11	0.89	<0.001	0.15	0.007	<0.001	129.8	0.35
Beech	% estimate	-23.43	0.76	<0.001	0.19	0.006	<0.001	125.9	0.19
	Count	-24.05	1.38	<0.001	0.19	0.011	<0.001	126.8	0.33
Oak	% estimate	-33.53	1.24	<0.001	0.25	0.009	<0.001	133.6	0.17
	Count	-33.68	1.12	<0.001	0.25	0.008	<0.001	133.6	0.15
Sycamore	% estimate	-22.46	1.38	<0.001	0.18	0.011	<0.001	123.1	0.37
	Count	-21.18	1.36	<0.001	0.17	0.011	<0.001	123.2	0.41

Fig 3.4. Comparison of 50% DOY values from visual counts of leaf expansion on tree sections and 50% DOY values from photo-derived greenness index on tree sections. Data is from counts and photos of 20 crown sections across eight different trees. The left-hand plot shows the relationship between 50% DOY values ($R^2 = 0.76$, $p < 0.001$). The right-hand plot shows the range of 50% DOY values from each method: the horizontal line shows the median, the box represents values within the 25–75% quartiles, and the error bars show the minimum and maximum values.



3.4 Discussion

This study suggests that first budburst dates could give unreliable information on the timing of canopy development, with important implications for studies of forest ecosystem dynamics. The order in which species reached first budburst did not reflect the order in which they reached 50% or full leaf expansion. Oak was a particularly notable case in this study, taking on average twice as long to reach 50% leaf expansion after first budburst, compared to all three other species. Interestingly this was not reflected in a difference in the rate of leaf expansion, which was based on time from first leaf expansion to 50% expansion, suggesting the delay was instead between first budburst and first leafing. As well as differences between species, there was also intra-species variation in the time taken from first budburst to 50% DOY. The curved relationship between first budburst dates and 50% DOY was noticeable for all species, particularly ash, demonstrating a tendency for individuals with later budburst to leaf more rapidly than conspecific individuals with earlier budburst, as has been observed elsewhere (Cole and Sheldon, 2017). Given that first budburst dates were a poor predictor of leaf expansion timing, I suggest that caution should be exercised when interpreting first budburst dates, as they do not fully characterise the trajectory of canopy development, or necessarily signal the order in which tree canopies mature. While first leaf expansion dates show more similar patterns to 50% DOY, they still identify a different ordering of phenology between species, and show different patterns of intra-species variation. In order to predict impacts of changing phenology on ecosystem processes and function, data sets that encapsulate the entire process of canopy development are critical. There will also be benefits to other areas of climate science. Later stages of leaf expansion correspond more closely to remote sensing indices, so can help to validate satellite data (Elmore et al., 2016; White et al., 2014). In addition, finer-scale detection of variation in leaf development timing between and within species will help to identify environmental cues for leafing phenology and improve predictive models for biosphere-climate modelling (Richardson et al., 2012).

Given the variability within species and the small sample size in this study, it is not possible to say whether the pattern observed for oak exists more broadly. It is interesting to note that Morecroft et al. (2003) found that a studied population of *Quercus robur* took two months from budburst to reach peak photosynthetic activity, suggesting that peak photosynthesis does not occur until well into summer. Satellite and near-surface remote-sensing data have also indicated that onset of peak photosynthetic activity lags canopy greening (Richardson et al., 2007), though usually to a lesser extent than reported by Morecroft et al. (2003). It would be interesting to identify whether other populations of oak show similar patterns to those observed in this study, and to what extent the delay in photosynthetic activity is a function of slow leaf expansion versus changes in leaf physiology after full canopy development. More studies incorporating monitoring of photosynthetic development for different species and populations will also be important, to improve understanding of the relationship between leaf expansion and photosynthesis, and how this varies between species.

In this study, there were no differences identified between species in terms of leaf expansion rate, but there was substantial intra-species variation. The majority of phenology studies focus on timing metrics, and the rate of a process is often ignored (Brown et al., 2017). However, these results indicate that by not considering leaf expansion rate, important information on within-species variability could be missed. The degree of variation in leaf expansion rate within a species could have important implications for fitness and resilience in a population. For example, two trees sharing similar 50% DOYs could have very different leaf emergence timing, making one individual more vulnerable to spring frosts and herbivory damage. This supports the argument that methods that collect time-series data are preferable to event monitoring.

Considerable intra-species variation was also observed in leaf expansion timing, in agreement with other studies that have monitored multiple individuals of a species at a single site (Capdevielle-Vargas et al., 2015; Cole and Sheldon, 2017; Delpierre et al., 2017). The level of intra-species variation itself varied between phenophases, further highlighting that snapshot assessments of tree phenology can be misleading. Ash was particularly variable in terms of both budburst and leaf expansion timing. Interestingly, in this study there was no significant difference in leaf expansion timing between ash and sycamore, though ash is typically a late-leafing species while sycamore is typically an early-leafing species (Morecroft et al., 2008; Roberts et al., 2015; Sparks and Carey, 1995). This variability in ash, if widespread, could increase its resilience to climate change, notwithstanding other threats. However, it is likely that intra-species variation masked differences between these species that might be identified with a larger sample size. This has been a finding of other studies (Cole and Sheldon, 2017), and backs up the need for methods that enable high levels of within-site and within-species replication. While ten individuals is the recommended minimum sample size by the USA-NPN (Denny et al., 2014), I recommend that larger sample sizes be used where possible (Elmendorf et al., 2016) and that data from these studies be used to identify ideal minimum samples sizes for target species.

Logistic growth models have been widely used to characterise the phenology of landscapes and forest stands from remote sensing data (Calders et al., 2015; Richardson et al., 2007; Zhang et al., 2003), and can also be fitted to the shorter time-series obtained from individual trees. Even when the data set was reduced by removing every other observation, the model still provided very similar estimates of 50% DOY and rate. The instances when the model failed to fit the data was where leaf expansion occurred very rapidly, leaving only three data points. In one of the time-series only four data points remained after removal of observations, but the model still produced a fit, though parameter estimates had higher standard errors. With five data points, the model performed well. This indicates that for individual trees, where the time series is relatively short, observations carried out every four days are sufficient to detect phenological patterns with good accuracy, but less frequent observations could reduce accuracy and limit the potential to model the phenological process using this approach.

Having highlighted the benefits and potential for collecting time-series data for individual trees, reliable methods for obtaining this data are needed. In comparing observational methods, I found that observing three relatively small sections of a tree gives comparable results to assessments of a whole tree crown. This is promising, as three sections can be assessed relatively quickly, and though more time consuming than a single estimate of a tree crown, observer bias may be reduced by the increase in objectivity (Galloway et al., 2006; Vittoz et al., 2010). However, the trees included in this study were relatively small mature trees. It follows that the comparability between counts of three crown sections and whole crown estimates could decrease as crown size increases, as a smaller proportion of the total crown is assessed. That said, large trees pose problems for phenology monitoring generally, both in terms of viewing buds in order to make counts, and in terms of making accurate estimates (Fuccillo et al., 2015; Vittoz and Guisan, 2007). Trials of count and estimate methods are needed with citizen scientists, to determine levels of error associated with both approaches, and the extent to which this varies with crown size, height and species.

Based on this study, ground-based photography offers potential to supplement data collection on individual tree phenology, though a number of issues need to be considered. Firstly, in a forest situation, the position from which photographs are taken must be carefully chosen. Two time-series had to be excluded because of the influence of background foliage, despite efforts taken prior to onset of leaf expansion to choose branch sections that would be unimpeded by surrounding vegetation. Given the potential difficulty in selecting appropriate regions to photograph, the use of fixed camera mounts (University of New Hampshire, 2017) might be necessary if this method was to be used with citizen scientists. This would also ensure photos were taken of the same branch sections, and would increase feasibility of obtaining complete time-series, as different surveyors could be involved in image capture.

The greenness index data was comparable to visual observations in terms of 50% DOY but not rate. Previous studies using fixed cameras on canopy towers, found greenness to be closely related to leaf expansion, though in one study greenness identified earlier 50% DOY than visual observations (Mizunuma et al., 2011). Greenness is a function of both leaf expansion and pigment changes, so while related, leaf expansion and greenness are different (Keenan et al., 2014a). This must be borne in mind when interpreting data from different methods. Greenness index data is an additional measure of leaf development, and should be seen as complementary to leaf expansion data, rather than a substitute for it. Furthermore, it is important to note that there was considerable variability within some of the time-series, resulting in poor model fits for three of the crown sections. This is likely due to day-to-day fluctuation in solar radiation, affecting image lighting (Mizunuma et al., 2011; Richardson et al., 2007), and also limitations in the quality of the consumer-grade digital camera used (Richardson et al., 2007). The selection of appropriate camera angles can help minimise the influence of light conditions (Inoue et al., 2014). This further emphasises that fixed camera mounts are likely to be necessary to ensure data quality with this method.

3.5 Conclusions

Citizen science phenology monitoring has the potential to provide large-scale data at fine resolutions, to help understand how tree leaf phenology varies according to a range of environmental and genetic factors. However, to do so effectively requires the collection of time-series data to track the development of individual tree crowns. Reliance on first event dates can lead to misinterpretation over the ordering of leaf development among species, and provides no indication of leaf development rate. Fixed mount photography from the ground could be used to supplement data on canopy greening currently collected through projects such as the Phenocams network. With technological development, consumer-grade digital cameras and smartphone cameras are becoming increasingly advanced in their capabilities, which could enhance future prospects for obtaining reliable data on canopy greening. However, further work is needed in this area, to ensure good data quality from handheld photography of individual tree crowns. Therefore visual observations remain the most viable option for widespread data collection on individual tree phenology at present. Further research is needed to assess volunteer accuracy using counts and percentage estimates to quantify leaf expansion.

4 A comparison of ground-based methods for estimating canopy closure for use in phenology research

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4.1 Introduction

Climate change is affecting forest ecosystems around the globe, with changes in tree phenology widely documented for temperate forests (Richardson et al., 2013; Roberts et al., 2015; Vitasse et al., 2011). Growing season extensions have been observed for many European tree species, most notably due to canopies coming into leaf earlier (Menzel and Fabian, 1999; Menzel et al., 2006; Thompson and Clark, 2008). The phenology of dominant canopy trees exerts strong influence on the understorey environment, as canopy openness is highly related to available photosynthetically active radiation (PAR) (Brusa and Bunker, 2014; Gonsamo et al., 2013; Promis et al., 2012), influencing microclimate, soil respiration (Giasson et al., 2013; Yuste et al., 2004) and understorey plant dynamics (Van Couwenberghe et al., 2011). Therefore, earlier canopy closure and later senescence is likely to have wide-ranging impacts on the phenology and life processes of understorey plants and wider forest biodiversity. Studies have indicated threats to spring ephemeral herbs that utilise the period before canopy closure for completing their life cycle (Kim et al., 2015). Many tree saplings depend on spring sunlight prior to canopy closure for their growth and survival (Augspurger, 2008). Understorey species that are shade tolerant or those with greater phenological plasticity are likely to gain competitive advantage (De Frenne et al., 2011), and invasive species could become more prevalent (Engelhardt and Anderson, 2011; Willis et al., 2010). As canopy openness is a key determinant of ecological processes in the understorey, effective methods for monitoring intra and inter-annual changes in the timing of canopy closure/openness would be very useful, especially if they allowed data to be collected across a variety of spatial scales, and with plenty of replication.

Canopy phenology has been extensively studied in recent years. Satellite remote sensing has enabled data collection of forest leaf phenology at large spatial scales (Boyd et al., 2011; Wang et al., 2016; White et al., 2009; Wu and Liu, 2013; Zhang et al., 2005). These methods focus on deriving estimates of canopy green-up dates from Normalised Difference Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI) data, for the purpose of tracking photosynthetic activity to assess forest productivity, gas exchange and phenological feedbacks to the climate system (Richardson et al., 2013). While remote sensing data is useful for identifying large-scale phenological trends, the coarse resolution means that local variations between forest stands are often masked (Fisher et al., 2006; White et al., 2014). Furthermore, loss of temporal resolution due to atmospheric conditions (Cleland et al., 2007b; White et al., 2014), and difficulties separating greening of the understorey from canopy greening (Hamunyela et al., 2013), can compromise the use of this data for identifying shifts in canopy closure timing.

A range of ground-based methods have been used to assess canopy structure and understorey light environments at the forest-level. Direct measures of understorey light are highly affected by sky conditions and accurate determination requires continuous measurement over several days (Engelbrecht and Herz, 2001; Gendron et al., 1998). This makes direct measurements inappropriate for phenology studies where the objective is to assess variation through time. As an alternative, hemispherical photography and Plant Canopy Analysers (PCAs) such as the LAI-2200, are commonly used to assess structural attributes of forest canopies (Frazer et al., 1997; Gonsamo et al., 2013; Hale and Edwards, 2002; Rich, 1990). Both instruments incorporate an extreme wide angle view to measure gap fraction – defined as the proportion of unobstructed sky in a given region of the projected image plane (Frazer et al., 1997) – at multiple zenith angles. For estimating understorey light levels, particularly during spring, wide viewing angles are an advantage as sunlight largely penetrates the canopy below the zenith. Using gap fraction measurements, Leaf Area Index (LAI) and canopy openness can be determined.

LAI is the most widely used metric of canopy structure (Jonckheere et al., 2005; Weiss et al., 2004), though it is also one of the most difficult to characterise accurately (Bréda, 2003). LAI is defined as one half the total green leaf area per unit ground surface area (Chen and Black, 1992). Hemispherical photography and PCAs assess the whole canopy as viewed from a single point, using gap fraction inversion principles and radiative transfer theory respectively (Chen et al., 1997; Macfarlane et al., 2007; Woodgate et al., 2015). As such, LAI derived from optical methods actually characterises 'Plant Area Index' (as trunks and branches are included as well as leaves), and is highly related to understorey light levels (Bréda, 2003; Jonckheere et al., 2004). However, both methods are costly, particularly PCAs, which in addition to high instrument costs, require simultaneous reference light readings outside the canopy. This is problematic in forests, as a wireless set up or remote data loggers are needed, adding additional resource implications and making the method impractical for large-scale use (Bréda, 2003). Furthermore, both methods for estimating LAI assume that canopy elements are randomly distributed. In reality, a degree of 'clumping' occurs both within and between plant canopies (Bréda, 2003; Chen et al., 1997; Ryu et al., 2010; Weiss et al., 2004). The degree of clumping varies depending on forest type and structure, and also shows strong seasonal variation according to the phenological stage (Ryu et al., 2010). Therefore accurate LAI estimation requires determination of a clumping index for a given canopy at a given time of year, and specialist equipment and/or software is required (Chianucci et al., 2015; Ryu et al., 2010).

Digital Cover Photography (DCP) using ordinary digital cameras can also be used to estimate LAI following the method proposed by Macfarlane et al. (2007). This method has a number of advantages as specialist equipment and software are not required, though a number of steps are involved in analysis to calculate effects of foliage clumping (Chianucci et al., 2014; Macfarlane et al., 2007). DCP has been successfully used to track canopy development in phenological studies concerned with photosynthesis and gas exchange (Ryu et al., 2012). However, the restricted viewing angle of DCP is less appropriate for tracking the progress of canopy closure, where the objective is to assess change in the relative timing of shading in the understorey. Although LAI is highly related to understorey light (particularly where it is based on gap fraction at multiple zenith angles) it is primarily used to quantify ecosphysiological attributes of forest canopies (photosynthetic and transpiration rates) to study climate-biosphere interactions (Bréda, 2003; Chen et al., 1997; Jonckheere et al., 2004; Macfarlane et al., 2007; Woodgate et al., 2015). Where the aim is to track changes in relative canopy closure to determine temporal variability in understorey light, canopy openness is a more appropriate and straightforward metric to use (Brusa and Bunker, 2014).

Canopy openness is the proportion of the entire sky hemisphere that is unobstructed by vegetation when viewed from a single point (Jennings et al., 1999), and is highly correlated with understorey light (Brusa and Bunker, 2014; Gonsamo et al., 2013; Pellikka, 2001; Promis et al., 2012; Roxburgh and Kelly, 1995; Whitmore et al., 1993). Hemispherical photography has been widely used to assess canopy openness, representing the sum of all gap fraction values, weighted according to zenith angle, and multiplied by 100 to give a percent visible sky value (Frazer et al., 1997). The advent of digital cameras and their increasing availability has made hemispherical photography more widely available for forest science (Brusa and Bunker, 2014; Frazer et al., 2001; Hale and Edwards, 2002; Inoue et al., 2004). However, cost and resource implications still preclude many forest managers from using it as a monitoring tool. While hemispherical photography does not require reference light readings to be made, images must be taken under specific weather conditions—on dry, still days, without direct sunlight, normally early or late in the day, or on a day with uniform overcast skies (Rich, 1990). This places considerable constraint on when data can be collected. Once images have been obtained, analysis can be time-consuming and expensive. Though free specialist software programmes now exist that provide comparable results to professional software (Promis et al., 2011), expertise is still required. Overall, the technique is prohibitively expensive, in terms of cost and time, for phenology studies that require high levels of replication.

A variety of cost-effective, rapid assessment alternatives to hemispherical photography have been used to assess canopy openness, including photography without a fisheye lens (Pellikka, 2001), the canopy scope (Brown et al., 2000), and simple visual estimations (Jennings et al., 1999). These methods differ in their view zenith angle; therefore canopy openness in this context is defined as the proportion of unobstructed sky within the total area viewed. While these methods are used to characterise coarse-level variation in canopy openness, their ability to detect fine-scale changes in canopies through time needs to be assessed. Another option has emerged in the last few years with the rise of smartphones that have high resolution cameras. Inexpensive fisheye lens attachments for smartphones have recently become available for less than US$10. Smartphone photography, if reliable, could provide an efficient means of collecting large quantities of data on the timing of canopy closure using citizen science.

The use of citizen science has proven highly successful in other areas of phenological research, including observational studies of plant bud-burst and leaf-out timing (Collinson and Sparks, 2008; Jeong et al., 2013; Mayer, 2010). The widespread and increasing ownership of smartphones means that many people now carry sophisticated cameras, making them ideal citizen science tools. However, a considerable range of makes and models exist. These vary in their camera specifications (*e.g.,* resolution, focussing capability and angle of view), which could affect canopy openness estimations (Frazer et al., 2001; Inoue et al., 2004; Jennings et al., 1999). Therefore, for this method to be practical for large-scale use, different makes and models of smartphone need to give comparable estimations.

In this study, we compared canopy openness values (% visible sky) from hemispherical photography, with estimates derived from visual estimation techniques and from smartphone photography, with and without the use of a fisheye lens attachment. Data were collected in winter, spring, summer and autumn, at fixed points across four broadleaved woodlands in south-west England, to assess the extent that surrogate methods can estimate variation in canopy openness. We then tested a basic means of analysing hemispherical photos and smartphone fisheye photos to derive canopy openness using non-specialist image analysis software. We did this by comparing simple canopy openness values (% visible sky) derived from the free image-analysis software, with weighted canopy openness values (% visible sky weighted as a function of gap fraction zenith angle) from professional specialist software. Recognising that different makes of smartphone camera might perform differently, we also compared three popular smartphone cameras in a separate trial. The different phone cameras were tested in broadleaved woodland under three levels of canopy density, and with multiple camera operators, to test reproducibility under different canopy conditions and with different users.

Our overall objectives were: a) to identify whether any of the proposed surrogate methods provide reliable estimates of variation in canopy openness; b) to identify whether non-specialist image analysis software can produce comparable estimates to specialist software; c) to test whether different smartphone camera models and different camera users yield similar canopy openness estimations. It is important to note that this study was not concerned with identifying methods to closely represent absolute values, since it has already been established that methods incorporating different view angles tend to give different absolute estimates of canopy openness (Bunnell and Vales, 1990; Cook et al., 1995). Our focus was to identify whether any of the alternative methods could reliably identify relative differences in canopy openness to monitor canopy closure timings, and promote data collection through large-scale citizen science.

4.2 Methods

4.2.1 Comparison of methods against hemispherical photography

Trials took place in 2014 at four woodlands in Devon, England. The suite of sites was purposely chosen to represent a range of canopy/understorey light conditions, with varying aspect, composition and structure (Table 4.1). Six fixed sample points or 'stations' were randomly selected in each of the four woodlands. At each station, canopy openness was estimated by a variety of methods in each season (related to leaf phenology): winter (no canopy), spring (around 50% leaf-out), summer (full canopy) and autumn (around 50% leaf-drop). All estimates were made concurrently for a woodland within each season, and the four woodlands all estimated within a week of each other.

Hemispherical photography

Hemispherical photographs were taken in colour using a Nikon Coolpix 990 3.34 MP camera with Nikon Fisheye Converter FC-E8 lens (Nikon Corporation, Tokyo, Japan). The circular fisheye lens provides a 180° field of view in all directions. Images were taken using the basic quality setting and stored in VGA-size, as canopy openness estimates are not affected by resolution or size settings with this camera model (Inoue et al., 2004).

Photos were taken without rain or direct sunlight entering the lens (Rich, 1989). The camera was mounted on a tripod at 1.2 m above ground, and levelled using a circular bubble level. Pictures were taken using the camera timer function to reduce movement during image capture (Rich, 1989). Aperture and shutter settings were set to automatic, and to minimise error from over-exposure (Brusa and Bunker, 2014; Hale and Edwards, 2002), exposure was checked using the histogram function in the camera playback facility, following the method outlined by Beckschafer et al. (2013). Where over-exposure was apparent, exposure settings were manually lowered to -2.0 EV, the minimum limit on this camera.

Images were analysed in HemiView Canopy Analysis Software v.2.1 (Delta-T Devices, Cambridge, UK). The Coolpix 900 lens settings in HemiView were selected to correct for lens distortion (Hale and Edwards, 2002). Various options exist for classifying a photograph into “sky” and “not sky” (binarization), using image analysis software (Glatthorn and Beckschafer, 2014; Zhao and He, 2016). In HemiView, it is only possible to use manual thresholding of black and white pixels, so we followed this method, which has been widely used in other studies (Bertin et al., 2011; Capdevielle-Vargas et al., 2015; Hale and Edwards, 2002; Machado and Reich, 1999; Zhang et al., 2005). Each photograph was individually processed to obtain the best contrast between vegetation and the background sky, by visual comparison with the original photograph (Rich, 1990). A decision was made, based on visual assessment during threshold setting, whether each photo should be included in the analysis. If it was not possible to gain a good contrast between sky and vegetation across the whole image, that photo was excluded. Canopy openness—in HemiView, “% visible sky”— was then derived for each image by the software. In HemiView this value represents a weighted canopy openness score based on gap fraction zenith angles (Rich et al., 1999).

Following analysis in HemiView, photos were also analysed using ImageJ (Rueden, 2016). Photos were converted to 8-bit binary black (“not sky”) and white (“sky”) images in ImageJ. Following the same procedure as we used for photos in HemiView, the manual thresholding function in ImageJ was used to individually process each image and obtain the best contrast between vegetation and background sky. This was done with reference to the original photograph (Rich, 1990). Hemispherical photos consist of a circular image inside a rectangular frame. As ImageJ is not designed specifically for such images, it cannot automatically exclude the framing pixels as is possible in HemiView. Therefore to calculate canopy openness (the proportion of pixels classified as sky) excluding the frame, we first calculated the number of pixels in a reference image containing only open sky. We then used the 'batch measure function' to calculate white (sky) pixels for all images, and calculated the canopy openness as a proportion of the circular hemispherical image, excluding the framing pixels.

Smartphone photography with fisheye lens

Photos were taken using a Sony Xperia L smartphone camera (Android Version 5.0) with magnetic fisheye lens attachment (Skimn FE-12 180° fisheye lens). Images were taken at 5 MP using a 16:9 aspect ratio – the camera's default settings. Using these settings, the fisheye lens gave a 125° x 75° field of view. The smartphone was held level, with the wider view orientated east-to-west when taking photos of the canopy, to ensure comparable images were obtained for each season. Photographs were taken in manual mode, with exposure lowered to -2.0 EV, the minimum limit on the camera. Images were stored as high quality JPEGs, between 2–3MB in size.

Smartphone fisheye photos were analysed in HemiView and ImageJ and visible sky values were calculated, following the same procedures outlined for hemispherical photo analysis. Lens equation coefficients relating zenith angles and radial distance were calculated from a calibration curve constructed from measurements taken from reference photographs. The resulting lens correction function ($y = 1.2213x - 1.396x^2 + 1.0855x^3 - 0.2761x^4$) was used by HemiView to adjust the calculations to correct for lens distortion.

Smartphone photography without a fisheye lens

Smartphone photos were also taken of the canopy without the fisheye lens attachment, giving a 70° x 40° field of view. Photos were taken of the canopy directly overhead (with the wider view orientated east-west), and of the canopy facing in three different bearings from the station—at 60°, 180° and 300° (with the camera positioned in a landscape orientation at a 45° angle from the horizontal). All photos were taken using the same settings as the photos with fisheye lens attachment, and exposure settings were manually adjusted as previously described. Photographs were then analysed using ImageJ, following the same procedure for binarization, to derive a canopy openness estimation based on % visible sky. Two sets of canopy openness estimates were derived from these photos: one based solely on the overhead canopy photo, and one calculated as an average from all four photographs to incorporate a wider area of view.

Non-photographic methods

Canopy openness was estimated visually on a simple percentage scale. Two sets of canopy openness estimates were derived, one based solely on an overhead estimation, and another based on an average of four estimations: one directly overhead, and at three different bearings from the station (60°, 180° and 300°) at a 45° angle from the horizontal.

Brown et al. (2000) proposed a canopy scope to aid in the visual estimation of canopy openness. The scope consists of a simple Perspex sheet with a grid of twenty-five dots, spaced 3 cm apart in a 5 x 5 array. A 20 cm length of string is attached to the corner, and ensures the scope is held at a constant distance from the eyes when making estimations. Canopy openness was estimated by focussing the scope on the largest canopy gap visible from the station, and counting the number of dots coinciding with sky. This number was then multiplied by four to obtain a percentage estimate. Brown et al. (2000) found a close correlation between largest gap canopy openness and total canopy openness, but acknowledged that for woodlands with several similar sized canopy gaps, the largest gap estimate may not give an accurate representation. Two alternative estimates were made: one by pointing the canopy scope at the canopy directly overhead; and another by taking the mean of four canopy scope estimates (using the overhead estimate and estimates made from viewing the canopy at bearings of 60°, 180° and 300° from north, at an approximately 45° angle from the horizontal).

Statistical analysis

We used linear regression to compare canopy openness derived from hemispherical photographs in HemiView, against each surrogate method. We first compared data from all seasons and sites together to assess which methods were able to estimate broad changes in canopy openness. We then compared methods on a season-by-season basis across the four sites, to understand whether methods were capable of estimating finer-scale variation in canopy openness. We also conducted method comparisons on a site-by-site basis using data from all four seasons, to assess whether methods performed well across the different woodlands.

For methods that performed consistently well across the comparisons, Analysis of Covariance (ANCOVA) was used to test whether the methods estimated canopy openness in similar ways under different conditions, with seasons and sites as covariates. A Tukey-Kramer test was used to explore differences that were found between seasons or sites. All statistical analyses were carried out in R 3.3 (R Core Team, 2016).

4.2.2 Comparison of smartphone models and operators

Field imagery

A second trial comparing smartphone models and phone users took place in mixed deciduous woodland at Mount Edgcumbe Estate, England (approximately 50°35'N and 4°16'W), during summer 2016 when trees were in full leaf. Three sampling locations or 'stations' were selected at the site, using visual assessment, to represent a 'closed', 'intermediate' and 'open' overhead canopy. We tested two popular Smartphone cameras – the iPhone 5 and Samsung Galaxy S4 – against the Sony Xperia used in the previous trials, to assess the comparability of canopy openness estimates. Photos taken with the iPhone 5 had a resolution of 8 MP and an aspect ratio of 16:9, providing a 61° x 48° field of view. Photos taken with the Samsung Galaxy S4 had a resolution of 9.6 MP and aspect ratio of 16:9, providing a 57° x 34° field of view. Photos were stored as high quality JPEGS, between 2–3 MB in size.

Twenty-two volunteers consecutively took an overhead photograph of the canopy with each camera, at each of the three stations. All photos were taken within a half-hour period. Volunteers were instructed to hold the phone at an estimated level position and take a photo of the canopy above, but were not told to orientate the phone in a particular direction, as we were interested to see the extent that individual user operation affected consistency in the results. Photos were analysed in ImageJ following the procedure outlined above.

Statistical analysis

The Aligned Rank Transform (ART) procedure in the R package ARTool (Kay and Wobbrock, 2016), followed by separate ANOVA using R 3.3 (R Core Team, 2016), was used to assess the effects of phone user, phone model and canopy treatment on canopy openness values. The ART procedure is an appropriate way to analyse datasets which are not normally distributed, and is described in more detail by Wobbrock et al. (2011). We performed *post hoc* contrasts using estimated marginal means with the emmeans package (Lenth, 2017).

4.3 Results

4.3.1 Hemispherical photography with HemiView v other methods

All hemispherical photos taken were suitably exposed in relation to sky conditions, for inclusion in the analysis, while four smartphone fisheye photos and six smartphone photos without the fisheye lens attachment were eliminated due to overexposure, out of 96 photos in each case.

Analysis of hemispherical photography with ImageJ produced reliable estimates of canopy openness values derived from analysis with HemiView (Table 4.2, Figs 4.1 A and D). With photos from spring, summer and autumn combined into a single ANCOVA analysis, the slope of the relationship was no different for all three seasons (Fig. 4.1 D, ANCOVA $F_{2,66} = 2.55$, $p = 0.09$). However, the intercepts of the relationships were significantly different (Fig. 4.1 D, ANCOVA $F_{2,68} = 8.09$, $p < 0.001$), with summer values estimated relatively lower than those of spring and autumn (Tukey-Kramer Test, summer v spring $p = 0.004$, summer v autumn $p < 0.001$, spring v autumn $p = 0.864$).

None of the other methods closely estimated absolute canopy openness values derived from hemispherical photography, but all smartphone photographic methods reliably estimated relative differences in canopy openness across all seasons for all sites (Table 4.2, Figs 4.1 B and C). The slopes of these relationships, which were all >1, indicate that smartphone fisheye photography results in higher estimates of canopy openness than hemispherical photography, and that the estimates differ more at higher values of canopy openness. During winter, when there were very high levels of canopy openness (*mean* = 37%, *sd* = 5%), smartphone fisheye photos did not correspond reliably to hemispherical photography (Table 4.2). This was also true for all other methods tested, and since winter is not a season where canopy change is expected and therefore not relevant to our aims, winter data were excluded from the rest of the analyses. Non-photographic methods (canopy scope and simple visual estimations) were much poorer estimators of change in canopy openness across all seasons and sites (Table 4.2).

Smartphone with fisheye lens estimates taken in different seasons had similar slope relationships (Fig. 4.1 E, ANCOVA: $F_{2,66} = 0.31$, $p = 0.73$; Fig. 4.1 F, ANCOVA: $F_{2,66} = 0.64$, $p = 0.53$), but they varied in intercept (Fig. 4.1 E, ANCOVA: $F_{2,64} = 33.56$, $p < 0.001$; Fig. 4.1 F, ANCOVA: $F_{2,64} = 48.73$, $p < 0.001$). For smartphone photographs analysed with HemiView canopy analysis software, spring and autumn intercepts were not significantly different (Tukey-Kramer $p = 0.796$), but both were significantly different from summer ($p < 0.001$ in each case). The same photographs analysed with ImageJ had different intercepts for each of the three seasons (spring v autumn $p = 0.020$, spring v summer $p < 0.001$, summer v autumn $p < 0.001$).

Since smartphone fisheye photography and ImageJ analysis reliably estimated variation in canopy openness, we tested whether the methods performed consistently between different sites (Fig. 4.2). Hemispherical imagery analysed with ImageJ showed similar slope relationships across all sites (Fig. 4.2 A; ANCOVA: $F_{3,64} = 1.17$, $p = 0.33$), but significant differences in intercept (ANCOVA: $F_{3,67} = 4.75$, $p = 0.005$). The intercept of Hardwick was different from Hunshaw and Whitleigh (Tukey-Kramer Test, $p = 0.018$ and $p = 0.007$), though all other intercepts were not different ($p = 0.288$ to 1.000).

Smartphone with fisheye photography, whether analysed with HemiView or ImageJ, resulted in different slope relationships for Hardwick compared to the other sites (Fig. 5.2 B, ANCOVA: $F_{3,60} = 4.10$, $p = 0.010$; Fig. 4.2 C, ANCOVA: $F_{3,60} = 7.07$, $p < 0.001$). As canopy openness increased, the estimates for Hardwick differed less from the hemispherical standard than the other sites. The intercepts of the other sites did not differ (Fig. 4.2 B, ANCOVA: $F_{2,46} = 0.91$, $p = 0.41$; Fig. 4.2 C, ANCOVA: $F_{2,46} = 0.54$, $p = 0.59$).

4.3.2 Comparison of smartphone models and operators

The three canopy treatments (closed, intermediate and open) were clearly different from each other in terms of canopy openness, but it did not matter which phone model or user took the photos (Fig. 4.3, Aligned Rank Transform + ANOVA, $p_{\text{canopy}} < 0.0001$, $p_{\text{user}} = 1.00$ and $p_{\text{model}} = 0.50$). However, variability in estimation of canopy openness increased markedly as canopy openness increased. For the closed canopy, standard deviations of the estimates ranged from 0.79–1.46% canopy openness, but were much greater for the open canopy (7.42–12.43%).

Table 4.1. Site descriptions of woodlands used to compare methods for estimating canopy openness. All sites were located in Devon, England.

Site	**Size (ha)**	**Stand density (trees/ha)**	**Average tree height (m)**	**Aspect**	**Dominant canopy species**	**Dominant shrub layer species**
Hardwick Wood (50°22′N, 4°4′W)	22	1360	16	Flat	*Acer pseudoplatanus, Fraxinus excelsior*	*Acer pseudeoplatanus, Ulmus* sp.
Hunshaw Wood (50°55′N, 4°7′W)	18	556	30	S	*Quercus robur* with *Fagus sylvatica* sub-canopy	*Corylus avellana, Sorbus aucuparia*
Newton Mill (50°52′N, 4°15′W)	25	456	35	NE	*Quercus robur*	*Corylus avellana, Fagus sylvatica*
Whitleigh Wood (50°25′N, 4°8′W)	20	1111	27	N	*Quercus robur* and *Betula pendula*	*Corylus avellana, Fagus sylvatica, Acer pseudoplatanus*

Table 4.2. Proportion of variation explained (R^2) and statistical significance (p) for relationships between hemispherical photography analysed with HemiView and alternative methods. Relationships were considered separately for each season, as well as across all seasons together.

Method	**All seasons**		**Spring**		**Summer**		**Autumn**		**Winter**	
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
Hemispherical photo (ImageJ)	0.96	<0.001	0.85	<0.001	0.77	<0.001	0.94	<0.001	0.69	<0.001
Smartphone fisheye photo (HemiView)	0.89	<0.001	0.83	<0.001	0.67	<0.001	0.79	<0.001	0.05	0.300
Smartphone fisheye photo (ImageJ)	0.84	<0.001	0.74	<0.001	0.76	<0.001	0.66	<0.001	0.08	0.170
Smartphone photo (overhead)	0.85	<0.001	0.57	0.002	0.43	<0.001	0.69	<0.001	0.04	0.380
Smartphone photo (average of 4)	0.81	<0.001	0.15	0.410	0.60	<0.001	0.72	<0.001	0.02	0.490
Canopy scope (overhead)	0.51	<0.001	0.24	0.240	0.01	0.170	0.41	<0.001	0.00	0.820
Canopy scope (largest gap)	0.52	<0.001	0.2	0.029	0.20	0.030	0.33	0.003	0.00	0.850
Canopy scope (average of 4)	0.55	<0.001	0.31	0.005	0.18	0.040	0.55	<0.001	0.00	0.910
Visual estimation (overhead)	0.39	<0.001	0.01	0.740	0.05	0.280	0.31	0.005	0.06	0.260
Visual estimation (average of 4)	0.52	<0.001	0.03	0.460	0.20	0.029	0.51	<0.001	0.04	0.350

Table 4.3. Proportion of variation explained (R^2) and statistical significance (*p*) for relationships at each woodland, between estimates of canopy openness from hemispherical photography analysed with HemiView versus estimates from other methods. Photographs were included from spring, summer and autumn, but not winter.

Method	**Hardwick**		**Hunshaw**		**Newton Mill**		**Whitleigh**	
	R^2	*p*	R^2	*p*	R^2	*p*	R^2	*p*
Hemispherical photo (ImageJ)	0.97	<0.001	0.85	<0.001	0.98	<0.001	0.81	<0.001
Smartphone photo fisheye (HemiView)	0.95	<0.001	0.86	<0.001	0.86	<0.001	0.86	<0.001
Smartphone photo fisheye (ImageJ)	0.84	<0.001	0.80	<0.001	0.81	<0.001	0.86	<0.001
Smartphone photo (overhead)	0.88	<0.001	0.78	<0.001	0.68	<0.001	0.85	<0.001
Smartphone photo (average of 4)	0.92	<0.001	0.93	<0.001	0.70	<0.001	0.85	<0.001
Canopy scope (overhead)	0.47	0.002	0.08	0.260	0.68	<0.001	0.19	0.072
Canopy scope (largest gap)	0.42	0.004	0.22	0.049	0.73	<0.001	0.12	0.160
Canopy scope (average of 4)	0.39	0.005	0.25	0.034	0.75	<0.001	0.16	0.100
Visual estimation (overhead)	0.42	0.004	0.1	0.200	0.60	<0.001	0.01	0.630
Visual estimation (average 4)	0.47	0.002	0.2	0.063	0.67	<0.001	0.01	0.740

Fig. 4.1. Canopy openness estimates from hemispherical photography with HemiView (HP+HV) compared with estimates from hemispherical photography with ImageJ (HP+IJ), smartphone fisheye photography with HemiView (SP+HV), and smartphone fisheye photography with ImageJ (SP+IJ). **Figs A–C.** Overall relationships across all seasons. R^2 and statistical significance of these relationships is presented in Table 4.2. **Figs D–F.** Separate relationships for each growing season (light green = spring, dark green = summer, dark red = autumn).

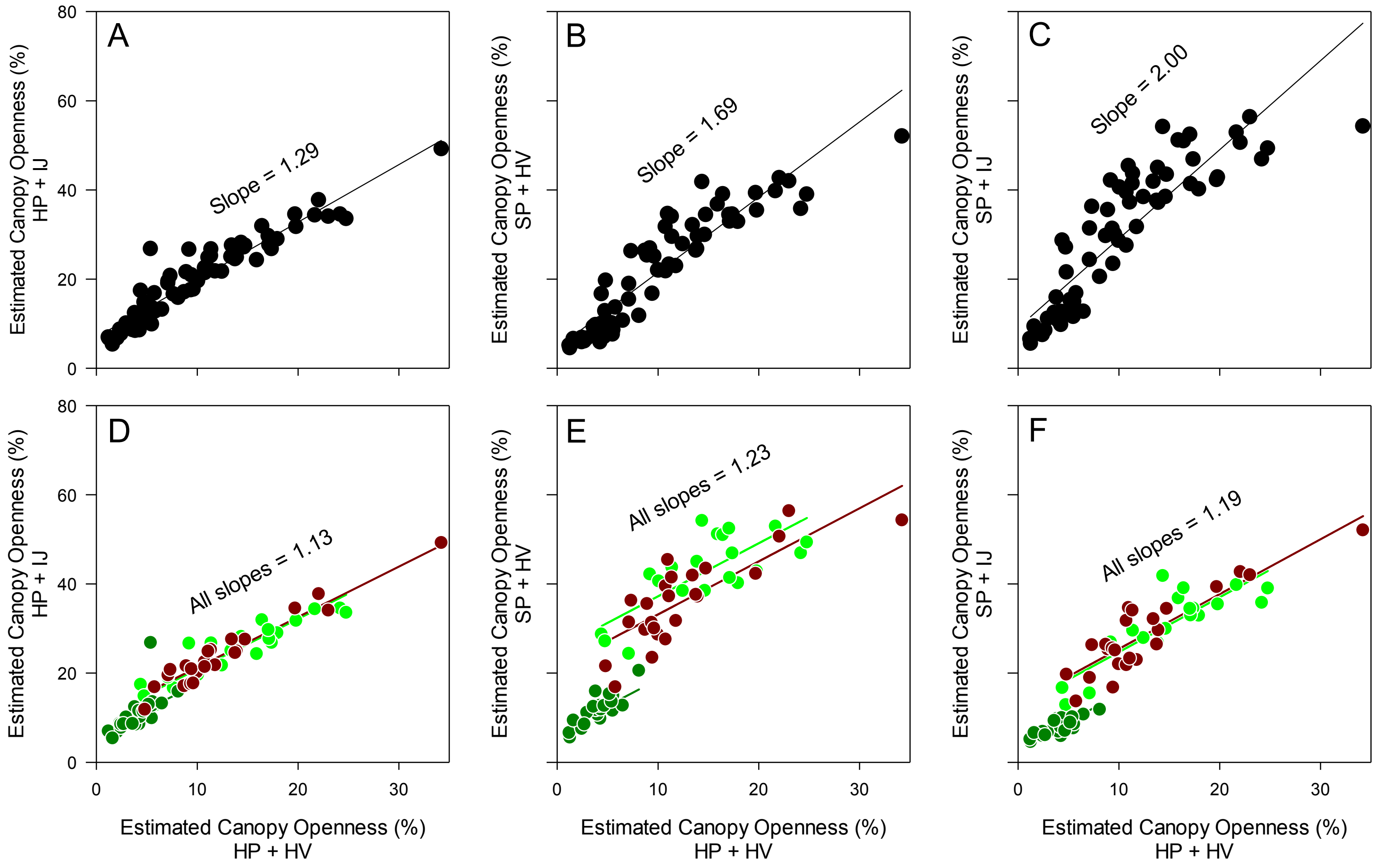


Fig. 4.2. Canopy openness by woodland, across spring, summer and autumn, from hemispherical photography with HemiView (HP+HV) compared with estimates from **(A)** hemispherical photography with ImageJ (HP+IJ), **(B)** smartphone fisheye photography with HemiView (SP+HV), and **(C)** smartphone fisheye photography with ImageJ (SP+IJ). R^2 and statistical significance of these relationships is presented in Table 4.3. Relationships are shown for each woodland (red = Hardwick, green = Hunshaw, blue = Newton Mill, grey = Whitleigh).

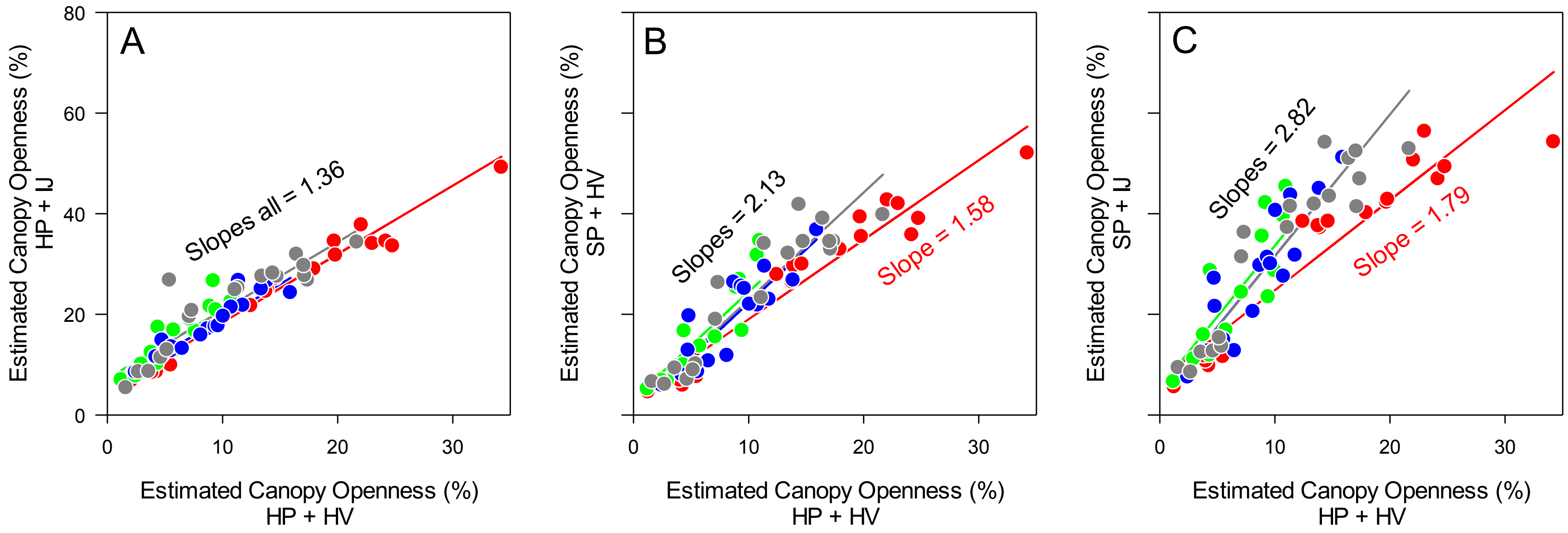
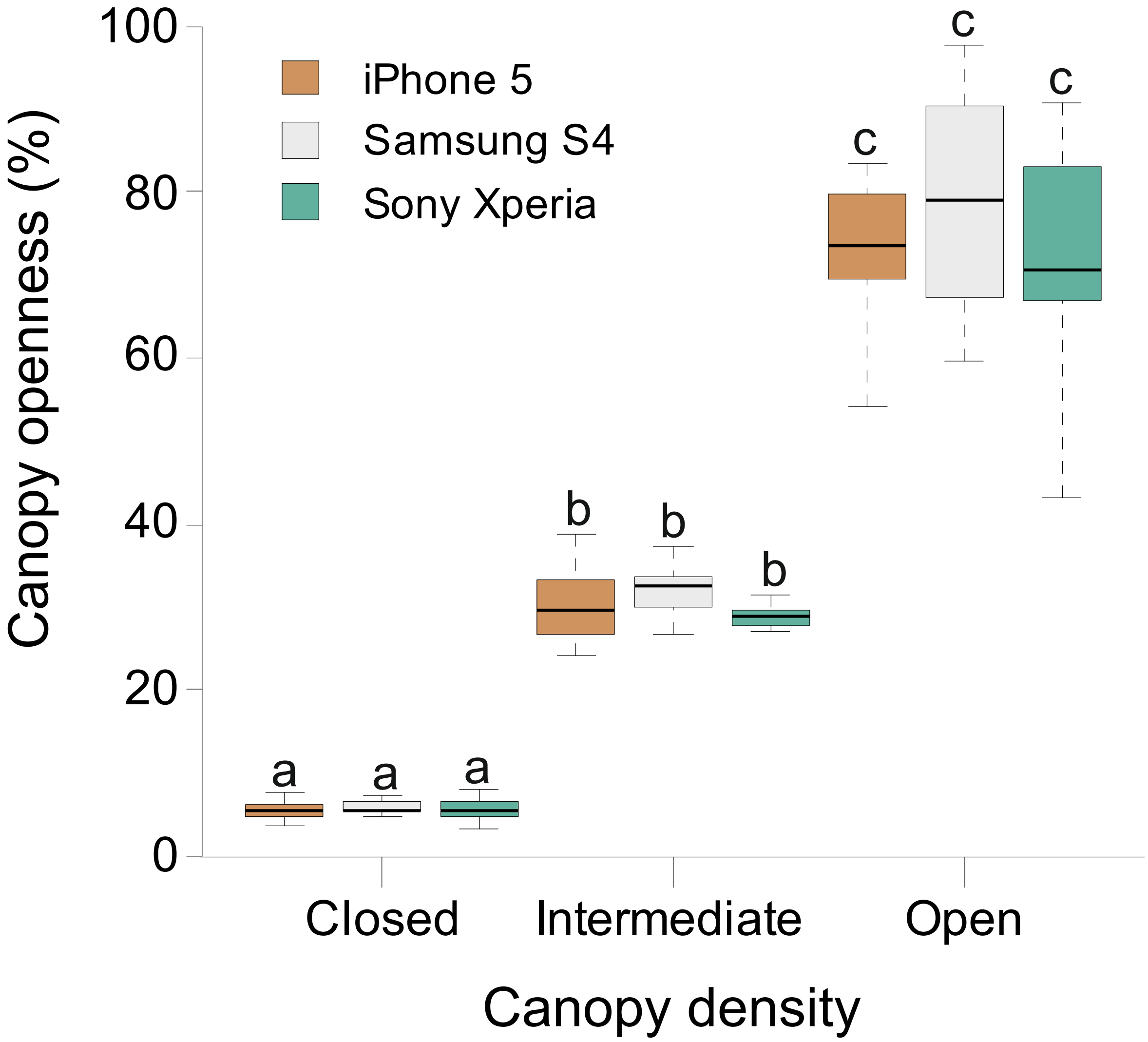


Fig. 4.3. Comparison of estimates of canopy openness using three different models of smartphone in three canopy densities. Every canopy density x phone combination was based on 22 photographs, each taken by a different user. The median is shown as a horizontal line, the box represents values within the 25–75% quartiles, and the error bars show the minimum and maximum values. Means sharing a letter were not significantly different according to *post hoc* contrasts using estimated marginal means.



4.4 Discussion

Our results showed that smartphone photographic methods estimated variation in canopy closure effectively, but rapid visual estimation methods did not. Basic visual estimations of canopies are known to lack consistency, varying considerably due to weather conditions (Jennings et al., 1999) and observer biases (Vales and Bunnell, 1988). The canopy scope is more a quantitative visual estimation method, allowing for greater consistency and has been shown to have low between-observer bias (Brown et al., 2000), so is potentially more suitable for citizen science. However, while the canopy scope can distinguish quite different degrees of canopy openness (Brown et al., 2000), it lacked the fine resolution needed to distinguish between similar canopies, and therefore is less suitable for monitoring changes through time. Smartphone photographic methods have now become a cost effective and practical alternative to visual estimation. Simple photographs using a smartphone camera without a lens attachment were sufficient for assessing the degree of variation in canopies across a whole season, but did not pick up fine-scale variations (*i.e.,* between similar canopies within a season) compared with hemispherical photography. This is unsurprising, as their narrow angle of view means they are essentially providing an estimate of canopy cover directly overhead, as opposed to canopy closure across a range of zenith angles (Chianucci et al., 2014; Jennings et al., 1999). With the addition of an inexpensive fisheye lens attachment, smartphone photographs were able to pick up finer variations in canopy openness in spring, summer and autumn, which would be important for monitoring seasonal dynamics.

As anticipated, smartphone fisheye photography gave higher canopy openness estimations than hemispherical photography, due to its narrower field of view. With hemispherical photography, an image taken within a forest will typically include a ring of tree trunks and shrubs around the periphery, with low gap fractions in the outer portions of the image (at larger zenith angles) (Chen et al., 1997). Although incorporating a greater field of view than non-fisheye photos, smartphone fisheye photos still omit the largest zenith angles containing most of the lower trunks and shrub layer. In its field of view, the gaps in a canopy contribute more to the overall image. Similarly, twigs and foliage have higher prominence in images. As smartphone fisheye photography misses gaps at larger zenith angles, it would not be a suitable method for detailed studies of canopy structure or plant growth. However, the method is suitable for monitoring timing of canopy closure, and its narrower field of view could actually make it a superior method for identifying leafing activity early in spring.

We found canopy structure affected the relationship between hemispherical photography and smartphone photography, meaning that canopy openness values must be converted to proportions of total canopy closure to be correctly interpreted. Where the overhead canopy was uniformly closed, the difference between canopy openness estimations from smartphone fisheye photos and hemispherical photos was lower—both sets of images show a closed canopy with few gaps. In more open situations, the difference between the two sets of estimations was greater. Similarly where stand density was higher and the height of the tree canopy was lower (*e.g.,* at Hardwick Wood, Table 5.1), the difference between canopy openness values from the two methods was smaller. Canopy height is known to effect openness estimations when the field of view is reduced (Jennings et al., 1999; Pellikka, 2001).

Due to the influence of canopy structure on canopy openness values, we propose the smartphone with fisheye photography method is appropriate for monitoring relative change in canopies through time. In order to compare the timing and rate of canopy closure across different forest locations we can standardize along a proportional scale of canopy closure, where 0% represents the winter canopy value prior to budburst, and 100% represents the summer canopy value once the canopy is fully in leaf. We note that canopies are dynamic, and small-scale fluctuations occur through summer. Therefore the summer canopy value would be determined from the point where the canopy reaches 'adjustment stability' (Margalef, 1969), after which only small changes of less than 2% canopy closure are observed. The progress of canopy closure can then be plotted through time from 0–100%, and a logistic growth model can be fitted to characterise the phenological pattern (Richardson et al., 2006; Zhang et al., 2003). An example using smartphone fish-eye photography is provided in Appendix 4.1.

In terms of photo analysis, we found that ImageJ is a reasonable alternative to professional specialist software such as HemiView, for deriving relative canopy openness values. It is clear that ImageJ overestimates values from HemiView to some degree, so again, this method would not be suitable for studies where absolute values were needed. The distortion of a hemispherical or fisheye lens causes the central part of the image, towards the zenith, to appear larger than peripheral elements towards the horizon (Herbert, 1987). Canopy openness derived from HemiView is based on a weighted gap fraction that takes into account the zenith angle of canopy gaps, and corrects for a given lens distortion (Promis et al., 2011). In contrast, canopy openness derived from ImageJ is simply the percentage visible sky across the image. However, values from ImageJ still consistently and reliably estimated relative differences in canopy openness in our study.

ImageJ has the benefits of being free, open access and relatively straightforward to use. It is not necessary to provide specifications of the fisheye lens to use it. Image binarization is still required, which can be time consuming. The manual thresholding technique used in this study would not be suitable for analysing large quantities of citizen science data. Many citizen science projects have successfully utilised internet crowd-sourcing applications (Kosmala et al., 2016) to involve the public in processing and classifying large numbers of images, so a similar approach could be used to binarize canopy photos, with multiple people classifying pixels for the same image to reduce error (Inoue et al., 2011). However, new methods for automatic thresholding of photos would improve efficiency (Brusa and Bunker, 2014; Glatthorn and Beckschafer, 2014; Inoue et al., 2004), and auto-thresholding plug-ins for ImageJ (Glatthorn and Beckschafer, 2014) could provide a viable option.

In terms of practicalities, smartphone fisheye photography is suitable for widespread use as part of citizen science projects, and if managed properly is a game-changer in terms of data quantity. The good agreement between smartphone models and users suggests the method can be reliably applied by citizen scientists. The three phone models tested varied in resolution and field of view, but still produced comparable results. While some variation was evident between photos taken with the same phone, under the same canopy conditions, there was no overall effect of phone user on canopy openness values. Variation between photos taken with the same smartphone was greatest at higher levels of canopy openness. This is not surprising, as under the dense canopy, gaps were small and uniformly distributed, whereas the open canopy comprised a very large central gap bordered by canopy. Small variation in camera positioning could therefore result in compositional differences between photographs. This could lead to significant differences in estimates, as has been observed with other methods for estimating canopy openness (Jennings et al. 1999). Therefore, we recommend that for best results camera position is standardised by installation of fixed camera mounts (University of New Hampshire, 2017) for citizen scientists to place their smartphones on in order to take repeat photographs of particular parts of the canopy.

The quality of photos obtained from smartphone fisheye photography is sufficient to obtain reliable data. The high resolution available with smartphone cameras is a clear advantage. Resolution is known to be an important factor influencing the quality of canopy openness measures from hemispherical photography (Brusa and Bunker, 2014; Woodgate et al., 2015), and in this study the smartphone camera resolution was superior to that of the hemispherical camera (with nearly 2,000,000 more pixels). It has also been noted that higher resolution images are less vulnerable to thresholding errors during image processing and analysis (Macfarlane et al., 2007). Some blurring was evident towards the perimeter of the smartphone fisheye photos, but this is also apparent with hemispherical photos (Frazer et al., 2001). Blurring from motion caused by holding the camera to capture images could also influence image quality (Woodgate et al., 2015). The use of fixed mounts for phone cameras would help alleviate this problem, as well as utilising the camera's timer function or earphone controls to remotely operate the camera shutter.

As with hemispherical photography, there are several logistical issues associated with the use of smartphone photography, relating to sky conditions and image exposure. The effects of over-exposure and the importance of taking photos under uniform sky conditions has been emphasised in many studies (Beckschafer et al., 2013; Brusa and Bunker, 2014; Rich, 1990; Woodgate et al., 2015; Zhang et al., 2005). In this study, a small proportion of smartphone photos had to be excluded due to over-exposure. While smartphone photographs were taken at -2.0 EV, the lowest exposure setting available, Beckschafer et al. (2013) showed that over-exposure can still occur at -2.0 EV under bright skies. This can also be a problem with hemispherical photography, as the Nikon Coolpix 990 had the same limits for exposure compensation. The histogram function allows a definitive check as to whether photos are over-exposed, and more advanced cameras allow for lowering below -2.0 EV (Beckschafer et al., 2013). We emphasise again that the smartphone fish-eye photography method would not be suitable for detailed studies of canopy structure or growth where small differences between sites must be detected, and therefore consistent exposure is paramount (Leblanc, 2005). However, to track the progress of canopy closure through time and compare trends in the timing of this phenological event over large spatial scales, a small degree of noise in the data is acceptable. The example in Appendix 4.1 demonstrates that the phenological process of canopy closure can be clearly modelled using this method. While the limits of exposure settings on smartphone cameras may mean some photos have to be discarded, the greater number of images obtained by utilising a citizen science approach should increase the number of suitable images that can be included in a study. Where possible citizen scientists should be encouraged to take photos early or late in the day, which is when sky conditions are generally most appropriate, and coincides with times when people are likely to be available to collect imagery.

4.5 Conclusions

Smartphone fisheye photography, with relatively simple image analysis, offers a practical method for comparing changes in the timing of canopy closure across different forests year on year, and may even be more suited to this task than hemispherical photography. Using this approach, trends in proportional changes in canopy closure could be identified across different spatial and temporal scales using citizen science. Further research is required to assess the temporal resolution of image capture needed to represent canopy changes adequately.

5 Using smartphone photography with a fisheye lens to monitor canopy closure phenology

5.1 Introduction

In temperate broad-leaved forests, the spring period is of key importance to understorey plants, as temperatures rise and the availability of photosynthetically active radiation is at its peak prior to canopy closure. The leaf phenology of overstorey trees determines spatial and temporal patterns of light availability as spring develops, influencing the structure and composition of the understorey (Kato and Komiyama, 2002). It is now well established that climate change is affecting the leaf phenology of temperate trees (Menzel and Fabian, 1999; Menzel et al., 2006; Parmesan, 2007; Sparks and Carey, 1995; Thompson and Clark, 2008; Wang et al., 2016; Wu and Liu, 2013). Warmer temperatures are causing leaf expansion to advance, bringing about the earlier closure of forest canopies and onset of light limitation in the understorey. As spatio-temporal patterns of light and shade are key determinants of forest plant dynamics (Valladares et al., 2016), changes in the timing of canopy closure would affect growth, reproduction and survival of understorey biodiversity.

Many tree saplings employ a strategy of 'phenological escape', leafing before the canopy closes to maximise photosynthesis (Gill et al., 1998). This high light period has been shown to be very important for the growth and survival of saplings in closed canopy forests. Many species are only able to survive in the shaded understorey because they obtain the majority of their light and carbon for the growing season prior to canopy closure (Augspurger, 2008; Lopez et al., 2008). Shading experiments have identified reduced growth and increased mortality when saplings were subjected to earlier canopy closure (Augspurger, 2008). Though some saplings leaf several weeks earlier than conspecific canopy trees, for many species the phenological escape is brief; in a study of 13 tree species, saplings were found to leaf on average six days earlier than conspecific canopy trees (Augspurger and Bartlett, 2003). The ability of saplings to adapt their leaf phenology in line with dominant canopy species could be important for their survival. While most research has focussed on sapling phenology in relation to canopy trees of the same species (Richardson and O'Keefe, 2009), temperate forests vary greatly in their species composition and most forests have mixed species canopies. Therefore monitoring canopy closure of mixed species stands will be important for understanding spatial patterns of light availability that could determine sapling growth and survival.

The herb-layer is also highly dependent on sunlight prior to canopy closure. Earlier canopy closure affects the growth and reproductive success of spring ephemerals, that rely on the brief period when temperature and light conditions are favourable (Augspurger and Salk, 2017; Kudo et al., 2004). In addition, summer-green and evergreen temperate forest herbs have also been shown to rely heavily on the spring period to gain a positive carbon balance for growth and reproduction after light has become limiting (Rothstein and Zak, 2001; Routhier and Lapointe, 2002). Earlier canopy closure will alter competitive dynamics in the understorey, and is likely to favour invasive species. Those species that can begin growth earlier in the year, tolerate deeper shade, or exhibit more plastic responses in their phenology will displace other woodland ground flora, with increases in non-native species already being attributed climate change (Engelhardt and Anderson, 2011; Willis et al., 2010). A better understanding of spatial patterns of spring canopy closure at the level of individual forests is important in order to predict herb-layer dynamics at local levels and across forested landscapes.

Given the influence of canopy phenology on understorey biodiversity, monitoring changes in the timing of canopy closure is critical for implementing effective forest conservation. In recent years the study of canopy phenology has gained increasing attention, though largely in relation to understanding climate-biosphere interactions at regional and global scales using satellite remote-sensing (Tang et al., 2016). A variety of indices can be derived from satellite data, with Enhanced Vegetation Index (EVI) and Leaf Area Index (LAI) being the most widely used (Wang et al., 2017), particularly in studies of primary productivity and biometeorology (Green et al., 2017; Keenan et al., 2014b; Richardson et al., 2013). However, loss of imagery due to atmospheric interference, and difficulty separating canopy greening from the influence of understorey vegetation, limits prediction accuracy to around seven days at best (Ahl et al., 2006; Doktor et al., 2009; White et al., 2014). Given that differences in canopy closure timing of several days could have considerable influence on understorey plant fitness, monitoring methods that provide a higher degree of temporal accuracy are needed.

Canopy phenology shows high levels of variation over small spatial scales, due to multiple interacting factors including species composition, genetic variability, topography and soils (Arend et al., 2016; Cole and Sheldon, 2017; Lapenis et al., 2017; White et al., 2014). Satellite data provides information that is averaged across coarse spatial scales, so variation within the landscape is missed (Doktor et al. 2009). Commonly used satellite products such as those derived from Moderate Resolution Imaging Spectroradiometer (MODIS) offer spatial resolution of around 1 km, though Landsat imagery offers higher resolution of 30 m. Even so, resolution is still too coarse to detect fine-scale differences within forests. Within single forest stands large differences in leaf-out timing are common. Differences of two weeks have been observed across a single stand with even structure and composition, due to micro-climatic variation (Fisher et al., 2006), and differences of more than one month have been reported for the same tree species at a single site due to phylogenetic factors (Cole and Sheldon, 2017). While satellite data are invaluable for characterising large-scale trends, the usefulness of coarse resolution data in studies of local ecosystem dynamics is limited. Methods that enable high temporal and fine spatial resolution data collection within forest stands are required to understand local-level changes in ecosystems. Many authors have also recognised the need for more extensive ground-based data to help validate satellite metrics and provide more realistic predictions for regional and global biosphere modelling (Doktor et al., 2009; Jeong et al., 2013; Richardson et al., 2012; Tang et al., 2016; White et al., 2009; Wu et al., 2017).

The longest standing approach to monitoring canopy phenology are visual observations of budburst and leaf expansion, which provide fine-resolution information at the level of individual trees. Such observations have been important in understanding drivers of leafing phenology between different species, and in helping to understand genetic and phenotypic variation within species (Cleland et al., 2007b; Polgar and Primack, 2011). Furthermore, visual observation networks have the potential to generate large data-sets through the involvement of citizen scientists (Beaubien and Hamann, 2011; Collinson and Sparks, 2008; Crimmins et al., 2017). However, the extent to which leaf expansion of individual trees can be related to forest canopy closure and light limitation in the understorey is unknown. Later stages of leaf development after leaf expansion, such as leaf enlargement and flattening, can be difficult to detect with visual observations (Keenan et al., 2014a), but contribute to canopy closure after leaves have expanded from the bud. Therefore, it is likely that leaf expansion dates predicted from visual assessment would be earlier than canopy closure dates. In addition, tree leaf expansion timing and rate varies between and within species (Chapter 3), so it is likely that a large number of observations would be needed in order to attempt to characterise canopy closure from individual tree phenology assessments.

In response to the need for fine-scale monitoring of canopy phenology, there is increasing interest in near-surface remote sensing techniques. Digital cameras positioned on towers above canopies, such as those used in the Phenocams network (Inoue et al., 2014; Richardson et al., 2007; Wingate et al., 2015), capture daily surface images. The recent development of unmanned aerial vehicles (UAVs) fitted with cameras offer even higher resolution and coverage (Klosterman et al., 2018). Both camera methods use colour channel analysis to derive indices of canopy greening that signal canopy development through spring, and the initial rise in greenness has been shown to correlate well with budburst dates from visual observations (Keenan et al., 2014a). Another promising high resolution technique is the use of Terrestrial LiDAR instruments to track Leaf Area Index (LAI) and quantify development of separate forest strata (Calders et al., 2015). However, these techniques are limited in terms of the spatial coverage that can be achieved, as they require considerable financial investment and/or suitable existing infrastructure for camera installation. There is also a requirement for technical expertise in processing data. This limits application to a relatively small, albeit increasing, number of research forests. There remains a need for methods that can be applied across a broader range of forests and regions.

Hemispherical photography has been widely used in studies of forest canopies and understorey light environments, to characterise canopy openness, or its inverse, canopy closure (Brusa and Bunker, 2014; Gonsamo et al., 2013). Recently, smartphone cameras with inexpensive fisheye lens attachments have been shown to provide comparable estimates of canopy closure (Bianchi et al., 2017; Smith and Ramsay, 2018), providing a cost-effective alternative. Free, non-specialist image analysis software can be used to extract data with similar results to professional software. Different smartphone models provide repeatable canopy closure estimates (Smith and Ramsay, 2018), and the widespread ownership of smartphones and inexpensive nature of fisheye lens attachments means they could be used widely through citizen science. Projects such as the USA National Phenology Network (Jeong et al., 2013) demonstrate the potential for gaining large data-sets from citizen science phenology studies.

While smartphone fisheye photography has been shown to provide comparable estimates of canopy closure compared to hemispherical photography, its effectiveness at tracking the progress of canopy closure from winter to summer has not been tested. In order to be useful, the method must be able to detect fine-scale changes as the canopy develops through spring, and it must be possible to derive meaningful phenological parameters from the time-series. Logistic growth models are commonly used in canopy phenology studies, to describe the timing and rate of canopy development (Ahl et al., 2006; Calders et al., 2015; Fisher et al., 2006; Richardson et al., 2006; Richardson et al., 2007; White et al., 2014; Zhang et al., 2003). If smartphone fisheye photography data on canopy closure can be used to derive similar phenological parameters to hemispherical photography, it could enable canopy phenology data to be collected at much larger scales than is currently achievable through existing methods. To facilitate widespread and efficient data collection, it would also be useful to understand how often data must be collected (*i.e.,* the temporal grain required) to obtain accurate estimates of canopy closure, capable of detecting annual and spatial variation.

It is important to note here that the various indices so far described—NDVI/EVI, camera-derived greenness indices, LAI and canopy openness—are all correlated to a greater or lesser extent, but also represent independent phenological measures. Canopy closure is strongly related to photosynthetically active radiation in the understorey (PAR) (Brusa and Bunker, 2014; Gonsamo et al., 2013; Pellikka, 2001), and represents the proportion of the sky hemisphere obscured by canopy elements when viewed from a single point (Gonsamo et al., 2013; Jennings et al., 1999). Greenness is related to canopy closure, and increases as green leaves fill gaps in the canopy (Brown et al., 2017; Keenan et al., 2014a; Wingate et al., 2015). However, greenness is not only a function of the size and spatial arrangement of leaves, but also relates to changes in colour pigmentation. The green signal has been shown to peak before full canopy closure and maximum LAI are reached, when leaves are only half their maximum size, due to production of carotenoids as leaves mature (Keenan et al., 2014a; Wingate et al., 2015). Further, canopy closure is reached before peak LAI, because canopy closure is based on viewing the canopy at multiple zenith angles from a fixed position in the understorey (or above the canopy), and therefore does not account for leaf layering. These differences mean that the metrics should not be seen as interchangeable, but represent complementary techniques that lend themselves to different applications: LAI relates most closely to changes in canopy physiology, while greenness can accurately detect the onset of leaf expansion and the end of growth season (Keenan et al., 2014a). For studies of understorey light dynamics, canopy closure is the most appropriate and straightforward metric to assess, and could be monitored widely with smartphone fisheye photography.

In this study, I trial the use of smartphone fish-eye photography to monitor the process of canopy closure at multiple locations in a mixed broadleaved forest, from a winter to summer canopy. Smartphone fisheye photos were taken every other day alongside traditional hemispherical photos and visual observations of leaf expansion. Time-series data were fitted using a logistic growth model to characterise the timing and rate of canopy closure for each forest plot. I compare canopy closure timing and rate parameters from the logistic growth model fit of smartphone canopy closure estimates, with those from hemispherical photography and visual estimates. These three methods are compared in relation to varying canopy composition and structure, to assess their relationships under different canopy types. Finally, I assess the effect of reduced temporal grain on canopy closure estimates to understand how often data should be collected to obtain reliable estimates, and I discuss how this novel method could be widely applied to provide new insights in forest phenology studies.

5.2 Methods

5.2.1 Study site and data collection

The study was conducted during spring 2017, in Elwell Woods, a small 0.9 ha mixed broadleaved woodland on the River Tamar, England (50°24 N, 4°12 W). The woodland was dominated by *Acer pseudoplatanus* with some *Fraxinus excelsior*, and a patchy understorey of *Crataegus monogyna*. Ten fixed points or 'stations' were established in early March prior to budburst. Stations were deliberately selected to represent a range of conditions in the woodland, with different species compositions and canopy openness levels. The site was monitored every other day from mid-March, to check for signs of imminent leaf expansion. Data collection began when budburst was first observed at the site, on April 1, Day of Year (DOY) 91. Data collection finished when all stations had full canopies, on May 25, DOY 145.

Hemispherical photos were taken using a Nikon Coolpix 990 3.34 MP camera with Nikon Fisheye Converter FC-E8 lens (Nikon Corporation, Tokyo, Japan), and corresponding photos were also taken with a Sony Xperia M4 Aqua smartphone camera (Android Version 5.0) with magnetic fish-eye lens attachment (Skimn FE-12 180° fish-eye lens). The former is a genuine hemispherical lens with 180° field of view in all directions. The smartphone camera with fisheye lens attachment has a narrower field of view. In this study, the smartphone camera was set to a 4:3 aspect ratio, providing 13MP and a 125° x 110° field of view with the fisheye lens attached. Both cameras were mounted on a tripod at 1.2 m above ground, to eliminate the influence of the field layer, and levelled using a circular bubble level. In both cases, photographs were taken in manual mode, and appropriate exposure settings were determined for the sky conditions. This was done using the histogram function on the Nikon Coolpix following the method outlined by Beckschafer et al. (2013), and by visual inspection of captured images with the smartphone camera. Exposure was lowered as required, ranging from 0 to -2.0 EV, the minimum limit on both cameras. To achieve even exposure across the photograph and avoid areas of bright sky or direct sunlight, images were taken at dusk, or in cases where weather conditions were prohibitive (*i.e.,* heavy rain or strong winds), just before dawn the following morning. To avoid blurring caused by pressing the camera shoot buttons, the timer function was used on the hemispherical camera, and earphone controls were used to remotely operate the smartphone camera.

Photographs were analysed using ImageJ, since ImageJ has been found to reliably estimate canopy closure values from hemispherical and smartphone fisheye photographs, and is widely available for use in citizen science projects (Smith and Ramsay 2018). Following the method in Smith and Ramsay (2018), manual thresholding of photographs was applied to binarise images into white ('sky') and black ('not sky') pixels, with reference to the original photograph. A canopy openness value was derived for each image, excluding the redundant framing pixels generated automatically by the two cameras. As this study is concerned with the process of canopy closure, canopy openness values were subtracted from 100 to give the absolute canopy closure percentage. To enable comparisons between different canopies, the canopy closure time-series for each station was standardised along a relative scale from 0 to 100, where 0 represents the winter canopy value without leaves, and 100 represents the summer canopy value with full leaf expansion, using the following equation:

$$Relative\ canopy\ closure\ (\%) = (x - canopy_{\mathrm{MIN}}) / \ (canopy_{\mathrm{MAX}} - canopy_{\mathrm{MIN}}) \tag{1}$$

Here x is the absolute canopy closure value for any given DOY, $canopy_{\mathrm{MIN}}$ represents the lowest absolute canopy closure value for a given station, and $canopy_{\mathrm{MAX}}$ represents the highest absolute canopy closure value for a given station.

In addition to the two sets of photographs, a canopy leaf expansion score was derived from visual observations of individual trees in the canopy above each station. Trees were included in the visual assessment if they were visible in the smartphone fisheye camera field of view. On each DOY, each tree was assigned a leaf expansion score based on the following categories: 0%, 10%, 25%, 50%, 75%. Trees were assigned the score that most closely matched their leaf expansion status. These broad categories were chosen to enable rapid assessment, which was important given the number of trees that had to be assessed in order to characterise the whole canopy. Similar percentage categories are used in citizen science phenology monitoring projects where participants are expected to record the leaf phenology of multiple individual trees (Denny et al., 2014; Elmendorf et al., 2016). Broad percentage categories can also improve between-observer precision (Morrison, 2016) so are often considered appropriate for citizen science. To obtain a leaf expansion score for the canopy above each station on a given DOY, leaf expansion scores for each tree were summed and divided by the total number of trees included in the visual assessment. This provided an estimate of canopy leaf expansion on a proportional scale from 0 to 100, for each station and DOY.

In order to consider canopy structure and composition in the analysis, heights of the overhead canopy at each station were estimated using a clinometer. Summer canopy openness for each station was estimated in ImageJ using the method outlined above to calculate the proportion of visible sky based on $canopy_{\mathrm{MAX}}$ images. This was done for hemispherical photographs and smartphone fisheye photographs separately. The percentage of non-deciduous canopy (*i.e.,* tree trunks, branches, twigs and ivy) for each station was calculated by subtracting the canopy openness value for $canopy_{\mathrm{MIN}}$ from 100. Deciduous foliage for the summer canopy was then calculated using equation (2):

$$Deciduous\ foliage = 100 - (canopy_{\mathrm{MAX}}\ openness + non\text{-}deciduous\ canopy) \tag{2}$$

Two estimates of canopy composition were then made at each station, based on $canopy_{\mathrm{MAX}}$ hemispherical photographs and smartphone fisheye photographs respectively. Proportions of ash, sycamore and hawthorn in each $canopy_{\mathrm{MAX}}$ image were calculated in ImageJ, using the freehand selection tool to fill the area containing each canopy species (ash, sycamore and hawthorn), and then analysing the area fraction of the filled pixels. The proportion of the deciduous foliage comprising each species was then calculated by dividing the area fraction for each species by the deciduous foliage total (equation 2), and multiplying by 100. Stations were then categorised according dominant species composition based on the smartphone fisheye photographs, with stations classed as either sycamore-dominant or hawthorn-dominant.

5.2.2 Deriving phenological metrics from the time-series data:

Data from each station and method (hemispherical photography, smartphone fisheye photography and visual estimations) were fitted using a logistic growth model in order to characterise the rate and timing of canopy closure. In addition, individual time series of leaf expansion for each tree were fitted with a logistic growth model, so that the timing of leaf expansion across each species could be characterised. Logistic growth uses non-linear regression to fit a sigmoidal curve, using the equation:

$$y = \frac{\theta_1}{1 + \exp\left[-(\theta_2 + \theta_3 x)\right]} \tag{3}$$

where y is response variable (proportion of canopy closure), x is the predictor variable (DOY), and θ_1, θ_2 and θ_3 are the model fitting parameters. θ_1 is the upper asymptote, which was fixed at 100 as the data were based on percentages so this value was known to be the true maximum. Using a fixed upper asymptote has been shown to improve model fit (Austin et al. 2011) and produce more realistic parameter estimates, whereas a free upper asymptote often produces biased estimates (Tjorve and Tjorve 2010). The logistic growth model provides two biologically meaningful parameters to describe the data: the rate parameter (θ_3) and the half-maximum (ψ). The rate parameter is based on the steepness of the curve at its mid-point and represents the proportional increase in canopy closure per day. The half-maximum is a measure of canopy closure timing, and represents the DOY when canopy closure reaches 50%, calculated as $\psi = \theta_2/\theta_3$, and hereafter referred to as 50% DOY. Standard error and statistical significance of model parameter estimates were assessed to provide a measure of confidence in the model fits for each data set. Logistic models were fitted using the car package and nls function in R (Fox and Weisberg, 2011).

5.2.3 Statistical analyses

In order to assess the effect of dominant canopy composition on canopy closure timing and rate, I conducted one-way analysis of variance (ANOVA) tests to compare 50% DOY and rate values between sycamore-dominated canopies and hawthorn-dominated canopies. This was done for each method—hemispherical photographs, smartphone fisheye photographs and visual estimations. In cases where data were not from a normally distributed population, according to a Shapiro-Wilks test, I used the Aligned Rank Transform (ART) procedure in the R package ARTool (Kay and Wobbrock, 2016), followed by one-way ANOVAs.

Linear regression was used to assess relationships between the 50% DOY and rate values obtained for individual stations from hemispherical photography, smartphone fisheye photography and visual estimation methods. One-way ANOVA, followed by post-hoc contrasts using estimated marginal means, was then used to test for significant differences between methods in terms of the range of 50% DOY values and rate values predicted across the stations. Additionally, I calculated a combined 50% DOY value and a combined rate value for each method. This was done by averaging the canopy closure proportions from all stations for each DOY, to derive a single-time series that was then fitted using a logistic growth model. This approach required only one logistic model to be run for each method. Using the combined 50% DOY and rate values, I compared how the three methods characterised the overall stand canopy closure, and how 50% DOY and rate values derived from the combined model compared with average 50% and rate values from the ten station models.

Finally, I investigated the effect of interval time between sampling days (temporal grain) on 50% DOY and rate values. The original data was collected every other day (2-day temporal grain). By removing data for different DOYs, I simulated 4, 6, 8, 10, 12 and 14-day temporal grains. Proportion canopy closure was then re-calculated based on the reduced time-series, and proportions for each DOY were averaged across the ten stations to obtain a time-series for the whole stand, for each temporal grain. I took the first day of data collection (Day 91) as the first day for all temporal grains. Where the DOY for $canopy_{\mathrm{MAX}}$ was removed as a result of altering the temporal grain, I inserted the maximum value on the next DOY when data collection would have been carried out (*e.g.,* using a 10 day temporal grain, data collection would have taken place on Day 91, 101, 110, 120, 130, 140, and 150; data collection ended on Day 145, so the highest canopy closure value from the original data set was inserted at day 150). I then re-ran the logistic growth model for each data set. In addition, with smartphone photograph data only, I used a 14-day temporal grain with varying start date, to assess how this impacted on 50% DOY and rate values. Logistic models were run using a 14-day temporal grain with start dates on Day 79, 81, 83, 85, 87 and 89. All statistical analyses were carried out in R 3.3 (R Core Team, 2016).

5.3 Results

Canopy composition varied considerably between stations (Table 5.1). Stations fell into two broad categories, sycamore-dominated with a minor ash component (stations 1–5) and hawthorn-dominated with some sycamore (stations 6–10). All but two of the sycamore-dominated canopies (stations 1 and 2) contained some hawthorn. Stations were ranked in numerical order ranging from the most sycamore-dominated/least hawthorn-dominated (station 1) to the least sycamore-dominated/most hawthorn-dominated (station 10). The proportion of each species in the field of view of the two cameras varied, so I based the 1–10 ranking on the smartphone fisheye photo compositions. In some cases the difference in composition between the two cameras was small, varying by only a few percent (station 2 and 4) or not at all (station 1). However, in other cases they varied by more than 20% (stations 6, 7 and 10). The summer canopy openness values between the two sets of images were similar, but it is clear that hemispherical photographs contained a higher proportion of non-deciduous canopy elements in their field of view.

All time-series from smartphone fisheye photographs and hemispherical photographs could be fitted using a logistic growth model to obtain parameter estimates with low standard error and high significance (Fig. 5.1 A–B, Appendix 5.2: Table A5.1). All time-series from visual estimates could also be fitted to logistic growth models, though the model fit for four of the hawthorn dominant stations were poorer, indicated by the higher standard errors of parameter estimates (Fig. 5.1 C, Appendix 5.2: Table A5.1). However, all parameter estimates were statistically significant. Time series from logistic model fits of individual tree leaf expansion could be fitted for all trees except for one hawthorn, where leaf expansion occurred very rapidly. Models from an additional three hawthorn trees produced poor model fits with non-significant parameter estimates ($p >$ 0.05) so these individuals were not included in the analysis of individual tree leaf expansion timing (Appendix 5.2: Table A5.2).

All tree species were significantly different in their leaf expansion timing according to 50% DOYs from logistic model fits (Fig. 5.2, ANOVA: $F_{2,49}$: 48.15, p <0.001; pairwise comparisons: hawthorn v sycamore p <0.001, hawthorn v ash p <0.001 and sycamore v ash p = 0.010). Across the stand, hawthorn was the earliest tree to leaf, with the majority of individuals reaching 50% leaf expansion before any sycamore individuals. Ash was the latest species to leaf. Hawthorn was consistent in its leafing timing, while sycamore showed a large degree of intra-species variation.

There was a significant difference in 50% DOY between the two canopy types, with later canopy closure apparent for sycamore-dominated canopies (Fig. 5.1 D–F) compared to hawthorn-dominated canopies. This was detected by hemispherical photographs (ANOVA: $F_{1,8}$ = 6.22, p = 0.037), smartphone fisheye photographs (ANOVA: $F_{1,8}$ = 4.88, p = 0.058) and visual estimations (ANOVA: $F_{1,8}$ = 16.60, p = 0.004). However, both photographic methods showed the canopy of station 1 closing earlier than three of the hawthorn-dominated canopies (Fig. 5.1 D and E). In terms of canopy closure rate, faster rates were apparent for sycamore-dominated canopies compared to hawthorn-dominated canopies, according to both hemispherical photographs (Fig. 5.1 G, ANOVA: $F_{1,8}$ = 13.20, p = 0.007) and smartphone photographs (Fig. 5.1 H, ANOVA: $F_{1,8}$ = 64.37, p < 0.001) . No significant difference in rate was observed between canopies using the visual estimates (Fig. 5.1 I, ANOVA: $F_{1,8}$ = 3.00, p = 0.122).

50% DOY and rate values estimated by hemispherical photography and smartphone fisheye photography for the different stations were related, but a linear model only explained 53–57% of the variation (Fig. 5.3 A and B). However, despite variability between 50% DOY values from the two methods, the average difference between the pairs of photos was only 2.15 days (s.d = 1.1). The largest difference in 50% DOY between the two methods was at station 4, where the smartphone fisheye photo method showed 50% DOY occurring 4.8 days earlier than the hemispherical photo method. The average difference in canopy closure rate between pairs of photos was relatively small (mean = 0.011, s.d = 0.008), representing only ~1% difference in canopy closure extent per day.

Comparison of smartphone fisheye photography and visual estimations showed a relationship between the 50% DOY values (Fig. 5.3 C). However, visual estimates predicted earlier 50% DOYs than smartphone fisheye photographs, particularly for the most hawthorn-dominated canopies (Fig. 5.1 F). No relationship was found between 50% DOY values from hemispherical photography and visual estimations (R^2 = 0.20, p = 0.20), nor between the rate of canopy closure from visual estimates and either smartphone photography (R^2 = 0.11, p = 0.35) or hemispherical photography (R^2 = 0.05, P = 0.54).

Overall, 50% DOY values across the stations were similar between the two photographic methods, but not visual estimations, which predicted earlier canopy closure (Fig. 5.4 A, ANOVA: $F_{2,27}$ = 10.00, p < 0.001; pairwise comparisons: hemispherical v smartphone photography p = 0.95, hemispherical photography v visual estimations p = 0.001, smartphone photography v visual esitmations p = 0.003). Canopy closure rates across the stations were similar for all three methods (Fig. 5.4 B, ANOVA: $F_{2,27}$ = 0.40, p = 0.67) but values were much more variable from visual estimates.

When data from all stations were combined into one logistic model, the two photographic methods showed almost identical logistic model fits (Fig. 5.5 A). From the combined model, photographic methods predicted the 50% DOY for the whole stand to within one day of each other, whereas the visual estimation method predicted 50% DOY 10–11 days earlier (Fig. 5.5 B). The predicted canopy closure rate for the stand was also similar from the photographic methods, but visual estimates predicted a slower rate of canopy development (Fig. 5.5 C). For all methods, the 50% DOY estimates derived from the combined logistic model fit for the whole stand were very similar to the average 50% DOYs derived from running separate logistic models for each station. Rate estimates from the combined model were very similar to average rate estimates from individual station models for the two photographic methods, but not for visual estimates.

When the time-series start date was held constant, the 50% DOY value from smartphone photography remained within one day of that predicted by the original model, even when temporal grain was reduced to fourteen days (Fig. 5.6 B). The 50% DOY values from hemispherical photographs and visual estimates were more variable as temporal grain was reduced, but still remained within two days of the original models (Fig. 5.6 A and C). The rate parameter was somewhat more variable, but this variability only represented a difference of around 0.02, which is a 2% difference in the extent of canopy closure per day (Fig. 5.6 D–F). Even with a variable start date for the time series, and a 14-day temporal grain, 50% DOY values from smartphone fisheye photography remained within two days of the original model (Fig. 5.7 A). The rate parameter did vary with different start dates but at worst resulted in a 3% difference in the extent of canopy closure per day (Fig. 5.7 B).

Table 5.1. Structural and composition features of the forest canopy at ten stations in Elwell Woods, England.

Station no.	Dominant species	Canopy height (m)	Canopy structure						Composition (% of deciduous foliage)					
			Smartphone fisheye photographs			Hemispherical photographs			Smartphone fisheye photographs			Hemispherical photographs		
			Canopy openness (%)	Non-deciduous canopy (%)	Deciduous foliage (%)	Canopy openness (%)	Non-deciduous canopy (%)	Deciduous foliage (%)	Ash	Hawthorn	Sycamore	Ash	Hawthorn	Sycamore
1	Sycamore	19	10	24	66	10	41	49	3	0	97	3	0	97
2	Sycamore	21	16	23	61	17	43	40	11	0	89	8	0	92
3	Sycamore	26	15	25	60	16	43	41	11	6	83	5	18	76
4	Sycamore	19	15	23	62	14	41	46	6	12	82	10	13	77
5	Sycamore	20	13	24	64	13	41	47	3	30	67	4	14	82
6	Hawthorn	21	12	35	54	13	47	40	0	48	52	0	74	26
7	Hawthorn	17	8	57	35	10	64	26	0	51	49	0	80	20
8	Hawthorn	11	11	32	57	14	51	35	0	71	29	0	57	43
9	Hawthorn	11	10	46	44	10	62	28	0	73	27	0	81	19
10	Hawthorn	13	10	35	56	11	49	40	0	92	8	0	70	30

Fig. 5.1. Canopy closure phenology derived from hemispherical photography (HP), smartphone fisheye photography (SP) and visual estimates (VE) for ten canopies. Sycamore-dominated canopies are shown in blue and hawthorn-dominated canopies in orange. **A–C.** Logistic growth model fits for all canopies. All model parameters were significant ($p < 0.001$). **D–F.** 50% DOY from logistic growth models. **G–I.** Canopy closure rate from logistic growth models. Error bars represent standard error of the model estimates and indicate goodness of fit. Statistically significant differences between the two canopy types are indicated by shaded circles ($p < 0.05$). Circles with a coloured diagonal line represent a borderline significant difference ($p = 0.058$). Circles with no fill indicate no significant difference ($p = 0.120$).

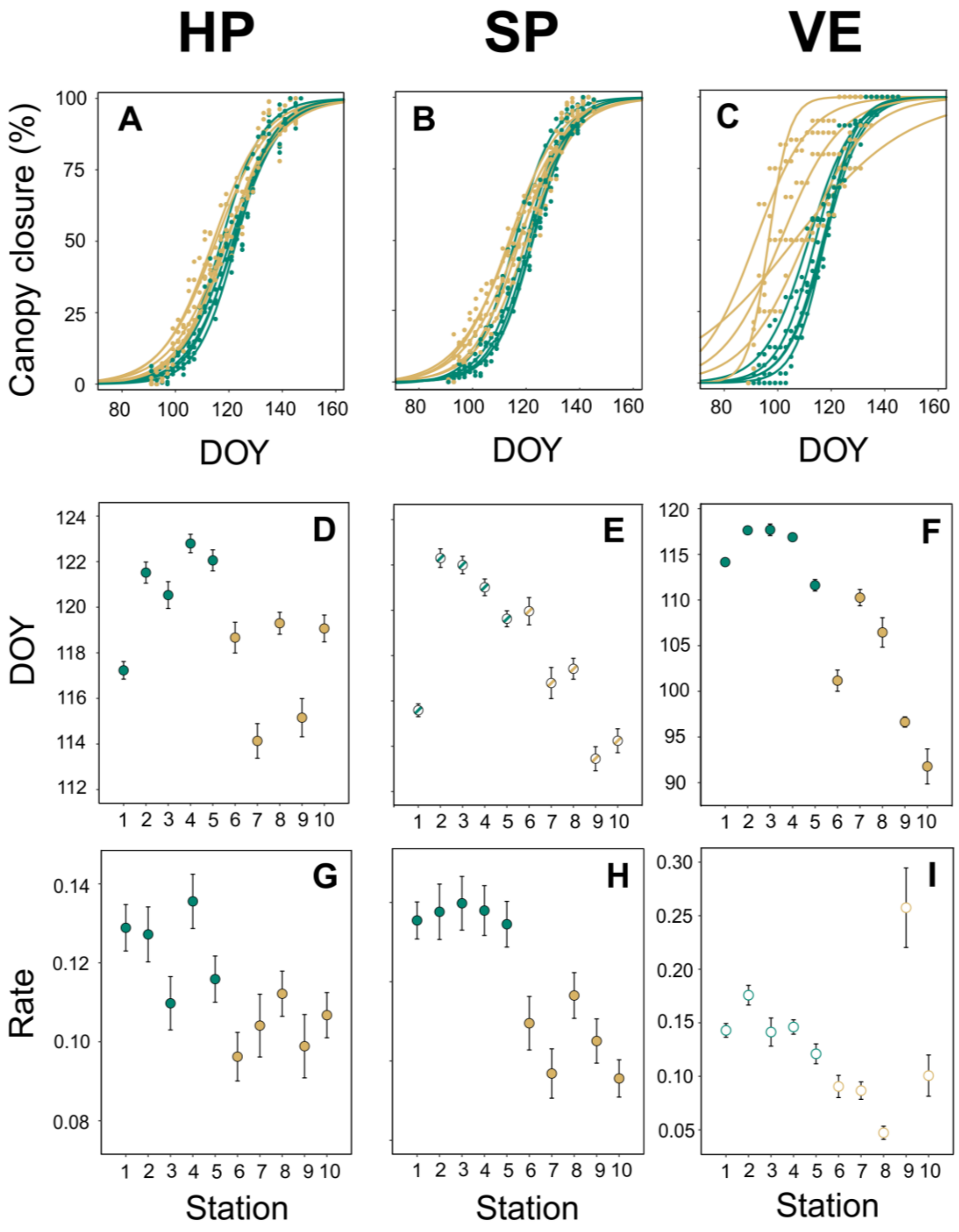


Fig 5.2. Comparison of leaf expansion timing for three tree species, based on 50% DOY derived from the logistic model fit of the time-series for each individual tree. Different colours denote significant differences between species.

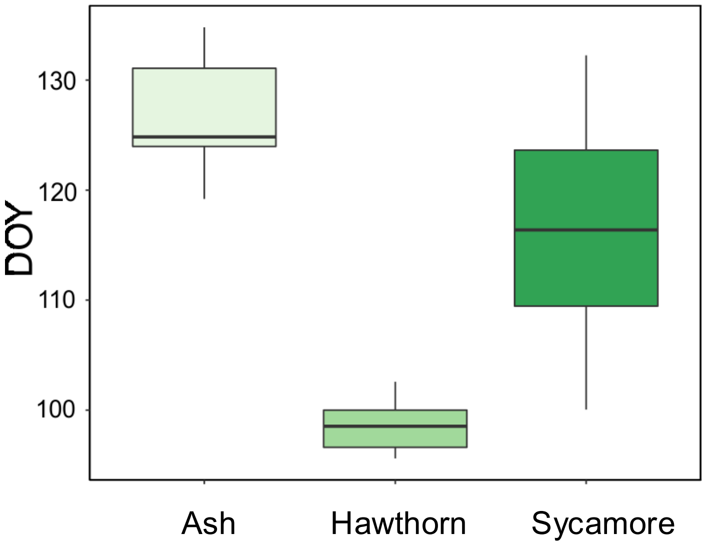


Fig. 5.3. Comparisons of individual station canopy closure timing and rate obtained from different methods. **A.** 50% DOY from hemispherical photography (HP) vs smartphone fisheye photography (SP), R^2 = 0.53, P = 0.018. **B.** Canopy closure rate from HP vs SP, R^2 = 0.57, P = 0.011. **C.** 50% DOY from SP vs visual estimation (VE), R^2 = 0.54, P = 0.015.

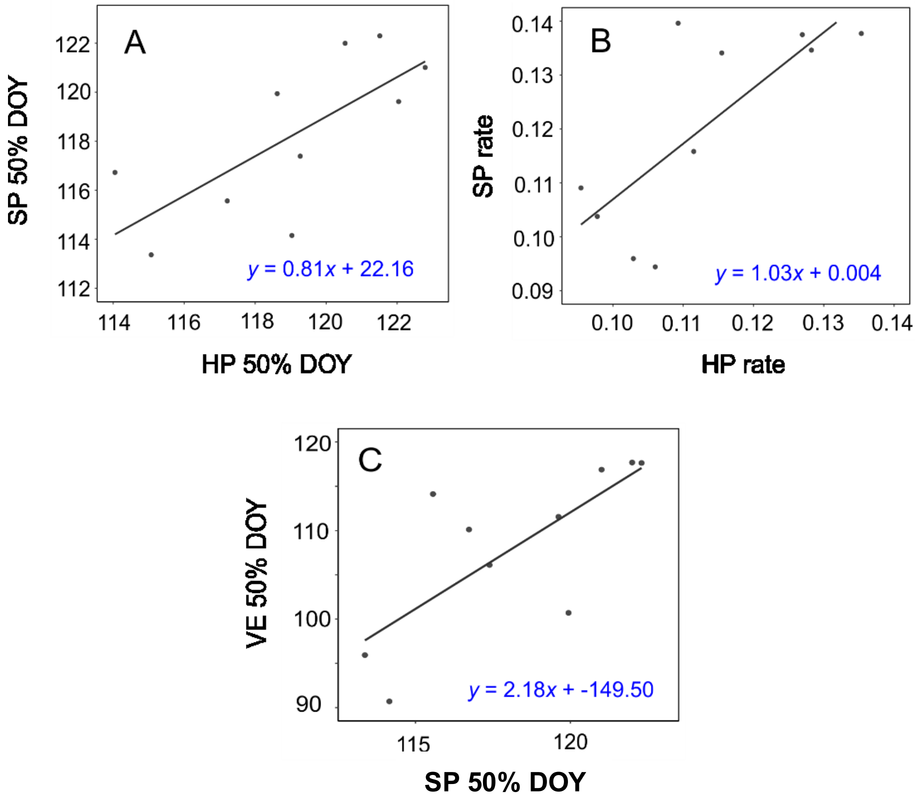


Fig. 5.4. Comparisons of canopy closure timing and rate across all ten stations, obtained from hemispherical photography (HP), smartphone fisheye photography (SP) and visual estimates (VE). **A.** 50% DOY values across the ten stations (mean values were HP = 119.02, SP = 118.21, VE = 108.14). **B.** Canopy closure rates from across the ten stations (mean values were HP = 0.11, SP = 0.12, VE = 0.13). The horizontal line shows the median, the box represents values within the 25–75% quartiles, and the error bars show the minimum and maximum values. Methods sharing a lower case letter were not significantly different according to post hoc contrasts using estimated marginal means.

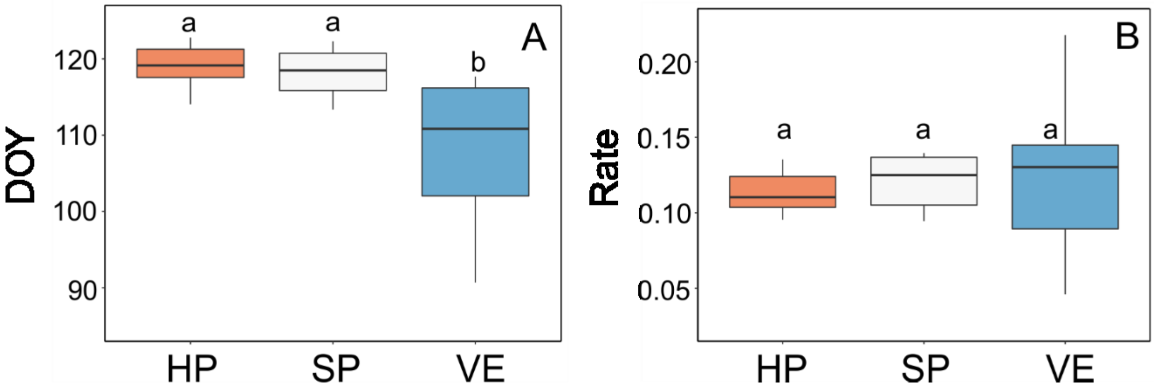


Fig 5.5. Canopy closure phenology based on logistic model fits for the overall stand (ten stations combined), from hemispherical photography (HP), smartphone fisheye photography (SP) and visual estimates (VE). **A.** Logistic models for overall stand. All parameter estimates were statistically significant ($p < 0.001$). **B.** 50% DOY values for the overall stand (HP = 119.12, SP = 118.34, VE = 109.01) **C.** Canopy closure rates for the overall stand (HP = 0.11, SP = 0.12, VE = 0.10). Error bars show standard error of the model estimates and are a measure of goodness of fit. Model parameter values, standard errors and significance are included in Appendix 5.2: Table A5.1.

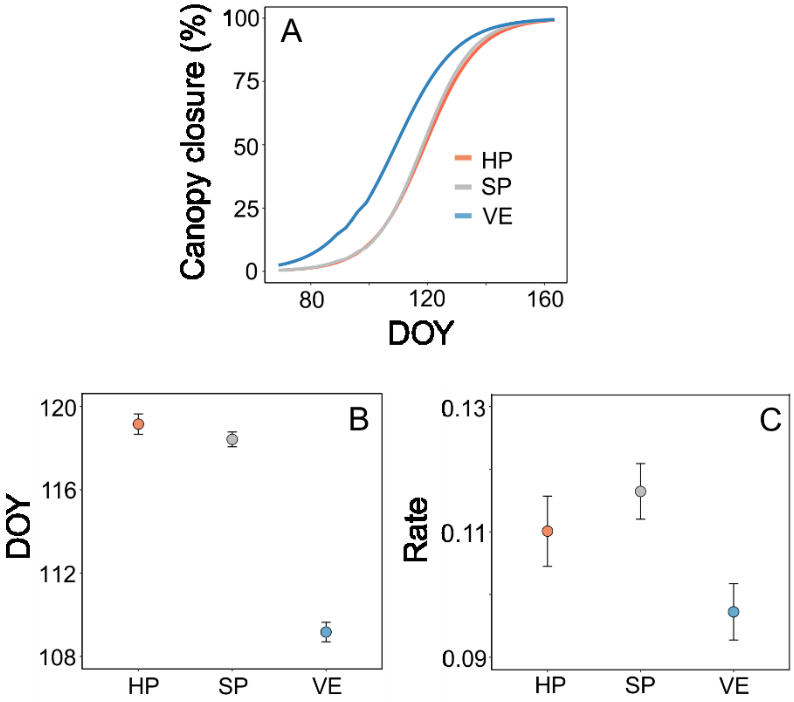


Fig 5.6. The effect of different temporal grains on 50% DOY and rate parameters based on combined forest canopy models for hemispherical photography (HP), smartphone fisheye photography (SP) and visual estimates (VE). Error bars represent standard error of the model parameter estimates. All parameter estimates were significant ($p < 0.007$). Model parameter values, standard errors and significance are included in Appendix 5.2: Table A5.3.

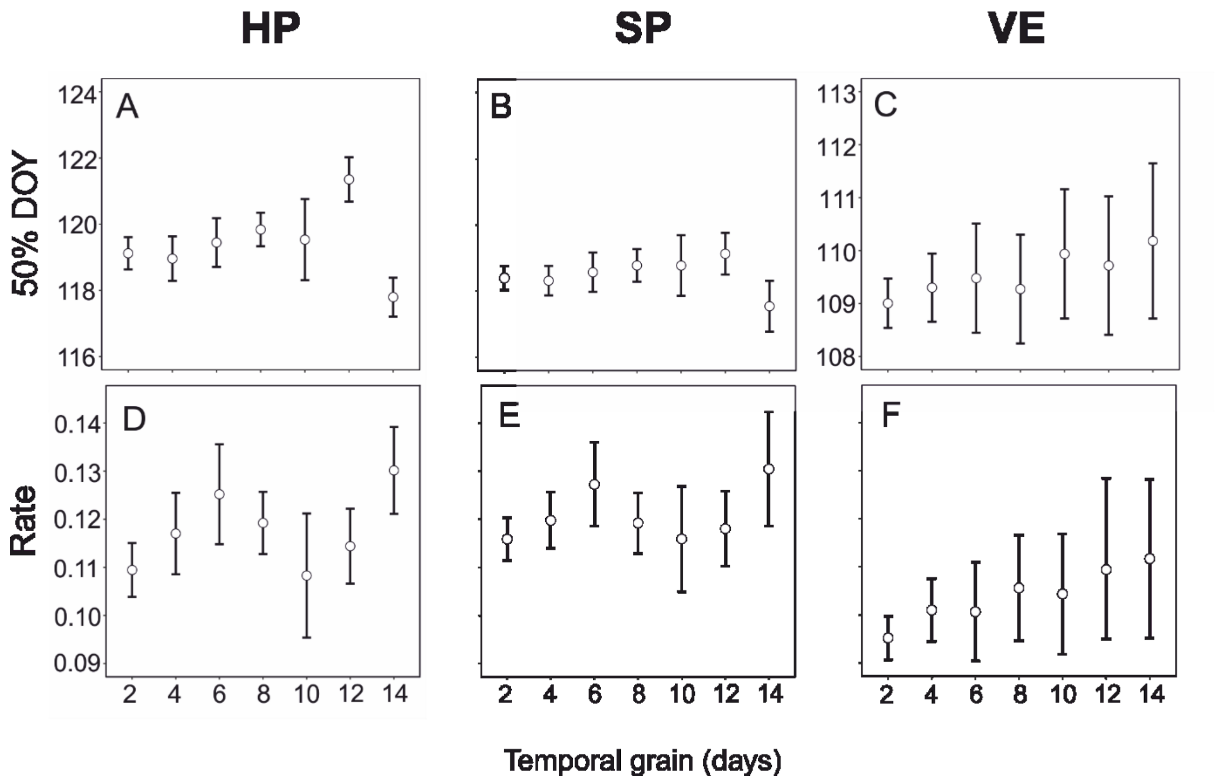
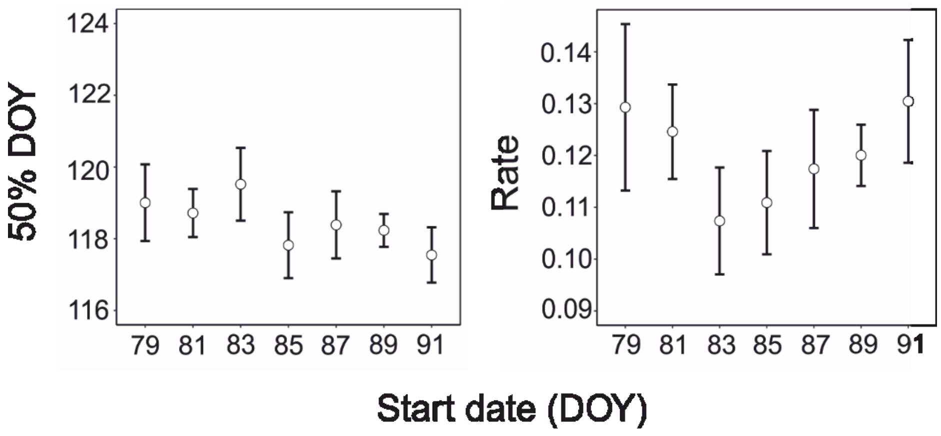


Fig 5.7. The effect of different start dates on 50% DOY and rate parameters based on combined forest canopy models, using smartphone photography data with a 14-day temporal grain. Day 91 was the original start DOY. Error bars represent standard error of the model parameter estimates. All parameter estimates were significant ($p < 0.002$). Model parameter values, standard errors and significance are included in Appendix 5.2: Table A5.4.



5.4 Discussion

Smartphone fisheye photography gives fine resolution measurements, capable of detecting small-scale variation in forest canopies (Bianchi et al., 2017; Smith and Ramsay, 2018). This trial demonstrates that when applied to monitoring canopy closure phenology, the method gives comparable results to hemispherical photography. Using logistic growth models with a fixed upper asymptote, the two methods have comparable model fits and parameter estimates. Other sigmoid models may also work well, but as logistic growth has been widely used in phenology studies (Ahl et al., 2006; Calders et al., 2015; Fisher et al., 2006; Richardson et al., 2006; Richardson et al., 2007; White et al., 2014; Zhang et al., 2003), it is a suitable choice for initial trials with a novel data collection method. The coarser resolution of the visual estimate method meant it was less able to detect small-scale changes in canopies. This gave rise to pulses and plateaus in leaf expansion activity, resulting in poorer model fits where canopies contained trees with contrasting leafing times.

It is not surprising that the visual estimation method produced earlier canopy closure dates and more variable canopy closure rates compared to photographic methods. The coarse resolution from assigning leaf expansion scores in percentage bands meant that a tree could gain a score of 100% leaf expansion, when just over 75% was in leaf. Perhaps a more important reason for the observed difference in visual estimation and photographic methods is that while leaf expansion and canopy closure are related, they assess different attributes and should be considered as independent descriptors of canopy phenology. Canopy closure, as assessed by the two photographic methods, is the proportion of sky obscured by leaves as viewed from a single point (where the photograph is taken), and is closely related to understorey light (Brusa and Bunker, 2014; Gonsamo et al., 2013). By contrast, estimates of leaf expansion do not consider how the leaves occupy space in the canopy. In this study, leaf expansion was defined as the point when the recognisable shape of the leaf was visible, which does not account for leaf flattening or enlargement. In other studies, measures of leaf emergence have been shown to peak prior to optical measures of canopy structural development (Capdevielle-Vargas et al., 2015; White et al., 2014). Similar to large-scale observational studies of leaf phenology, the visual method used here did not weight leaf expansion scores according to basal area or crown size, so scores for small crowns were weighted equally to those of large crowns. For this reason the visual method showed particularly early canopy closure for hawthorn-dominated canopies, as early-leafing hawthorn had a strong effect on leaf expansion scores but weaker effect on canopy closure. These issues demonstrate the importance of studying canopy closure directly, in order to understand understorey light dynamics, rather than inferring canopy closure timing from observations of leaf phenology.

The timing and rate of canopy closure characterised by the two photographic methods at the different stations can be explained in terms of leaf phenology and canopy composition. Hawthorn is a light-demanding, early leafing sub-canopy species, which takes advantage of high light periods prior to overstorey canopy closure (Roberts et al., 2015). The earlier leafing of hawthorn observed in this study corresponded with the earlier closure of hawthorn-dominated canopies. With the exception of station 1, there was a general pattern of earlier canopy closure where there was a greater proportion of hawthorn in the canopy. Furthermore, canopies containing the highest proportions of the later leafing ash were the latest canopies to close. As well as variation in the timing of leaf expansion between species, considerable intra-species variation is common even over small spatial scales (Delpierre et al., 2017). In this study, sycamore had the highest intra-species variation. This variation explains the earlier closure of station 1 compared to three of the hawthorn-dominated canopies (stations 6, 7 and 8). Sycamore came into leaf on average 13 days earlier at station 1 compared to sycamore at stations 6, 7 and 8.

Smartphone fisheye photography differs from hemispherical photography in its narrower field of view, which results in the former method producing images with a higher proportion of foliage elements and overhead canopy, as tree trunks and foliage at wider zenith angles are missed (Smith and Ramsay, 2018). However, there is no evidence that this difference affected canopy closure timing or rate estimates, as neither method consistently showed earlier or faster closure than the other. The differences observed between canopy closure estimates from smartphone and hemispherical photographs can be explained by the different proportions of the three canopy species captured in each camera's field of view. Where the overhead canopy was dominated by hawthorn, smartphone fisheye photos contained a higher ratio of hawthorn to sycamore, and therefore detected earlier canopy closure (stations 5, 8, and 10). By contrast, where hawthorn was present in the image periphery, hemispherical photos captured a greater proportion of hawthorn in their field of view than smartphone photos, and subsequently detected earlier canopy closure (stations 6 and 7). The difference in canopy closure timing between the two methods was greater where the compositional difference was highest.

Overall, the results show that smartphone fisheye photographs yield very similar 50% DOY and rate values to hemispherical photography, when values are averaged across the stand, or when proportions of canopy closure across the stand are combined into one logistic model. The narrower field of view of the smartphone camera with fisheye lens means fewer individual tree crowns are included compared to a full hemispherical image (Pellikka, 2001). Given the variability in leaf expansion timing between species and individuals, it could be expected that an image containing fewer trees would a) yield more variable estimates of canopy closure timing across the stations, and b) yield faster estimates of canopy closure rate for individual stations. However, there was no overall difference in rate of canopy closure between the two photographic methods, and variability in rate and timing estimates were very similar. These results suggest that the smartphone fisheye camera field of view is large enough to capture variability in a canopy comparably to hemispherical photography.

The woodland sampled in this study was small, with similar canopy openness, aspect and topography, so ten stations enabled the smartphone fisheye photography method to characterise stand canopy closure comparably to hemispherical photography. Both methods also identified very similar levels of absolute canopy openness for $canopy_{\mathrm{MAX}}$ in contrast to Smith and Ramsay (2018). This may reflect the fairly uniform nature of canopy gaps in the woodland in this study, as well as the wider angle of view of the smartphone camera set up used here. In forests with more uneven structure, more stations may be required for smartphone fisheye photography to characterise canopy closure timing accurately. In addition, given the effects of microclimate and topography on leaf expansion timing (Fisher et al., 2006) it is recommended that in larger and more heterogeneous forests, ten stations are randomly assigned per 1 ha plot, and multiple plots are chosen to represent different stand conditions *e.g.,* elevational gradients, species compositions and stand structures. Where the aim is to investigate local-level variation in forest canopy closure, for detailed studies of canopy-understorey dynamics, individual models should be run for each station, in order to understand the degree of variability across each stand.

Where the aim is to assess differences between forests across large geographic areas, a time-saving approach of combining data from ten stations into one logistic model could be used, as this resulted in similar canopy closure timing and rate metrics for the stand.

There was a surprising degree of consistency in the logistic model estimates of canopy closure timing and rate between data sets obtained from a 2-day temporal grain and data sets from a 14-day temporal grain. A 14-day temporal grain is considerably less frequent than required for studies of leaf expansion on individual trees, where the rate of canopy development is much faster (Chapter 3). In this study the time from budburst to full canopy closure was 54 days, which is longer than reported in some other studies of both mixed species (Richardson et al., 2007) and single species stands (Capdevielle-Vargas et al., 2015). The longer duration of canopy closure in this study is likely a result of the species composition in the stand, which included early leafing hawthorn and late-leafing ash. In addition, while in this study it did not seem to matter when observations began around a 14-day window of first leaf expansion, this may have been due to the fact that most early leafing in this study was a result of hawthorn, which had a relatively low impact on overall canopy closure. In forests where early leafing trees have higher leaf area, early leafing activity could influence canopy closure more strongly, which would make capturing that activity more important for accurate prediction of canopy closure timing and rate. Further studies investigating the effect of temporal grain on canopies with different species compositions would be important to determine standard guidance on appropriate minimum sampling effort to obtain accurate canopy closure estimates.

5.5 Conclusions

The present study has highlighted the potential of smartphone fisheye photography to provide meaningful data on the timing of canopy closure in forest ecology studies. While this trial is based on a small sample size in a single mixed species stand, the results clearly demonstrate that the method can detect small variations in canopy closure timing and rate, with potential to assess variation in canopy closure dynamics both between and within forests, and between different years. Further work is now needed test how the method performs in forests with different structures and compositions, so that standard guidance can be given to citizen scientists on how often photos should be taken. In addition, while the logistic model provided good fits and estimates of canopy closure timing and rate, the half-maximum parameter can be difficult to define in a biologically meaningful sense (Hufkens et al., 2012). Investigating alternative model fits that yield parameters of time when canopy closure rate peaks, and time when canopy closure reaches 75% and 95%, would be useful next steps (Yin et al., 2003).

There is a gap in current forest phenology monitoring, as few methods assess canopy closure directly (though see Korhonen et al. 2011 and Moeser et al. 2014) . The advantage of this method is its potential for widespread application, which is much needed to inform both landscape-scale and local-level conservation management, given the wide-range of factors that influence canopy phenology. With widespread and increasing ownership of smartphones, and the inexpensive nature of fisheye attachments, this method could be widely applied to enable comparisons of canopy closure timing between forests across large spatial scales. There could also be potential for data from smartphone fisheye photography to add valuable ground-based information to assist in the validation of satellite indices, though further research would be needed to characterise the relationship between different indices and canopy closure across a range of forest types.

6 Monitoring impacts of climate change on forest ecosystem dynamics using citizen science

6.1 Introduction

It is well-established that climate change is affecting temperate broadleaved forests, with changes to tree phenology causing earlier and more prolonged closure of forest canopies (Menzel and Fabian, 1999; Roberts et al., 2015; Vitasse et al., 2009b). Broad-scale monitoring is conducted through remote sensing to characterise trends at regional and landscape scales (Ahl et al., 2006; Boyd et al., 2011; Hamunyela et al., 2013; Zhang et al., 2003). Meanwhile, impacts of future climate change have been investigated in experimental studies on specific species in particular sites and conditions (De Frenne et al., 2011; Fu et al., 2012; Jacques et al., 2015; Kim et al., 2015; Rollinson and Kaye, 2012; Vitasse et al., 2009a). However, there remain large gaps in our understanding of how climate change will affect forest ecosystem dynamics at local scales, inhibiting effective conservation management to mitigate impacts on biodiversity.

The present research has underlined the fact that forests vary greatly, even over small spatial scales, and therefore high levels of replication are necessary to predict impacts on different forests, in order to implement effective biodiversity conservation at local and landscape-scales. A large range of factors including soil type, topography, structure and composition interact to affect the way different forests respond to environmental change (Vanhellemont et al., 2014; Verstraeten et al., 2013). Seasonal vegetation dynamics vary between forests, and this has implications for monitoring methods. For example, existing phenology monitoring of forest understorey plants focuses heavily on spring ephemerals (*e.g.,* Nature's Calendar, 2017), but some forests may be dominated by summer-green or evergreen flora (Chapter 2). In developing widespread monitoring of forest understorey dynamics, it is important to maintain a flexible approach that enables the selection of species that are most relevant to individual study sites (Chapter 2). Furthermore, at the site-level, considerable intra-species variation can be found in the phenology of canopy trees over short distances (Chapter 3 and 5), and small differences in canopy openness can have large effects on herb-layer vegetation (Chapter 2). Therefore high replication is needed within forests as well as between them.

Models have been designed in attempts to predict impacts of climate change on forests, but there is a lack of information on how community dynamics and site factors interact to determine the response of different species and ecosystems (Aaheim et al., 2011; McMahon et al., 2011). Numerous researchers have called for more widespread ground data to validate satellite remote sensing and improve parameterization for predictive models (Morgan et al., 2001; Peng et al., 2017a; Richardson et al., 2012; Wu et al., 2017). Furthermore, many ecologists interested in local forest conservation have also called for more integrated studies that consider forest ecosystem dynamics at a range of temporal and spatial scales (Baeten et al., 2010; Cole and Sheldon, 2017; Groffman et al., 2012; Murphy and McCarthy, 2014). It would be prohibitively expensive for this to be done by professional researchers, so the only realistic way to achieve this is through the involvement of non-professional scientists in data collection.

This thesis aimed to identify methods that could be used more widely in monitoring of forest ecosystem dynamics in relation to climate change. A key outcome of the thesis is the development of an effective method for monitoring canopy closure timing, which has the potential to be widely used through citizen science. Light is the main mechanism controlling understorey growth, with the spring period being the most dynamic in terms of understorey development (Chapter 2). Therefore, monitoring changes in the timing of when understorey light becomes limiting is key. As the period of phenological escape is brief for many species (Augspurger and Bartlett, 2003; Richardson and O'Keefe, 2009), monitoring methods must be sensitive enough to detect small-scale variation in canopy closure through space and time. Canopy closure is a reliable surrogate attribute to estimate the understorey light environment across different forests, in place of more complex attributes such as Global Site Factor (Chapter 2). Visual estimates of canopy openness and leaf expansion are too coarse to detect small variation in canopy closure (Chapter 4 and 5), and ordinary smartphone photography is too restricted in its angle of view (Chapter 4). However, smartphone photography with a fisheye lens is able to detect small variations in canopy closure, and can characterise canopy closure phenology comparably to sophisticated hemispherical photography (Chapter 5). My research has also demonstrated that this method is suitable for widespread use. Free image analysis software can be used to derive canopy closure estimates comparable to professional software, and different phone models and users can give reproducible results (Chapter 4).

As well as monitoring canopy closure timing, monitoring individual tree phenology is important for predicting changes in forest composition and biodiversity. Another important finding of my research is that first event dates frequently used to monitor tree phenology can be misleading. Due to differences in the rate of leaf development between and within species, it is important that phenology monitoring involves collection of time-series data that enable more accurate determination of leaf expansion timing and rate. This is particularly important in studies of ecosystem dynamics, as the rate of leaf expansion affects how quickly a tree begins photosynthesis, and can also affect vulnerability to herbivory and frost damage (Augspurger, 2009). Furthermore, the timing and rate of tree leaf expansion across a population has important implications for trophic interactions (Cole and Sheldon, 2017). In my research, I found that both visual estimation methods of leaf expansion—counts of tree sections and percentage estimates of whole crowns—yielded similar estimates of timing and rate using logistic growth models (Chapter 3). However, before being used, these methods would need to be trialled with citizen scientists to assess reliability with multiple surveyors, and with different crown sizes and heights. Ensuring reproducible estimates of leaf expansion timing and rate will be important for predicting local and landscape-level impacts of phenological changes on tree health and biodiversity.

Based on the research in this thesis, I present a summary of key recommendations for widespread monitoring of forest ecosystem dynamics in relation to climate change (Fig. 6.1). I then provide details of a citizen science pilot study that I have developed, as a first step to implementing this. Finally, I discuss recommendations for further research, and highlight opportunities for development.

Fig. 6.1. Monitoring recommendations based on key findings

Monitoring canopy closure with smartphone fisheye photography

- Photographs should be taken as frequently as possible to enable accurate characterisation of canopy closure under canopies with different compositions and development rates. Every two days is ample, but as a minimum photos should be taken once every two weeks.

- A minimum of ten stations should be selected for each stand (*i.e.*, an area of forest with similar structure, composition and topography). These stations should be far enough apart that the photos taken capture different canopy elements, to avoid pseudoreplication.

- Guidance on camera settings and optimum conditions for photography, outlined in Chapters 5 and 6 and Appendix 7.1 should be carefully followed to maximise data quality.

Monitoring herb-layer dynamics

- Herb-layer vegetation should be monitored alongside canopy closure at the same locations and time intervals. 3 x 3 m is an appropriate plot size, as larger sizes are likely to increase error in percentage estimates (Vittoz and Guisan 2007).

- Percentage cover of overall vegetation and bare ground should be estimated, alongside percentage cover estimates for key species.

- Species selected should represent dominant species in the stand, and also include species of conservation interest (e.g. rare or declining species and potential invasives).

- In addition to intensive monitoring in spring, percentage cover estimates should be carried out at least once in summer, autumn and winter (at the same time each year), to identify other effects of climate change (*e.g.,* changing rainfall patterns, extreme temperatures, mild winters *etc*.).

Monitoring individual tree phenology

- Time-series data on leaf expansion should be collected using visual observations* conducted at least once every four days.

- A large sample size (>10) replicate individuals should be chosen for each species and age class being studied. Replicate individuals should be of a similar size and in similar habitat and micro-climatic conditions (*i.e.,* be chosen from within a single stand, and occupying a similar position in the canopy *e.g.*, all dominant trees, or all sub-canopy trees).

*Further research is needed to determine whether counts or estimates are the most reliable method with multiple observers, across different crown sizes, heights and species.

6.2 Putting findings into practice: citizen science pilot study

As a first step to implementing more widespread monitoring of forest ecosystem dynamics in relation to climate change, I have established a pilot citizen science project to monitor spring canopy closure and understorey dynamics in a local woodland. The pilot study is taking place in Budshead Local Nature Reserve, Plymouth, England (50°25 N, 4°10 W). The site is an estuarine Plantation on an Ancient Woodland Site (PAWS) comprising a mature canopy of beech and hornbeam, with an understorey of beech, sycamore and ash. The pilot study has been coordinated in partnership with Active Neighbourhoods, a community project run by Devon Wildlife Trust and Plymouth City Council. Ten members of the public have been recruited to participate in data collection during spring 2018.

The study design brings together several key elements of my research findings, and involves: smartphone fisheye photography to monitor canopy closure, counts of leaf expansion (on tree saplings), and percentage cover estimates of key herbaceous plants. In addition, volunteers will record flowering abundance of herbs. Small saplings (< 1.5 m tall) from three species (ash, beech and sycamore) that were common in the forest understorey were selected for monitoring, and fitted with removable identification tags. The saplings act as the 'stations' where canopy photographs and herb-layer assessments are conducted. In total 21 saplings have been tagged (seven of each species). As the woodland in this study has a canopy of mature beech and hornbeam, the summer conditions in the understorey are very shaded and the herb-flora is dominated by spring ephemerals, hence their selection as the species being monitored in this pilot study.

Data quality considerations are important in all research, particularly so when multiple surveyors are used, and especially when those surveyors are inexperienced (Crall et al., 2011; MacKenzie et al., 2017). Data quality in citizen science has gained increasing attention, as citizen science has become more important for gathering data at scales needed to answer questions on complex and rapidly changing conservation issues. Training has been shown to improve data quality, as has the provision of clear instructions (Dickinson et al., 2010; Fuccillo et al., 2015). A half-day training session was delivered for volunteers to provide instruction on how to take canopy photographs, carry out leaf expansion counts and estimate herb-layer cover. Detailed written and pictorial instructions were also provided (Appendix 6.1). In addition, each station will be assessed by two different volunteers, and a graduate Conservation Biology student has been trained to oversee the project. She will be repeating observations and photographs at all stations, and this will provide a comparison between data collected by volunteers and data from an experienced surveyor.

Volunteer motivation is another important factor in determining data quality in citizen science (Beaubien and Hamann, 2011; Worthington et al., 2012). If participants are not motivated, projects can be hampered by incomplete or inaccurate data sets (Frensley et al., 2017). Having a dedicated person to oversee volunteers and provide regular communication should help maintain volunteer motivation and retention (Beaubien and Hamann, 2011). In addition, it is important to consider reasonable expectations on people's time. I found that canopy closure timing estimates were reliable if photos were taken as infrequently as once every two weeks (Chapter 5). However, leaf expansion counts on individual trees needed to be conducted once every four days to yield accurate predictions of phenology timing and development rate (Chapter 3). Therefore it was decided that volunteers should be asked to carry out monitoring twice a week at regular intervals (*i.e.,* every three to four days). While saplings might leaf more rapidly than mature trees, it was decided that asking volunteers to visit more frequently than twice a week could reduce involvement. A three- to four-day temporal grain, should still enable good prediction accuracy using logistic growth models.

Having volunteers take canopy photos at a higher temporal grain than necessary could be beneficial for two reasons. Firstly, while volunteers have been instructed on measures to maximise photo data quality, it is possible that some photographs may be unusable due to weather conditions and depending on individual user-expertise. Furthermore, the forest being studied has a different species composition and age structure to that studied in Chapter 5, so it is possible that canopy closure rate will be more rapid.

In this pilot it was decided that volunteers would take photographs without the use of a mount or tripod. The marked sapling is used to mark where photos should be taken. Volunteers have been instructed to stand next to their sapling to take the photo, and to face the same direction each time, so the smartphone camera is orientated consistently. The canopy at each station will be monitored by three people—twice by volunteers and once by the project coordinator. This will enable a comparison of canopy closure timing and rate from the three sets of photographs. If all three sets provide comparable estimates, it would indicate that tripods and mounts may not be necessary to ensure consistent images. This would be useful, as requiring fixed mounts would reduce the potential for this method to be widely applied.

The cost-effective nature of the methods employed in this research have facilitated this pilot, and makes such studies feasible longer term. As different smartphone cameras perform comparably (Chapter 4), volunteers are using their own smartphones to take photographs. The inexpensive nature of the smartphone fisheye lens attachments has meant that the project was able to purchase one for each volunteer. In addition, two volunteers have expressed interest in being involved in analysing images. Since ImageJ software is open access and simple to use, it will be possible for volunteers to install the software on their own computers. This could enable a follow-up trial to assess volunteer accuracy in analysing canopy images. This would speed up the process of analysis, and could provide insights as to whether canopy images would be appropriate for analysis through online crowdsourcing (Kosmala et al., 2016).

6.3 Future research and areas for development

To take the proposals in this thesis forward there are several key areas for future work. These include: further research to refine methods; data quality research with citizen scientists using the methods; development of smartphone apps to enable efficient data submission and analysis; and the engagement of partners to support the roll-out of a national project.

Research to refine the methods and to assess the quality of data collected by citizen scientists could be achieved at the same time, with an extended roll-out of the current pilot project. It would be useful to test the smartphone fisheye photography method in a wider range of forest types, to provide more specific guidance on how frequently photos must be taken. With regards tree phenology assessments, trials with citizen scientists are needed to assess accuracy of counts versus percentage estimates of leaf expansion using different trees species, and with canopies of different heights. Two of the main data quality challenges in citizen science arise when participants are required to identify species and make subjective visual assessments of abundance (Crall et al., 2011; Delaney et al., 2008; Fuccillo et al., 2015; Galloway et al., 2006). As recommended herb-layer monitoring will focus on key species for each study site, citizen scientists should have a manageable number of species to become familiar with, but some form of data validation and training will be required. In addition, it will be important to assess citizen scientist accuracy in percentage cover estimates. Data quality testing should be carried out routinely as part of citizen science monitoring schemes, so mechanisms for ongoing data quality checks should be built into any monitoring programme that is developed.

A time-consuming element of the present study was the processing of canopy imagery to derive canopy closure percentage estimates. If this method is to be used on a large scale, it is important to speed up the process of image analysis to reduce project management costs. There are two possible options for this. One option is to utilise a crowd-sourcing approach, where images are added to an online repository (*e.g.,* Zooniverse.org) to enable multiple citizen scientists from around the world to classify the canopy and sky pixels, and then analyse images to calculate the percentage canopy closure. This sort of approach has already been used to validate plant phenology data from webcam images (Kosmala et al., 2016) and to classify images of crown health in tropical rainforests (Zooniverse, No date). Each image is analysed by tens of users, to derive a consensus value, with confidence weightings applied according to level of between-user agreement. Zooniverse currently has 1.1 million users, and is a growing community, so this offers considerable potential (Kosmala et al., 2016).

Another option is to utilise the rapidly developing technology in smartphone apps. Tichy (2016) developed an app for calculating canopy cover (*i.e.,* the vertical projection of the tree canopy onto the ground surface) from canopy photos taken with a smartphone or tablet. The app can be used to analyse images taken with or without a fisheye lens, with the user inputting the camera angle of view and threshold settings for image classification. The aim of the study by Tichy (2016) was to identify methods for estimating canopy cover, which relates to the dominance of tree cover at a site and is often used to calculate stand volume, rather than understorey light, which can be inferred from canopy closure (Gonsamo et al., 2013; Jennings et al., 1999; Tichy, 2016). Although the app does provide a ‘canopy closure’ calculation, this was not tested against canopy openness/closure values derived from professional software. Having established the potential for smartphone fisheye photography to obtain canopy openness estimates in my research, it would be useful to assess the reliability of this app as an analysis tool. Ideally an app would be developed that can enable reliable automatic calculation of canopy openness. Newly developed image analysis algorithms are able to detect and eliminate poor quality images (*e.g.,* those with lens flare), and select appropriate thresholds for separating canopy and sky pixels (Glatthorn and Beckschafer, 2014). This would remove subjectivity in analysis and increase efficiency.

The potential use of smartphones and apps in ecological research is only just starting to be recognised (Teacher et al., 2013). A major advantage of using apps for data collection is the ability to integrate rapid data submission. The UK-wide citizen science project, Open Air Laboratories (OPAL), required participants to enter data online or send data by post, and found that only about 10% of completed surveys were returned (Lakeman-Fraser et al., 2016). Increasing the ease by which people submit data is likely to improve submission rates. An app that enables citizen scientists to enter data, capture images, analyse them and then submit their automatically geo-referenced data-sets would improve data quality, save time and make the project more cost effective. To be practical, the app would need to have offline functionality to input and store data when the user does not have internet signal, which is becoming increasingly possible as technology develops (Teacher et al., 2013).

Smartphone app technology continues to advance apace, and exciting new opportunities are arising for obtaining additional data that could be used in studies of forest ecosystem dynamics. Recently, an app for estimating chlorophyll content of individual leaves has been tested, and shown to be a reasonable cost-effective alternative to professional chlorophyll meters (Vesali et al., 2015). This technology is based on analysing colour channels, similar to analysis used to derive greenness indices (Chapter 3). This could be extended to assess greenness indices for plant canopies or forest understories, using automatic algorithms to correct for lighting variation (Brown et al., 2016) This could provide opportunities for citizen scientists to use photography of forest understories alongside smartphone fisheye photos of the canopy, to track the green-up of the herb and shrub layers in spring, in relation to canopy closure.

A smartphone app has also been developed to provide estimates of canopy Leaf Area Index in grasslands and crop fields (Confalonieri et al., 2013; Francone et al., 2014). This app has been shown to provide a reasonable rapid assessment alternative to LAI from sophisticated plant canopy analysis in broadleaved forests (Orlando et al., 2015). The app requires testing in forests with different composition and structure, but could be used to collect widespread data on forest phenology in relation to forest productivity. If citizen scientists are taking photographs of canopy closure using smartphone fisheye photography, it could take them less than a minute to open this app and take an additional photo to characterise LAI. The efficiency with which data can be collected and analysed using smartphone apps is a huge advantage.

In summary, developing an app to enable analysis and submission of canopy photographs will be an important next step. In addition, following the pilot study in spring 2018, I intend to extend the project more widely, working with my current employer, Plantlife. Exmoor National Park and the National Trust in the South West are interested in engaging citizen scientists in a forest monitoring programme. Further, as over 40% of forests in the UK are owned privately by individuals for 'personal use' (Smith and Gilbert, 2003), engaging with the private woodland owner sector will be important. I have begun discussions with the Sylva Foundation—a UK charity supporting private woodland owners with conservation objectives—on potential to incorporate phenology monitoring into their existing MyForest App, which provides a facility for landowners to enter data about their woodlands (Snaddon et al., 2013). Through Plantlife I am also involved in national discussions with the Woodland Trust, who lead the UK's current phenology monitoring project, Nature's Calendar. Building this new monitoring project into existing networks will be important, to learn from existing experience and maximise the project reach.

The work presented in this thesis has made a useful contribution to understanding how citizen science could contribute valuable data for monitoring impacts of climate change on temperate forest ecosystem dynamics. The work has emphasised the need for high replication of phenology monitoring in forests—few studies have compared seasonal dynamics across woodlands, but this research highlighted that considerable differences can be found even over small spatial scales. Furthermore, little work has been done previously to quantify the reliability of first event dates in tree phenology research, but the research presented here suggests these are unreliable, and monitoring projects should focus on collecting time-series data from visual observations or photographic methods. The research presented here emphasises the need for widespread and integrated monitoring of forests in relation to climate change, and crucially, offers a way forward. Smartphone fisheye photography has been identified as a novel method suitable for monitoring canopy closure timing, with potential for widespread use. It is already clear that citizen science can make significant contributions to fields such as phenology and ecology, and that there is considerable interest in this area. However, with citizen science trials just beginning, and technological advances continuing, work is now needed to develop the methods proposed into a cohesive monitoring package ready for widespread roll-out.

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8 Appendices

Appendix numbering relates to chapter numbering, *e.g.,* Appendix 2.1 is the first appendix relating to Chapter 2. Tables within Appendices relate to chapter numbers, *e.g*. A2.1 is the first table relating to chapter 2, A2.2 is the second table relating to chapter 2 *etc*.

Appendix 2.1

Woodland and plot-level species composition for four Devon woodlands.

Table A2.1. Overall woodland species composition justifying NVC classifications for four Devon woodlands. NVC community descriptions based on Hall et al. 2004.

	Hardwick	**Hunshaw**	**Newton Mill**	**Whitleigh**
NVC community	W8e *Fraxinus excelsior – Acer campestre – Mercurialis perennis* (*Geranium robertianum* sub-community)	W16b *Quercus spp.* – *Betula spp.* – *Deschampsia flexuosa* (*Vaccinium myrtillus – Dryopteris dilatata* sub-community)	W11a *Quercus petraea – Betula pubescens – Oxalis acetosella* (*Dryopteris dilatata* sub-community)	*Quercus robur – Pteridium aquilinum – Rubus fruticosus* (typical sub-community)
Description of species composition relating to NVC community	Abundant *Hedera helix, Galium aparine, Urtica dioica* and *Phyllitis scolopendrium* are characteristic of this sub-community, and were key understorey species across the woodland. *Geranium robertianum* was also scattered throughout, though not present in survey plots. *Kindbergia praelonga* is an abundant bryophyte in this community, and was the most common bryophyte species in the woodland.	*Pteridium aquilinum* and ericoid shrubs are characteristic, as well as *Vaccinium myrtillus and Dryopteris dilatata,* all present at the site. *Calluna vulgaris* was common along woodland rides, though not in the surveyed plots. Typical bryophytes for this community were common at the site: *Leucobryum glaucum, Dicranum scoparium* and *Hypnum cupressiforme.*	Dominant oak with frequent downy birch and some ash is characteristic, and both species were common at the site. *Corylus avellana* is a locally common species in this community, present here. *Hyacinthoides non-scripta, Dryopteris spp.* and *Rubus fruticosus* are abundant. *Oxalis acetosella* and *Anemone nemorosa* are also characteristic herbs that were present.	Oak is dominant, but sweet chestnut is frequently found in this community, and was an important component at the site, outside of the surveyed area. The field layer typically has *Hyacinthoides non-scripta*, which was present in specific areas of the site. Other dominant field layer species for this community were common throughout: *Rubus fruticosus, Pteridium aquilinum* and *Lonicera periclymenum.*

Table A2.2. Species composition by growth form in the six studied plots at each of the four Devon Woodlands

Plant growth form category	**Hardwick**	**Hunshaw**	**Newton Mill**	**Whitleigh**
Gb Bulbous geophytes	*Hyacinthoides non-scripta*	N/A	*Hyacinthoides non-scripta*	N/A
Gn Non-bulbous geophytes	*Arum maculatum,* *Circaea lutetiana,* *Ficaria verna*	*Pteridium aquilinum*	*Anemone nemorosa,* *Pteridium aquilinum*	*Pteridium aquilinum*
hc Herbaceous hemicryptophytes	*Geum urbanum,* *Mercurialis perennis,* *Silene dioica,* *Urtica dioica,* *Rumex sanguineus,* *Poa trivialis*	N/A	*Milium effusum,* *Oxalis acetosella,* *Geranium robertianum*	N/A
hc (Pt) Fern hemicryptophytes	*Phyllitis scolopendrium,* *Dryopteris filix-mas,* *Polytichum setiferum*	*Dryopteris dilatata,* *Dryopteris affinis,* *Blechnum spicant,* *Athyrium filix-femina*	*Dryopteris dilatata,* *Dryopteris affinis*	*Dryopteris dilatata,* *Blechnum spicant*
Th Therophytes	*Galium aparine*	*Melampyrum pratense*	N/A	N/A
Pn Nano-phanaerophytes	*Rubus fruticosus* agg.	*Rubus fruticosus* agg., *Vaccinium myrtillus*	*Rubus fruticosus* agg.	*Rubus fruticosus* agg.
Ph Phanaerophytes (excluding shrubs and young trees)	*Hedera helix*	*Hedera helix,* *Lonicera periclymenum*	*Hedera helix,* *Lonicera periclymenum*	*Hedera helix,* *Lonicera periclymenum*
Ch Chamaephytes	N/A	N/A	*Stellaria holostea*	N/A

Appendix 2.2

Statistical comparisons showing differences in vegetation structure between plots and months for four Devon woodlands.

Table A2.3. Hardwick Wood pairwise comparisons of plots for bare ground cover, point frequency and vegetation height. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Mains-test results are reported in Chapter 2.

Bare Ground Cover (%)

Plots	2	3	4	5	6
1	1.00	1.00	1.00	1.00	0.006
2		1.00	1.00	1.00	0.007
3			1.00	0.72	<0.001
4				1.00	<0.001
5					0.12

Point Frequency

Plots	2	3	4	5	6
1	1.00	1.00	0.57	0.07	<0.001
2		1.00	0.78	0.10	<0.001
3			1.00	1.00	<0.001
4				1.00	0.01
5					0.15

Vegetation Height

Plots	2	3	4	5	6
1	1.00	1.00	0.56	<0.001	<0.001
2		0.71	0.045	<0.001	<0.001
3			1.00	<0.001	0.007
4				0.02	0.17
5					1.00

Table A2.4. Newton Mill pairwise comparisons of plots for bare ground cover, point frequency and vegetation height. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Mains-test results are reported in Chapter 2.

Bare Ground Cover (%)

	2	3	4	5	6
1	1.00	<0.001	<0.001	<0.001	<0.001
2		<0.001	<0.001	<0.001	<0.001
3			0.56	1.00	1.00
4				0.27	1.00
5					1.00

Point Frequency

	2	3	4	5	6
1	1.00	<0.001	<0.001	0.04	<0.001
2		<0.001	<0.001	<0.001	<0.001
3			1.00	0.40	1.00
4				0.24	1.00
5					0.005

Vegetation Height

	2	3	4	5	6
1	0.08	0.38	0.13	<0.001	1.00
2		<0.001	<0.001	<0.001	<0.001
3			1.00	<0.001	1.00
4				<0.001	1.00
5					<0.001

Table A2.5. Hunshaw Wood pairwise comparisons of plots for bare ground cover, point frequency and vegetation height. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Mains-test results are reported in Chapter 2.

Bare Ground Cover (%)

	2	3	4	5	6
1	1.00	<0.001	0.490	<0.001	<0.001
2		<0.001	0.84	<0.001	<0.001
3			<0.001	0.006	0.054
4				<0.001	<0.001
5					<0.001

Point Frequency

	2	3	4	5	6
1	1.00	<0.001	0.03	<0.001	<0.001
2		<0.001	1.00	<0.001	<0.001
3			<0.001	0.02	0.005
4				<0.001	<0.001
5					1.00

Vegetation Height

	2	3	4	5	6
1	1.00	<0.001	0.35	<0.001	<0.001
2		<0.001	0.47	<0.001	<0.001
3			<0.001	1.000	1.00
4				<0.001	<0.001
5					<0.001

Table A2.6. Whitleigh Wood pairwise comparisons of plots for bare ground cover, point frequency and vegetation height. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Mains-test results are reported in Chapter 2.

Bare Ground Cover (%)

	2	3	4	5	6
1	1.00	<0.001	<0.001	<0.001	<0.001
2		<0.001	<0.001	<0.001	<0.001
3			<0.001	0.03	1.00
4				<0.001	<0.001
5					0.007

Point Frequency

	2	3	4	5	6
1	1.00	<0.001	<0.001	<0.001	<0.001
2		<0.001	0.008	<0.001	<0.001
3			0.03	<0.001	0.72
4				<0.001	<0.001
5					0.16

Vegetation Height

	2	3	4	5	6
1	1.00	<0.001	<0.001	<0.001	<0.001
2		0.004	0.03	<0.001	<0.001
3			1.00	<0.001	0.004
4				<0.001	<0.001
5					<0.001

Table A2.7. Hardwick Wood pairwise comparisons of months for bare ground cover, point frequency and vegetation height. The matrix shows p values for each comparison, and un-shaded cells highlight significant differences. Repeated measures ANOVAs revealed significant differences between months for all parameters: bare ground cover, $F_{1,10}$ = 5.32, p <0.001; point frequency, $F_{1,10}$ = 20.95, p <0.001; vegetation height, $F_{1,5}$ = 9.83, p (G-G) = 0.025. G-G is the Greenhouse-Geisser corrected p-value for cases when sphericity was violated according to Mauchly's sphericity test.

Bare Ground Cover (%)

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	0.19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.04	0.02
4			1.00	1.00	1.00	1.00	0.91	0.41	<0.001	<0.001
5				1.00	1.00	1.00	1.00	1.00	0.01	0.006
6					1.00	1.00	1.00	1.00	0.02	0.01
7						1.00	1.00	1.00	0.10	0.06
8							1.00	1.00	0.60	0.35
9								1.00	1.00	1.00
10									0.97	0.78
11										1.00

Point Frequency

Months	3	4	5	6	7	8	9	10	11	12
2	0.28	<0.001	<0.001	<0.001	0.01	1.00	1.00	1.00	1.00	1.00
3		0.01	0.003	0.16	1.00	1.00	1.00	0.10	0.01	0.006
4			1.00	1.00	0.18	<0.001	<0.001	<0.001	<0.001	<0.001
5				1.00	0.06	<0.001	<0.001	<0.001	<0.001	<0.001
6					1.00	0.002	<0.001	<0.001	<0.001	<0.001
7						1.00	0.10	0.005	<0.001	<0.001
8							1.00	1.00	0.89	0.44
9								1.00	1.00	1.00
10									1.00	1.00
11										1.00

Vegetation Height

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	0.04	<0.001	<0.001	0.006	0.005	0.09	0.79	1.00	1.00
3		1.00	0.007	0.01	0.58	0.53	1.00	1.00	1.00	1.00
4			1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.39
5				1.00	1.00	1.00	1.00	0.14	0.01	<0.001
6					1.00	1.00	1.00	0.28	0.03	0.001
7						1.00	1.00	1.00	0.10	0.07
8							1.00	1.00	0.96	0.07
9								1.00	1.00	0.82
10									1.00	1.00
11										1.00

Table A2.8. Newton Mill pairwise comparisons of months for bare ground cover, point frequency and vegetation height. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Repeated measures ANOVAs revealed significant differences between months for all parameters: bare ground cover, $F_{1,10} = 23.00$, $p < 0.001$; point frequency, $F_{1,5} = 11.19$, p (G-G) = 0.017; vegetation height, $F_{1,5} = 7.85$, p (G-G) = 0.037. G-G is the Greenhouse-Geisser corrected p-value for cases when sphericity was violated according to Mauchly's sphericity test.

Bare Ground Cover (%)

Months	3	4	5	6	7	8	9	10	11	12
2	0.002	<0.001	<0.001	<0.001	<0.001	0.31	1.00	1.00	1.00	1.00
3		0.01	<0.001	0.47	1.000	1.00	1.00	1.00	0.04	0.002
4			1.00	1.00	0.11	<0.001	<0.001	<0.001	<0.001	<0.001
5				1.00	0.01	<0.001	<0.001	<0.001	<0.001	<0.001
6					1.00	0.003	<0.001	<0.001	<0.001	<0.001
7						0.64	0.13	0.09	0.002	<0.001
8							1.00	1.00	1.00	0.31
9								1.00	1.00	1.00
10									1.00	1.00
11										1.00

Point Frequency

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	<0.001	<0.001	<0.001	<0.001	1.000	1.00	1.00	1.00	1.00
3		<0.001	<0.001	<0.001	0.010	1.00	1.00	1.00	1.00	1.00
4			<0.001	1.00	1.00	<0.001	<0.001	<0.001	<0.001	<0.001
5				0.002	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
6					1.00	<0.001	<0.001	<0.001	<0.001	<0.001
7						0.06	0.003	<0.001	<0.001	<0.001
8							1.00	1.00	1.00	1.00
9								1.00	1.00	1.00
10									1.00	1.00
11										1.00

Vegetation Height

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	0.05	<0.001	<0.001	<0.001	0.02	0.02	0.03	0.53	1.00
3		0.365	<0.001	<0.001	0.009	0.16	0.15	0.24	1.00	1.00
4			0.44	0.99	1.00	1.00	1.00	1.00	1.00	0.57
5				1.00	1.00	0.94	0.99	0.66	0.04	<0.001
6					1.00	1.00	1.00	1.00	0.10	<0.001
7						1.00	1.00	1.00	1.00	0.02
8							1.00	1.00	1.00	0.26
9								1.00	1.00	0.24
10									1.00	0.37
11										1.00

Table A2.9. Hunshaw Wood pairwise comparisons of months for bare ground cover, point frequency and vegetation height. The matrix shows p values for each comparison, and un-shaded cells highlight significant differences. Repeated measures ANOVAs revealed significant differences between months for all parameters: bare ground cover, $F_{1,5} = 51.07$, p (G-G) <0.001; point frequency, $F_{1,10} = 11.02$, $p = 0.021$; vegetation height, $F_{1,5} = 10.06$, p (G-G) = 0.025. G-G is the Greenhouse-Geisser corrected p-value for cases when sphericity was violated according to Mauchly's sphericity test.

Bare Ground Cover (%)

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	1.00	0.06	0.004	0.001	<0.001	<0.001	<0.001	<0.001	0.01
3		1.00	0.15	0.01	0.004	<0.001	<0.001	<0.001	<0.001	0.03
4			1.00	1.00	0.91	0.10	0.10	0.06	0.25	1.00
5				1.00	1.00	1.00	1.00	1.00	1.00	1.00
6					1.00	1.00	1.00	1.00	1.00	1.00
7						1.00	1.00	1.00	0.10	0.06
8							1.00	1.00	0.60	0.35
9								1.00	1.00	1.00
10									0.97	0.78
11										1.00

Point Frequency

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	1.00	0.005	<0.001	<0.001	0.002	0.02	0.19	1.00	1.00
3		1.00	0.029	<0.001	0.006	0.01	0.12	0.83	1.00	1.000
4			0.89	0.007	0.22	0.48	1.00	1.00	1.00	1.00
5				1.00	1.00	1.00	1.00	1.00	1.00	0.10
6					1.00	1.00	1.00	0.39	0.03	<0.001
7						1.00	0.10	0.005	<0.001	<0.001
8							1.00	1.00	1.00	0.05
9								1.00	1.00	0.37
10									1.00	1.00
11										1.00

Vegetation Height

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	0.01	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
3		0.006	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
4			0.03	0.32	0.79	0.39	1.00	1.00	1.00	1.00
5				1.00	1.00	1.00	1.00	1.00	1.00	1.00
6					1.00	1.00	1.00	1.00	1.00	0.79
7						1.00	1.00	1.00	1.00	1.00
8							1.00	1.00	1.00	1.00
9								1.00	1.00	1.00
10									1.00	1.00
11										1.00

Table A2.10. Whitleigh Wood pairwise comparisons of months for bare ground cover and point frequency at Whitleigh. The matrix shows *p* values for each comparison, and un-shaded cells highlight significant differences. Repeated measures ANOVAs revealed significant differences between months for bare ground cover, $F_{1,10}$ = 16.36, p = 0.010 and point frequency, $F_{1,5}$ = 11.11, p (G-G) = 0.020. No significant differences were found between months for vegetation height, $F_{1,5}$ = 6.28, p (G-G) = 0.053. G-G is the Greenhouse-Geisser corrected p-value for cases when sphericity was violated according to Mauchly's sphericity test.

Bare Ground Cover (%)

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	1.00	0.03	0.002	<0.001	0.002	0.005	0.03	0.05	1.00
3		1.00	0.02	<0.001	<0.001	<0.001	0.003	0.02	0.03	1.00
4			1.00	0.67	0.30	0.67	1.00	1.00	1.00	1.00
5				1.00	1.00	1.00	1.00	1.00	1.00	1.00
6					1.00	1.00	1.00	1.00	1.00	0.99
7						1.00	1.00	1.00	1.000	0.45
8							1.00	1.00	1.00	0.99
9								1.00	1.00	1.00
10									1.00	1.00
11										1.00

Point Frequency

Months	3	4	5	6	7	8	9	10	11	12
2	1.00	1.00	0.17	<0.001	0.14	0.020	0.15	1.00	1.00	1.00
3		1.00	0.08	<0.001	0.006	0.008	0.06	1.00	1.00	1.00
4			0.06	<0.001	0.01	0.01	0.05	1.00	1.00	1.00
5				1.00	1.00	1.00	1.00	1.00	1.00	0.16
6					1.00	1.00	1.00	0.06	0.007	<0.001
7						1.00	1.00	1.00	0.29	0.01
8							1.00	1.00	0.39	0.02
9								1.00	1.00	0.13
10									1.00	1.00
11										1.00

Appendix 3.1

Logistic growth model statistics from tree phenology data

Table A3.1. Statistics from logistic growth models of leaf expansion data for individual trees and species from count method.

	Tree no.	θ2	SE	*t*	*p*	θ3	SE	*t*	*p*	DOY	SE
Ash	1	-45.45	3.57	-12.75	<0.001	0.37	0.029	12.75	<0.001	123.8	0.24
	2	-41.48	4.90	-8.47	<0.001	0.32	0.038	8.47	<0.001	128.1	0.40
	3	-67.72	5.09	-13.31	<0.001	0.50	0.038	13.31	<0.001	134.5	0.17
	4	-67.20	6.60	-10.18	<0.001	0.49	0.048	10.19	<0.001	136.9	0.23
	5	-87.29	10.64	-8.21	<0.001	0.65	0.079	8.21	<0.001	134.4	0.21
	6	-59.10	8.42	-7.02	<0.001	0.47	0.068	7.02	<0.001	124.7	0.33
	7	-90.18	3.27	-27.55	<0.001	0.64	0.023	27.55	<0.001	141.3	0.06
	8	-96.76	8.27	-11.71	<0.001	0.67	0.058	11.71	<0.001	143.5	0.14
	9	-47.20	4.27	-11.04	<0.001	0.40	0.036	11.04	<0.001	117.5	0.25
	10	-113.77	18.97	-6.00	<0.001	1.02	0.171	6.00	0.004	111.3	0.18
	Combined	-19.11	0.89	-21.43	<0.001	0.15	0.007	21.47	<0.001	129.8	0.35
Beech	1	-129.81	12.69	-10.23	<0.001	0.99	0.097	10.23	<0.001	130.7	0.11
	2	-115.96	17.11	-6.78	0.006	0.88	0.130	6.78	0.007	131.9	0.19
	3	-37.52	5.13	-7.32	<0.001	0.32	0.044	7.33	<0.001	116.3	0.45
	4	-19.11	3.08	-6.21	<0.001	0.16	0.251	6.23	<0.001	122.0	0.94
	5	-39.20	3.59	-10.93	<0.001	0.33	0.030	10.94	<0.001	119.7	0.31
	6	-75.38	8.18	-9.22	<0.001	0.60	0.065	9.22	<0.001	125.5	0.20
	7	-98.03	9.48	-10.34	<0.001	0.71	0.069	10.34	<0.001	138.2	0.15
	8	-73.14	7.60	-9.62	<0.001	0.57	0.060	9.62	<0.001	127.5	0.20
	9	-105.38	11.83	-8.91	<0.001	0.78	0.088	8.91	<0.001	135.3	0.16
	10	-33.03	3.91	-8.45	<0.001	0.28	0.034	8.46	<0.001	116.3	0.43
	Combined	-24.05	1.38	-17.49	<0.001	0.19	0.011	17.5	<0.001	126.8	0.33
Oak	1	-48.46	8.29	-5.85	<0.001	0.40	0.068	5.85	<0.001	121.5	0.47
	2	-51.21	4.59	-11.15	<0.001	0.39	0.035	11.16	<0.001	130.3	0.25
	3	-107.53	14.10	-7.63	0.005	0.79	0.103	7.63	0.005	136.4	0.19
	4	-32.82	5.90	-5.56	<0.001	0.25	0.045	5.55	<0.001	130.0	0.71
	5	-129.10	9.46	-13.64	<0.001	0.95	0.069	13.64	<0.001	136.3	0.09
	6	-60.00	4.06	-14.78	<0.001	0.42	0.028	14.79	<0.001	142.4	0.18
	7	-38.73	3.27	-11.86	<0.001	0.28	0.024	11.86	<0.001	137.4	0.32
	8	-66.29	5.77	-11.48	<0.001	0.51	0.045	11.48	<0.001	129.4	0.19
	9	-93.73	16.45	-5.70	0.002	0.72	0.126	5.70	0.002	130.7	0.27
	10	-106.98	18.38	-5.82	0.010	0.77	0.133	5.82	0.010	138.6	0.25
	Combined	-33.68	1.12	-30.05	<0.001	0.25	0.008	30.07	<0.001	133.6	0.15
Sycamore	1	-36.66	5.18	-7.07	<0.001	0.30	0.042	7.08	<0.001	123.6	0.53
	2	-35.71	2.49	-14.36	<0.001	0.28	0.020	14.36	<0.001	127.0	0.27
	3	-77.13	6.04	-12.77	<0.001	0.59	0.046	12.77	<0.001	131.7	0.15
	4	-81.53	7.84	-10.40	<0.001	0.62	0.060	10.40	<0.001	131.6	0.18
	5	-24.45	1.67	-14.68	<0.001	0.20	0.014	14.72	<0.001	121.6	0.35
	6	-61.69	8.18	-7.54	<0.001	0.51	0.068	7.54	<0.001	120.6	0.29
	7	-68.45	9.10	-7.52	0.002	0.62	0.082	7.52	0.002	110.6	0.24
	8	-78.60	8.15	-9.64	<0.001	0.71	0.074	9.64	<0.001	110.0	0.17
	9	-83.48	13.91	-6.00	<0.001	0.63	0.106	6.00	<0.001	131.9	0.30
	10	-31.24	1.86	-16.77	<0.001	0.26	0.015	16.77	<0.001	121.3	0.25
	Combined	-21.18	1.36	-15.54	<0.001	0.17	0.011	15.56	<0.001	123.2	0.41

Table A3.2. Statistics from logistic growth models of leaf expansion data for individual trees and species from percentage estimate method.

Species	**Tree no.**	**ө2**	**SE**	***t***	***p***	**ө3**	**SE**	***t***	***p***	**DOY**	**SE**
Ash	1	-53.16	3.13	-16.99	<0.001	0.42	0.025	17.00	<0.001	125.6	0.16
	2	-40.55	3.81	-10.65	<0.001	0.32	0.299	10.65	<0.001	127.3	0.33
	3	-65.04	3.43	-18.94	<0.001	0.48	0.025	18.94	<0.001	135.2	0.12
	4	-57.88	6.38	-9.08	<0.001	0.42	0.046	9.08	<0.001	138.1	0.30
	5	-108.70	9.59	-11.34	<0.001	0.80	0.071	11.34	<0.001	135.1	0.12
	6	-60.08	3.48	-17.27	<0.001	0.48	0.028	17.28	<0.001	124.5	0.13
	7	-101.33	3.50	-28.92	<0.001	0.72	0.025	28.92	<0.001	141.3	0.05
	8	-91.09	5.07	-17.96	<0.001	0.63	0.035	17.97	<0.001	144.2	0.10
	9	-50.47	3.93	-12.84	<0.001	0.43	0.034	12.84	<0.001	116.3	0.20
	10	-112.85	23.12	-4.88	0.005	1.02	0.208	4.88	0.005	111.1	0.22
	Combined	-18.72	0.88	-21.19	<0.001	0.14	0.007	21.22	<0.001	130.2	0.36
Beech	1	-70.04	6.49	-10.79	<0.001	0.53	0.050	10.79	<0.001	131.1	0.19
	2	-75.03	7.28	-10.31	<0.001	0.57	0.055	10.31	<0.001	131.3	0.19
	3	-31.30	3.22	-8.80	<0.001	0.26	0.030	8.81	<0.001	118.3	0.45
	4	-36.05	3.53	-10.20	<0.001	0.31	0.300	10.23	<0.001	117.4	0.34
	5	-39.66	3.08	-12.87	<0.001	0.32	0.252	12.87	<0.001	122.2	0.26
	6	-50.69	5.67	-8.94	<0.001	0.41	0.046	8.94	<0.001	124.2	0.30
	7	-73.08	7.41	-9.86	<0.001	0.52	0.053	9.86	<0.001	139.4	0.22
	8	-35.70	3.50	-10.19	<0.001	0.29	0.028	10.19	<0.001	123.8	0.37
	9	-96.21	10.80	-8.91	<0.001	0.71	0.080	8.91	<0.001	135.1	0.18
	10	-31.85	3.57	-8.91	<0.001	0.27	0.030	8.92	<0.001	118.3	0.43
	Combined	-23.43	0.76	-30.82	<0.001	0.19	0.006	30.87	<0.001	125.9	0.19
Oak	1	-48.09	5.38	-8.94	<0.001	0.40	0.044	8.94	<0.001	121.3	0.32
	2	-44.21	1.98	-22.31	<0.001	0.34	0.015	22.31	<0.001	131.7	0.15
	3	-114.33	9.88	-11.57	<0.001	0.84	0.072	11.57	<0.001	136.5	0.12
	4	-36.29	3.01	-12.06	<0.001	0.28	0.023	12.06	<0.001	129.6	0.33
	5	-118.13	3.54	-33.34	<0.001	0.86	0.026	33.34	<0.001	137.0	0.04
	6	-55.13	2.80	-19.66	<0.001	0.39	0.020	19.67	<0.001	141.8	0.15
	7	-41.58	1.91	-21.81	<0.001	0.31	0.014	21.82	<0.001	135.7	0.17
	8	-62.46	4.02	-15.53	<0.001	0.48	0.031	15.53	<0.001	129.2	0.15
	9	-91.17	9.86	-9.99	<0.001	0.69	0.070	9.99	<0.001	131.3	0.16
	10	-93.45	4.59	-20.38	<0.001	0.67	0.033	20.38	<0.001	138.7	0.08
	Combined	-33.53	1.24	-26.99	<0.001	0.25	0.009	27.01	<0.001	133.6	0.17
Sycamore	1	-46.70	2.99	-15.63	<0.001	0.38	0.024	15.63	<0.001	123.5	0.19
	2	-35.15	1.72	-20.42	<0.001	0.28	0.014	20.43	<0.001	127.3	0.20
	3	-75.45	4.45	-16.94	<0.001	0.57	0.034	16.94	<0.001	131.7	0.12
	4	-134.99	6.35	-21.25	<0.001	1.04	0.049	21.25	<0.001	130.1	0.05
	5	-54.43	2.96	-18.39	<0.001	0.45	0.024	18.39	<0.001	121.3	0.14
	6	-50.66	8.12	-6.24	<0.001	0.41	0.066	6.24	<0.001	123.7	0.44
	7	-116.03	27.55	-4.21	0.008	1.04	0.247	4.21	0.008	111.5	0.26
	8	-69.49	5.43	-12.79	<0.001	0.62	0.049	12.79	<0.001	111.2	0.14
	9	-67.38	5.11	-13.19	<0.001	0.51	0.039	13.19	<0.001	131.8	0.17
	10	-24.95	2.12	-11.76	<0.001	0.21	0.018	11.79	<0.001	116.7	0.41
	Combined	-22.46	1.38	-16.30	<0.001	0.18	0.011	16.32	<0.001	123.1	0.37

Table A3.3. Statistics from logistic growth models of Greenness Index data for crown sections and whole crowns

Species	Tree section	ɵ2	SE	*t*	*p*	ɵ3	SE	*t*	*p*	DOY	SE
Ash	4a	-65.36	18.44	-3.55	0.009	0.47	0.13	3.56	0.009	140.57	0.71
	4b	-64.64	9.79	-6.60	<0.001	0.46	0.07	6.60	<0.001	141.04	0.35
	4c	-101.26	17.40	-5.82	0.001	0.72	0.12	5.79	0.001	141.49	0.27
	Whole crown	-77.56	12.03	-6.45	<0.001	0.55	0.09	6.44	<0.001	141.13	0.31
Ash	5a	-124.75	16.18	-2.38	0.005	0.92	0.12	2.37	<0.001	134.98	0.43
	5b	-85.71	18.76	-2.21	0.010	0.64	0.14	2.21	0.010	133.73	0.26
	5c	Model unable to find a fit in 50 iterations									
	Whole crown	-102.04	20.75	-3.42	0.010	0.76	0.16	3.41	0.010	133.99	0.27
Ash	7a	-133.46	60.68	-2.20	0.079	0.95	0.43	2.20	0.079	141.09	0.53
	7b	-64.64	9.79	-6.60	<0.001	0.46	0.07	6.70	<0.001	141.04	0.35
	7c	-57.46	12.64	-4.54	0.006	0.41	0.09	4.54	0.006	140.37	0.56
	Whole crown	-90.77	17.31	-5.24	0.003	0.64	0.12	5.24	0.003	140.90	0.33
Ash	8a	-74.74	25.52	-2.93	0.033	0.51	0.17	2.93	0.033	146.31	0.68
	8b	-130.80	54.80	-2.39	0.063	0.89	0.37	2.39	0.063	146.48	0.52
	8c	-59.02	17.65	-3.35	0.020	0.41	0.12	3.34	0.122	144.94	0.75
	Whole crown	-69.56	20.41	-3.41	0.020	0.48	0.14	3.41	0.020	145.86	0.63
Beech	1a	-47.27	13.46	-3.51	0.017	0.37	0.10	3.54	0.017	130.88	0.08
	1b	-58.16	11.97	-4.86	0.008	0.45	0.09	4.87	0.008	131.06	0.17
	1c	-83.07	25.60	-3.25	0.032	0.63	0.19	3.24	0.032	130.27	0.13
	Whole crown	-56.70	0.80	-7.06	0.001	0.43	0.06	7.07	0.001	130.68	0.33
Beech	9a	-305.81	244.86	-1.25	0.267	2.29	1.84	1.25	<0.001	133.39	0.35
	9b	-96.15	30.31	-3.17	0.019	0.72	0.23	3.17	<0.001	132.90	0.49
	9c	-193.07	69.11	-2.79	0.038	1.45	0.52	2.79	0.443	133.59	0.31
	Whole crown	-94.31	20.08	-4.70	0.003	0.70	0.15	4.70	0.003	133.79	0.34
Oak	5a	-44.88	9.82	-4.57	0.001	0.34	0.07	4.57	0.001	133.29	0.69
	5b	-15.44	3.36	-4.59	0.001	0.12	0.03	4.70	0.001	128.94	1.52
	5c	-33.16	11.85	-2.80	0.021	0.25	0.10	2.80	0.021	135.19	1.40
	Whole crown	-31.20	6.37	-4.90	0.001	0.24	0.05	4.92	0.001	132.13	0.80
Sycamore	3a	-60.01	5.70	-10.54	<0.001	0.46	0.04	10.55	<0.001	131.50	0.22
	3b	-40.54	12.99	-3.12	0.021	0.31	0.10	3.13	0.020	131.81	1.00
	3c	-54.63	4.18	-13.07	0.000	0.41	0.03	13.08	<0.001	131.71	0.19
	Whole crown	-60.44	10.69	-5.65	<0.001	0.46	0.08	5.66	0.001	131.13	0.41

Table A3.4. Statistics from logistic growth models of leaf expansion (based on count data) for same crown sections that were included in photograph trial, for comparison with Table A4.3.

Species	**Tree section**	**ɵ2**	**SE**	***t***	***p***	**ɵ3**	**SE**	***t***	***p***	**DOY**	**SE**
Ash	4a	-56.52	6.99	-8.09	<0.001	0.42	0.05	8.09	<0.001	135.39	0.33
	4b	-76.57	15.18	-5.04	0.002	0.56	0.11	5.05	0.002	137.22	0.40
	4c	-130.20	24.12	-5.40	0.002	0.94	0.17	5.94	0.002	137.93	0.23
	Whole crown	-67.20	6.60	-10.18	<0.001	0.49	0.05	10.19	<0.001	136.86	0.23
Ash	5a	-124.75	16.18	-7.71	0.005	0.92	0.12	7.71	0.005	135.87	0.16
	5b	-85.71	18.76	-4.57	0.010	0.64	0.14	4.57	0.010	133.44	0.38
	5c	-79.23	10.36	-7.65	0.001	0.59	0.08	7.65	0.001	133.52	0.25
	Whole crown	-87.29	10.64	-8.21	<0.001	0.65	0.08	8.21	<0.001	134.37	0.21
Ash	7a	-88.68	7.60	-11.67	<0.001	0.63	0.05	11.67	<0.001	141.70	0.15
	7b	-93.80	7.20	-13.02	<0.001	0.66	0.05	13.02	<0.001	141.41	0.13
	7c	-90.73	4.66	-19.46	<0.001	0.64	0.03	19.46	<0.001	140.76	0.09
	Whole crown	-90.18	3.27	-27.55	<0.001	0.64	0.02	27.55	<0.001	141.28	0.06
Ash	8a	-94.70	12.10	-7.83	<0.001	0.66	0.84	7.83	<0.001	143.75	0.22
	8b	-88.73	7.21	-12.31	<0.001	0.62	0.05	12.31	<0.001	143.02	0.15
	8c	-107.14	13.13	-8.16	<0.001	0.75	0.09	8.16	<0.001	143.57	0.19
	Whole crown	-96.76	8.27	-11.71	<0.001	0.67	0.06	11.71	<0.001	143.45	0.14
Beech	1a	-124.41	8.88	-14.00	<0.001	0.95	0.07	14.01	0.001	130.88	0.08
	1b	-101.81	12.32	-8.27	<0.001	0.78	0.09	8.27	<0.001	131.06	0.17
	1c	-217.58	31.19	-6.98	0.006	1.67	0.24	6.99	0.006	130.27	0.13
	Whole crown	-129.81	12.69	-10.23	<0.001	0.99	0.10	10.23	<0.001	130.69	0.11
Beech	9a	-128.24	9.48	-13.53	0.000	0.95	0.07	13.53	0.000	135.64	0.09
	9b	-97.56	13.26	-7.36	0.002	0.72	0.10	7.36	0.002	134.99	0.21
	9c	-95.79	16.05	-5.97	0.002	0.71	0.12	5.97	0.002	135.04	0.27
	Whole crown	-105.38	11.83	-8.91	0.000	0.78	0.09	8.91	0.000	135.25	0.16
Oak	5a	-115.78	14.97	-7.73	0.005	0.85	0.11	7.73	0.005	136.38	0.17
	5b	-140.32	27.80	-5.05	0.037	1.04	0.21	5.05	0.037	135.55	0.22
	5c	-161.04	30.14	-5.34	0.006	1.18	0.22	5.35	0.006	136.84	0.16
	Whole crown	-129.10	9.46	-13.64	<0.001	0.95	0.07	13.64	<0.001	136.29	0.09
Sycamore	3a	-85.97	7.47	-11.51	<0.001	0.65	0.06	11.51	<0.001	131.27	0.15
	3b	-72.17	6.62	-10.90	<0.001	0.55	0.05	10.91	<0.001	131.80	0.19
	3c	-73.30	7.65	-9.58	<0.001	0.55	0.06	9.59	<0.001	132.08	0.21
	Whole crown	-77.13	6.04	-12.77	<0.001	0.59	0.05	12.77	<0.001	131.70	0.15

Table A3.5. Statistics from logistic growth models of leaf expansion (based on count data), with a four-day temporal grain.

Species	Tree no.	θ2	SE	*t*	*p*	θ3	SE	*t*	*p*	DOY	SE
Ash	1	-44.53	3.14	-14.17	<0.001	0.36	0.03	14.18	<0.001	123.47	0.22
	2	-41.59	6.05	-6.87	0.001	0.32	0.05	6.87	<0.001	128.06	0.50
	3	-79.72	4.83	-16.50	<0.001	0.59	0.04	16.48	<0.001	134.31	0.12
	4	-65.02	10.60	-6.13	0.004	0.47	0.08	6.13	0.004	137.15	0.38
	5	-99.29	2.69	-36.86	<0.001	0.74	0.02	36.75	<0.001	134.43	0.05
	6	-58.22	10.82	-5.38	0.006	0.47	0.09	5.38	0.006	124.99	0.42
	7	-91.77	5.34	-17.17	<0.001	0.65	0.04	17.16	<0.001	141.27	0.08
	8	-108.81	9.67	-11.26	0.002	0.76	0.07	11.28	0.001	143.28	0.18
	9	-46.53	4.95	-9.40	0.001	0.40	0.04	9.38	<0.001	117.35	0.32
	10	-144.88	20.89	-6.94	0.006	1.30	0.19	6.93	0.006	111.35	0.10
Beech	1	-122.24	5.41	-22.59	<0.001	0.93	0.04	22.61	<0.001	131.06	0.09
	2	Model could not run: only three data points remained									
	3	-40.91	6.91	-5.92	0.002	0.35	0.06	5.91	0.002	116.13	0.56
	4	-21.51	4.67	-4.60	0.004	0.18	0.04	4.60	0.004	122.39	1.31
	5	-40.32	4.98	-8.10	0.000	0.34	0.04	8.10	<0.001	119.45	0.43
	6	-78.31	12.35	-6.34	0.003	0.63	0.10	6.34	0.003	125.20	0.24
	7	-89.19	8.93	-9.99	0.010	0.65	0.06	9.97	0.010	138.11	0.18
	8	-66.95	10.96	-6.11	0.026	0.52	0.09	6.11	0.026	127.59	0.37
	9	-102.04	3.47	-29.42	0.001	0.76	0.03	29.40	0.001	134.85	0.07
	10	-34.79	3.09	-11.26	<0.001	0.30	0.03	11.22	<0.001	116.17	0.34
Oak	1	-46.20	9.79	-4.72	0.009	0.38	0.08	4.72	0.009	120.82	0.62
	2	-48.68	2.65	-18.39	<0.001	0.37	0.02	18.39	<0.001	130.25	0.16
	3	Model could not run: only three data points remained									
	4	-34.82	7.97	-4.37	0.012	0.27	0.06	4.37	0.012	129.59	0.91
	5	Model could not run: only three data points remained									
	6	-57.26	5.94	-9.64	<0.001	0.40	0.04	9.65	<0.001	142.28	0.30
	7	-38.32	5.03	-7.62	<0.001	0.28	0.04	7.62	<0.001	137.26	0.53
	8	-61.85	8.05	-7.69	0.005	0.48	0.06	7.68	0.005	129.62	0.30
	9	-88.25	6.18	-14.28	<0.001	0.67	0.05	14.29	<0.001	131.05	0.15
	10	-104.68	5.46	-19.16	0.003	0.76	0.04	19.09	0.003	138.23	0.09
Sycamore	1	-35.37	7.36	-4.81	0.005	0.29	0.06	4.81	0.005	123.44	0.81
	2	-37.55	3.03	-12.38	<0.001	0.29	0.02	12.38	<0.001	127.54	0.31
	3	-71.85	5.48	-13.11	<0.001	0.55	0.04	13.12	0.001	131.27	0.17
	4	-76.28	6.95	-10.98	0.002	0.58	0.05	10.99	0.002	131.36	0.20
	5	-24.94	2.91	-8.56	<0.001	0.21	0.02	8.56	<0.001	121.55	0.63
	6	-55.78	12.18	-4.58	0.020	0.46	0.10	4.58	0.020	120.71	0.52
	7	-74.96	5.12	-14.64	<0.001	0.68	0.05	14.70	<0.001	110.92	0.09
	8	-71.75	6.20	-11.57	0.001	0.65	0.06	11.64	0.001	109.64	0.18
	9	-68.27	11.89	-5.74	0.011	0.52	0.09	5.75	0.011	131.67	0.39
	10	-33.08	2.09	-15.84	<0.001	0.27	0.02	15.83	<0.001	121.36	0.27

Table A3.6. Statistics from logistic growth models of leaf expansion (based on estimate data), with a four-day temporal grain.

Species	**Tree no.**	**ɵ2**	**SE**	***t***	***p***	**ɵ3**	**SE**	***t***	***p***	**DOY**	**SE**
Ash	1	-54.40	2.77	-19.65	<0.001	0.43	0.02	19.65	<0.001	125.27	0.13
	2	-41.84	6.23	-6.72	0.001	0.33	0.05	6.72	0.001	127.12	0.51
	3	-63.35	4.29	-14.75	<0.001	0.47	0.03	14.75	<0.001	134.96	0.17
	4	-56.14	9.84	-5.71	0.005	0.41	0.07	5.71	0.005	138.43	0.49
	5	-116.78	3.31	-35.27	<0.001	0.87	0.02	35.27	<0.001	135.00	0.06
	6	-63.20	3.05	-20.71	<0.001	0.51	0.02	20.74	<0.001	124.28	0.10
	7	-105.50	4.05	-26.03	<0.001	0.75	0.03	26.00	<0.001	141.25	0.04
	8	-89.99	10.04	-8.97	0.001	0.62	0.07	8.99	0.001	144.15	0.20
	9	-55.72	3.08	-18.09	<0.001	0.48	0.03	18.07	<0.001	116.15	0.14
	10	-185.93	6.27	-29.64	<0.001	1.67	0.06	29.60	<0.001	111.24	0.01
Beech	1	-71.79	8.46	-8.48	<0.001	0.55	0.06	8.49	<0.001	131.38	0.26
	2	-82.62	12.47	-6.63	0.003	0.63	0.09	6.64	0.003	131.62	0.30
	3	-32.72	4.53	-7.22	0.001	0.28	0.04	7.21	0.001	118.40	0.58
	4	-41.96	5.75	-7.30	<0.001	0.36	0.05	7.29	<0.001	117.34	0.45
	5	-40.14	3.30	-12.16	<0.001	0.33	0.03	12.16	<0.001	122.04	0.29
	6	-51.62	9.55	-5.41	0.003	0.42	0.08	5.41	0.003	124.19	0.50
	7	-64.42	7.78	-8.28	<0.001	0.46	0.06	8.28	<0.001	139.23	0.30
	8	-35.40	5.11	-6.92	0.001	0.29	0.04	6.92	0.001	123.93	0.57
	9	-103.37	5.81	-17.80	<0.001	0.77	0.04	17.77	<0.001	134.76	0.11
	10	-29.73	4.01	-7.41	0.001	0.25	0.03	7.40	0.001	118.21	0.61
Oak	1	-49.89	9.20	-5.42	0.003	0.41	0.08	5.42	0.003	121.12	0.51
	2	-43.69	2.47	-17.66	<0.001	0.33	0.02	17.66	<0.001	131.63	0.19
	3	-120.42	1.96	-61.50	<0.001	0.88	0.01	61.74	<0.001	136.30	0.02
	4	-36.69	4.27	-8.60	<0.001	0.28	0.03	8.60	<0.001	129.36	0.46
	5	-113.48	8.61	-13.18	0.001	0.83	0.06	13.19	0.001	136.98	0.06
	6	-51.42	2.29	-22.49	<0.001	0.36	0.02	22.50	<0.001	141.67	0.14
	7	-39.79	2.34	-17.03	<0.001	0.29	0.02	17.04	<0.001	135.62	0.23
	8	-61.80	4.51	-13.71	<0.001	0.48	0.03	13.71	<0.001	129.41	0.17
	9	-103.85	10.81	-9.61	0.001	0.79	0.08	9.65	0.001	131.65	0.18
	10	-89.32	6.15	-14.53	0.005	0.64	0.04	14.52	0.005	138.77	0.14
Sycamore	1	-46.88	3.95	-11.87	<0.001	0.38	0.03	11.87	<0.001	123.43	0.25
	2	-34.79	1.39	-24.98	<0.001	0.27	0.01	25.00	<0.001	127.45	0.17
	3	-158.54	14.99	-10.57	<0.001	1.22	0.12	10.51	<0.001	129.90	0.09
	4	-71.26	2.35	-30.26	<0.001	0.54	0.02	30.29	<0.001	131.47	0.07
	5	-50.84	1.88	-27.07	<0.001	0.42	0.02	27.08	<0.001	121.01	0.10
	6	-48.87	11.36	-4.30	0.013	0.39	0.09	4.30	0.013	124.10	0.67
	7	-169.32	11.21	-15.10	0.001	1.52	0.10	15.07	0.001	111.56	0.05
	8	-65.10	8.85	-7.36	0.005	0.59	0.08	7.38	0.005	111.23	0.21
	9	-62.60	4.54	-13.77	<0.001	0.47	0.03	13.78	<0.001	131.97	0.17
	10	-26.44	3.30	-8.02	<0.001	0.23	0.03	8.01	<0.001	116.73	0.60

Table A3.7. Statistics from logistic growth models of leaf expansion (based on count data), with a six-day temporal grain.

Species	**Tree no.**	**ɵ2**	**SE**	***t***	***p***	**ɵ3**	**SE**	***t***	***p***	**DOY**	**SE**
Ash	1	47.08	4.51	-10.43	<0.001	0.38	0.04	10.42	<0.001	123.55	0.31
	2	-48.60	11.51	-4.22	0.013	0.38	0.09	4.22	0.014	128.62	0.72
	3	-61.76	2.18	-28.26	<0.001	0.46	0.02	28.15	<0.001	134.82	0.10
	4	-62.74	1.72	-36.42	<0.001	0.46	0.01	36.46	<0.001	136.14	0.09
	5	Model could not run: only three data points remained									
	6	-57.01	4.73	-12.05	0.001	0.46	0.04	12.05	0.001	123.92	0.26
	7	-95.64	0.82	-117.20	<0.001	0.68	0.01	116.10	<0.001	141.11	0.02
	8	-93.48	5.39	-17.34	<0.001	0.65	0.04	17.49	<0.001	142.97	0.14
	9	-48.74	4.04	-12.06	0.007	0.42	0.03	12.03	0.007	117.40	0.26
	10	Model could not run: only three data points remained									
Beech	1	-118.20	0.45	-260.60	<0.001	0.90	0.00	264.10	<0.001	130.99	0.01
	2	Model could not run: only three data points remained									
	3	-36.40	9.76	-3.73	0.065	0.31	0.08	3.73	0.065	116.60	0.96
	4	-21.12	5.56	-3.80	0.019	0.17	0.05	3.81	0.019	121.28	1.62
	5	-40.21	5.37	-7.49	0.005	0.34	0.04	7.50	0.005	119.54	0.45
	6	-57.63	5.60	-10.30	0.009	0.46	0.04	10.35	0.009	125.59	0.23
	7	Model could not run: only three data points remained									
	8	Model could not run: only three data points remained									
	9	-106.87	1.08	-99.15	<0.001	0.79	0.01	98.03	<0.001	134.75	0.02
	10	-38.71	11.65	-3.32	0.080	0.33	0.10	3.32	0.080	115.86	0.97
Oak	1	-65.66	8.35	-7.86	0.016	0.54	0.07	7.84	0.016	121.59	0.18
	2	-48.67	5.55	-8.77	0.013	0.37	0.04	8.77	0.013	130.14	0.38
	3	Model could not run: only three data points remained									
	4	-32.65	5.53	-5.90	0.010	0.25	0.04	5.90	0.010	129.17	0.75
	5	Model could not run: only three data points remained									
	6	-64.10	2.57	-24.99	<0.001	0.45	0.02	25.07	<0.001	142.68	0.12
	7	-37.32	6.48	-5.76	0.010	0.27	0.05	5.77	0.010	136.85	0.72
	8	-65.24	2.43	-26.88	0.001	0.50	0.02	26.78	0.001	129.46	0.11
	9	Model could not run: only three data points remained									
	10	Model could not run: only three data points remained									
Sycamore	1	-40.92	3.03	-13.49	<0.001	0.33	0.02	13.48	<0.001	123.58	0.27
	2	-34.80	4.21	-8.26	0.004	0.28	0.03	8.27	0.004	126.43	0.49
	3	-99.08	2.85294 -	34.73	0.001	0.75	0.02	35.02	0.001	131.83	0.04
	4	-84.78	1.52	-55.76	<0.001	0.65	0.01	56.27	<0.001	131.44	0.03
	5	-25.71	2.96	-8.68	0.001	0.21	0.02	8.69	0.001	121.19	0.60
	6	-66.13	17.74	-3.73	0.065	0.55	0.15	3.72	0.065	121.16	0.32
	7	Model could not run: only three data points remained									
	8	-79.76	2.10	-38.06	<0.001	0.72	0.02	37.66	0.001	110.31	0.04
	9	-60.39	5.86	-10.30	0.009	0.46	0.04	10.35	0.009	131.59	0.23
	10	-30.77	2.82	-10.93	<0.001	0.25	0.02	10.93	<0.001	121.55	0.40

Table A3.8. Statistics from logistic growth models of leaf expansion (based on estimate data), with a six-day temporal grain.

Species	Tree no.	ɵ2	SE	*t*	*p*	ɵ3	SE	*t*	*p*	DOY	SE
Ash	1	-48.73	3.83	-12.73	<0.001	0.39	0.03	12.77	<0.001	125.77	0.22
	2	-43.45	10.11	-4.30	0.013	0.34	0.08	4.30	0.013	127.34	0.73
	3	-59.25	1.86	-31.91	<0.001	0.44	0.01	31.80	<0.001	134.97	0.09
	4	-48.48	5.98	-8.11	0.004	0.35	0.04	8.12	0.004	137.50	0.40
	5	-105.50	0.60	-174.60	<0.001	0.78	0.00	172.70	<0.001	135.22	0.01
	6	-58.47	4.77	-12.27	0.001	0.47	0.04	12.31	0.001	124.64	0.24
	7	-109.97	2.53	-43.46	<0.001	0.78	0.02	43.01	<0.001	141.23	0.06
	8	-86.97	1.79	-48.55	<0.001	0.60	0.01	48.84	<0.001	143.97	0.03
	9	-55.05	6.80	-8.10	0.015	0.47	0.06	8.06	0.015	115.95	0.25
	10	-97.35	0.84	-115.30	<0.001	0.88	0.01	113.80	<0.001	110.57	0.01
Beech	1	-57.94	3.41	-16.97	<0.001	0.44	0.03	17.04	<0.001	131.01	0.17
	2	-67.52	3.69	-18.29	<0.001	0.51	0.03	18.41	<0.001	131.32	0.13
	3	-30.08	7.35	-4.10	0.026	0.25	0.06	4.10	0.026	118.14	1.07
	4	-40.22	5.16	-7.80	0.001	0.34	0.04	7.79	0.001	116.60	0.42
	5	-38.54	4.58	-8.41	0.004	0.32	0.04	8.41	0.004	121.90	0.42
	6	-46.36	3.02	-15.35	0.001	0.37	0.02	15.35	0.001	123.94	0.22
	7	-122.84	33.99	-3.62	0.036	0.88	0.24	3.60	0.037	139.46	0.14
	8	-37.17	4.49	-8.27	0.004	0.30	0.04	8.27	0.004	123.79	0.46
	9	-114.88	22.32	-5.15	0.004	0.85	0.17	5.09	0.004	134.62	0.34
	10	-35.67	9.19	-3.88	0.060	0.30	0.08	3.88	0.060	118.78	0.97
Oak	1	-55.98	9.26	-6.05	0.009	0.46	0.08	6.03	0.009	121.71	0.33
	2	-42.52	2.82	-15.07	<0.001	0.32	0.02	15.10	<0.001	131.49	0.23
	3	-106.70	0.62	-170.80	<0.001	0.78	0.00	172.70	<0.001	136.78	0.01
	4	-37.63	4.13	-9.12	<0.001	0.29	0.03	9.12	<0.001	129.32	0.43
	5	-106.70	0.62	-170.80	<0.001	0.78	0.00	172.70	<0.001	136.78	0.01
	6	-58.98	3.14	-18.79	<0.001	0.41	0.02	18.83	<0.001	142.29	0.17
	7	-41.65	2.06	-20.21	<0.001	0.31	0.02	20.21	<0.001	135.25	0.19
	8	-59.97	3.53	-16.98	<0.001	0.46	0.03	16.93	<0.001	129.31	0.17
	9	-88.90	1.99	-44.75	<0.001	0.68	0.01	45.18	<0.001	131.37	0.04
	10	Cannot rungular gradient			only 3 data points						
Sycamore	1	-45.87	0.72	-64.01	<0.001	0.37	0.01	63.93	<0.001	123.26	0.05
	2	-34.99	3.59	-9.76	<0.001	0.28	0.03	9.76	0.001	126.77	0.41
	3	-168.60	0.01	-126.9	<0.001	1.30	0.00	126.92	<0.001	130.00	0.00
	4	-66.51	0.61	-108.80	<0.001	0.51	0.00	109.40	<0.001	131.33	0.02
	5	-47.79	2.12	-22.51	<0.001	0.39	0.02	22.51	<0.001	121.09	0.11
	6	-65.97	5.12	-12.89	0.001	0.54	0.04	12.81	0.001	123.00	0.20
	7	-80.17	0.95	-84.65	<0.001	0.72	0.01	83.56	<0.001	110.92	0.03
	8	-80.17	0.95	-84.65	<0.001	0.72	0.01	83.56	<0.001	110.92	0.03
	9	-62.38	6.29	-9.92	0.002	0.47	0.05	9.96	0.002	132.05	0.20
	10	-24.30	2.29	-10.60	<0.001	0.21	0.02	10.62	<0.001	116.33	0.50

Appendix 4.1

Suggested protocol for analysing canopy closure phenology using image analysis of canopy photographs

Canopy closure estimates can be calculated from smartphone fisheye photos. Canopy closure is the inverse of the canopy openness estimates typically derived from fish-eye photographs, and is more meaningful in phenology studies during the spring and early summer, when we are concerned with bud burst and leaf expansion.

Fig. A4.1 A. shows canopy closure estimates plotted through time for three example canopies. Data were collected using smartphone fisheye photography and ImageJ analysis, following the methods outlined in Chapter 5. Photos were taken every other day during spring 2017, in a small woodland in Cornwall, UK, from before budburst until after the canopy was fully in leaf. In order to make meaningful comparisons between these different canopies, canopy closure was standardised along a proportional scale between minimum and maximum values, where the minimum equals zero, and represents the canopy without leaves, and the maximum equals 100, representing the canopy in full leaf. This enables visual comparisons of spring canopy closure between different canopies (**Fig. A4.1** B.). It would also allow comparisons across different years in cases where the canopy develops through time, or where the canopy has opened up through management or other factors.

I have used a logistic growth function as described by Fox and Weisberg (2011) to plot the estimated development of each canopy (**Fig. A4.1** C), and to estimate the rate of canopy development (**Fig. A4.2** A) and the day of year when canopy development reaches the half-maximum (**Fig. A4.2** B). The model uses the following equation:

$$y = \frac{\theta_1}{1 + \exp\left[-(\theta_2 + \theta_3 x)\right]}$$

where y represents the response variable (proportion of canopy development), x represents the predictor variable (day of year), θ_1 is the upper asymptote (in this case $\theta_1 = 100$), and θ_2 and θ_3 are fitting parameters. θ_3 controls the steepness of the curve so represents the rate of the process (Fox and Weisberg, 2011)

Fig. A4.1. Standardization of canopy closure estimates from three forest canopies, and fitting of the logistic growth model. Canopy X = red, Canopy Y = blue, Canopy Z = green. **A.** Raw (absolute) estimated canopy closure values from image analysis. **B.** Standardization of each data set between the minimum and maximum values. **C.** Fitted models using the logistic growth equation

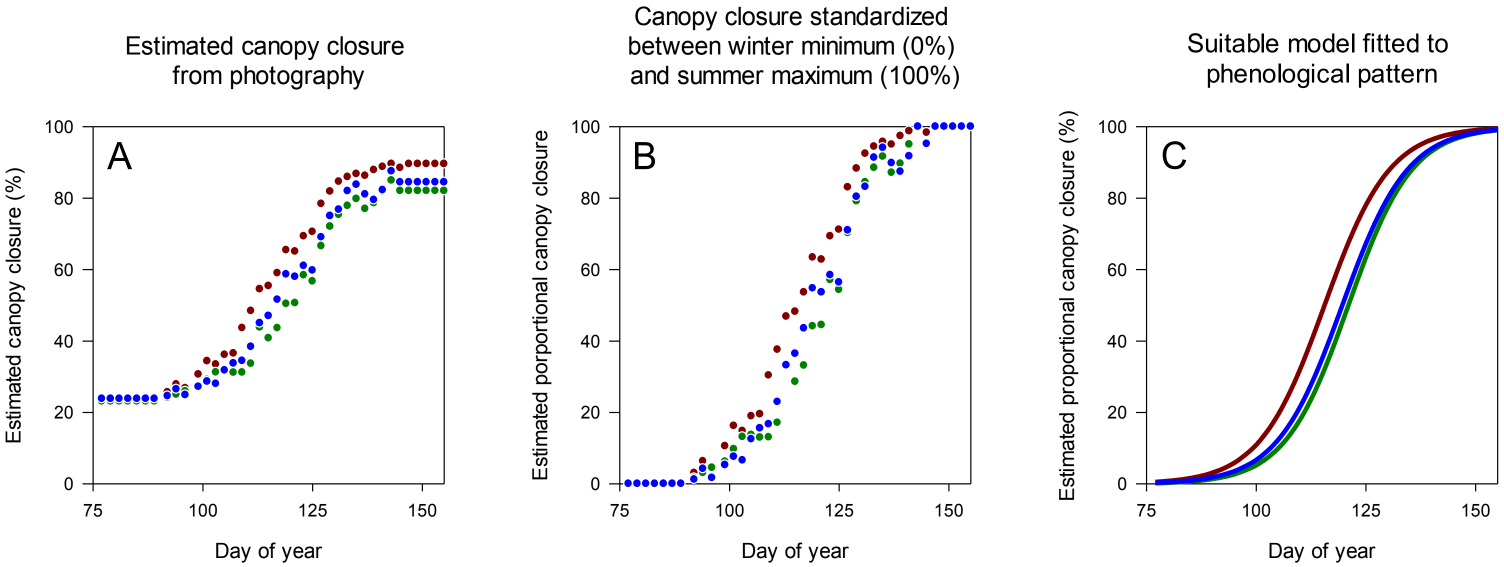
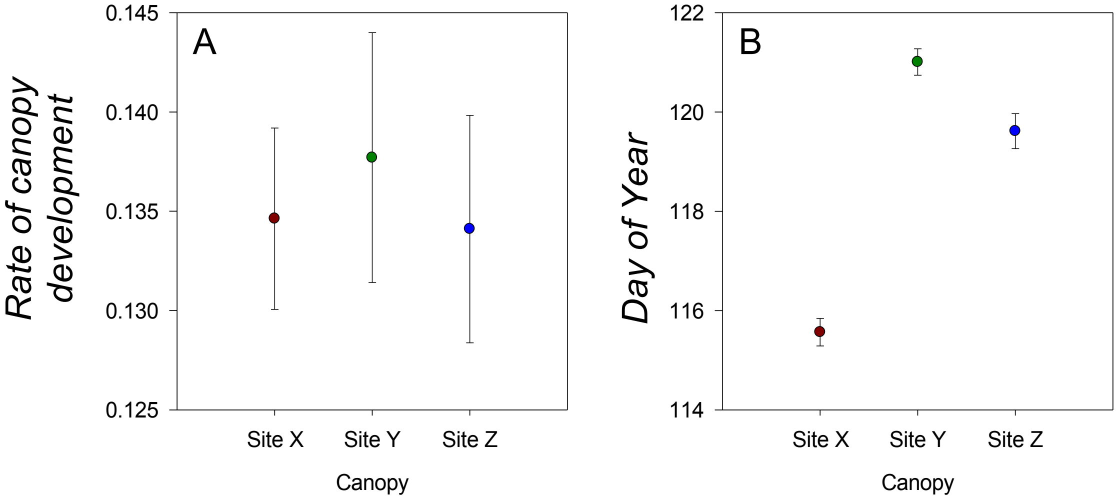


Fig. A4.2. Distribution of canopy closure rate and day of year when canopies reached 50% closure, for three forest canopies, with standard errors of estimates from the logistic growth model.



Appendix 5.1

Example hemispherical and smartphone fisheye photographs, demonstrating difference in field of view

Both photographs were taken from the same position on 5th May 2017, as part of the field trial conducted at Elwell woods. Photograph A is taken with the hemispherical camera, and Photograph B is taken with the smartphone camera with fisheye lens attached, using a 4:3 aspect ratio.

Appendix 5.2

Logistic model statistics from canopy phenology data

Table A5.1. Statistics from logistic growth models of canopy closure phenology data from hemispherical photography, smartphone fisheye photography and visual estimates

Method	Station	θ2	SE	*t*	*p*	θ3	SE	*t*	*p*	DOY	SE
Hemispherical photos	1	-15.11	0.69	-21.88	<0.001	0.13	0.006	21.91	<0.001	117.23	0.39
	2	-16.65	0.84	-19.74	<0.001	0.14	0.007	19.72	<0.001	122.80	0.40
	3	-14.14	0.71	-19.84	<0.001	0.12	0.006	19.81	<0.001	122.05	0.46
	4	-12.71	0.76	-16.65	<0.001	0.11	0.006	16.66	<0.001	119.07	0.59
	5	-13.23	0.81	-16.28	<0.001	0.11	0.007	16.27	<0.001	120.53	0.59
	6	-13.38	0.68	-19.60	<0.001	0.11	0.006	19.60	<0.001	119.30	0.48
	7	-11.42	0.73	-15.64	<0.001	0.10	0.006	15.65	<0.001	118.67	0.67
	8	-11.39	0.93	-12.27	<0.001	0.10	0.008	12.33	<0.001	115.15	0.84
	9	-11.88	0.91	-13.02	<0.001	0.10	0.008	13.09	<0.001	114.13	0.76
	10	-15.46	0.85	-18.27	<0.001	0.13	0.007	18.25	<0.001	121.52	0.46
	Combined	-13.12	0.67	-19.63	<0.001	0.11	0.006	19.63	<0.001	119.15	0.49
Smartphone fisheye photos	1	-15.66	0.54	-28.95	<0.001	0.14	0.005	29.03	<0.001	115.59	0.28
	2	-16.69	0.76	-21.92	<0.001	0.14	0.006	21.96	<0.001	121.01	0.37
	3	-16.09	0.69	-23.31	<0.001	0.13	0.006	23.36	<0.001	119.63	0.35
	4	-10.92	0.54	-20.16	<0.001	0.10	0.005	20.32	<0.001	114.24	0.53
	5	-17.05	0.83	-20.64	<0.001	0.14	0.007	20.67	<0.001	122.00	0.38
	6	-13.68	0.68	-20.15	<0.001	0.12	0.006	20.22	<0.001	117.42	0.46
	7	-13.14	0.81	-16.20	<0.001	0.11	0.007	16.24	<0.001	119.96	0.60
	8	-11.92	0.64	-18.70	<0.001	0.11	0.006	18.84	<0.001	113.45	0.53
	9	-11.31	0.73	-15.48	<0.001	0.10	0.006	15.56	<0.001	116.79	0.69
	10	-16.83	0.86	-19.68	<0.001	0.14	0.007	19.71	<0.001	122.30	0.41
	Combined	-13.79	0.53	-26.14	<0.001	0.12	0.004	26.21	<0.001	118.42	0.36
Visual estimates	1	-16.31	0.73	-22.22	<0.001	0.14	0.006	22.28	<0.001	114.15	0.35
	2	-17.07	0.79	-21.71	<0.001	0.15	0.007	21.74	<0.001	116.88	0.35
	3	-13.51	1.03	-13.06	<0.001	0.12	0.009	13.06	<0.001	111.61	0.63
	4	-9.24	1.92	-4.82	<0.001	0.10	0.019	5.23	<0.001	91.77	1.94
	5	-16.63	1.55	-10.73	<0.001	0.14	0.013	10.67	<0.001	117.68	0.63
	6	-5.03	0.68	-7.39	<0.001	0.05	0.006	7.70	<0.001	106.45	1.61
	7	-9.15	1.09	-8.37	<0.001	0.09	0.010	8.72	<0.001	101.17	1.16
	8	-24.88	3.61	-6.88	<0.001	0.26	0.037	6.93	<0.001	96.64	0.56
	9	-9.55	0.90	-10.62	<0.001	0.09	0.008	10.65	<0.001	110.26	0.90
	10	-20.67	1.08	-19.08	<0.001	0.18	0.009	19.09	<0.001	117.63	0.32
	Combined	-10.62	0.50	-21.29	<0.001	0.10	0.005	21.59	<0.001	109.17	0.47

Table A5.2. Statistics from logistic growth models of individual leaf expansion estimates for ash, sycamore and hawthorn

Species	Tree	Station	θ2	SE	*t*	*p*	θ3	SE	*t*	*p*	DOY	SE
Sycamore	1	1	-30.50	7.08	-4.31	0.004	0.28	0.066	4.29	0.004	108.20	0.80
	2	1	-51.16	13.18	-3.88	0.012	0.47	0.121	3.88	0.012	109.47	0.57
	3	1	-48.13	11.38	-4.23	0.004	0.44	0.104	4.22	0.004	109.42	0.56
	4	1	-10.60	3.80	-2.78	0.018	0.08	0.033	2.43	0.033	131.04	7.35
	5	1	-23.69	4.25	-5.58	<0.001	0.20	0.036	5.53	<0.001	120.45	0.90
	6	1	-46.25	15.99	-2.89	0.034	0.46	0.160	2.89	0.034	100.05	0.76
	7	2	-40.32	10.37	-3.89	0.008	0.33	0.085	3.88	0.008	122.48	0.78
	8	2	-26.52	5.44	-4.87	<0.001	0.23	0.047	4.84	<0.001	115.45	0.87
	9	2	-58.28	14.17	-4.11	0.006	0.45	0.110	4.11	0.006	129.44	0.56
	10	2	-29.16	6.29	-4.63	0.001	0.24	0.051	4.61	0.001	123.47	0.89
	11	2	-35.71	9.18	-3.89	0.008	0.33	0.085	3.88	0.008	108.48	0.78
	12	2	-25.92	6.66	-3.89	0.006	0.23	0.059	3.87	0.006	113.31	1.03
	13	3	-28.29	5.45	-5.19	<0.001	0.22	0.043	5.15	<0.001	127.91	0.84
	14	3	-92.04	24.71	-3.73	0.034	0.85	0.228	3.73	0.034	108.57	0.35
	15	3	-21.94	4.19	-5.23	<0.001	0.17	0.034	5.18	<0.001	126.29	1.03
	16	3	-26.08	5.93	-4.40	0.002	0.22	0.051	4.37	0.002	117.26	0.96
	17	3	-33.27	15.84	-2.10	0.126	0.31	0.146	2.11	0.126	108.37	1.18
	18	4	-35.68	8.46	-4.21	0.003	0.30	0.071	4.19	0.003	118.93	0.78
	19	4	-31.56	6.80	-4.64	0.002	0.27	0.060	4.62	0.002	116.17	0.78
	20	4	-29.59	6.86	-4.31	0.003	0.24	0.057	4.29	0.003	121.50	0.92
	21	4	-28.56	7.34	-3.87	0.006	0.25	0.065	3.87	0.006	113.54	0.97
	22	4	-22.65	8.21	-2.76	0.033	0.20	0.073	2.75	0.033	112.70	1.43
	23	5	-27.32	8.14	-3.36	0.015	0.26	0.077	3.35	0.016	105.60	1.06
	24	5	-32.69	6.71	-4.88	<0.001	0.26	0.054	4.84	<0.001	124.14	0.76
	25	5	-37.16	9.32	-3.99	0.005	0.31	0.079	3.97	0.005	118.95	0.79
	26	5	-19.14	5.66	-3.38	0.010	0.17	0.049	3.36	0.010	115.77	1.45
	27	6	-38.84	10.12	-3.84	0.009	0.29	0.077	3.83	0.009	132.25	0.85
	28	6	-31.79	8.28	-3.84	0.009	0.29	0.076	3.83	0.009	108.25	0.85
	29	7	-22.98	5.19	-4.42	0.002	0.18	0.041	4.39	0.002	126.35	1.12
	30	8	-32.87	6.54	-5.03	<0.001	0.26	0.051	5.00	<0.001	128.13	0.76
	31	9	-22.91	5.28	-4.34	0.002	0.20	0.046	4.31	0.002	116.59	1.09
	32	10	-17.60	3.97	-4.43	0.001	0.15	0.034	4.39	0.001	115.46	1.28
Ash	1	1	-29.06	6.06	-4.80	<0.001	0.23	0.049	4.76	0.001	123.94	0.86
	2	1	-36.74	10.11	-3.64	0.008	0.28	0.075	3.62	0.009	134.80	0.96
	3	2	-24.99	4.88	-5.12	<0.001	0.21	0.041	5.08	<0.001	119.20	0.90
	4	3	-19.54	3.48	-5.61	<0.001	0.16	0.028	5.55	<0.001	124.07	1.05
	5	4	-29.19	8.48	-4.76	<0.001	0.24	0.056	4.76	<0.001	125.60	0.84
	6	5	-33.59	11.21	-4.00	0.005	0.28	0.052	3.98	0.005	132.90	0.70

Species	**Tree**	**Station**	**ɵ2**	**SE**	***t***	***p***	**ɵ3**	**SE**	***t***	***p***	**DOY**	**SE**
Hawthorn	1	3	-34.56	12.85	-2.69	0.045	0.36	0.133	2.69	0.046	96.62	0.98
	2	4	-34.56	12.85	-2.69	0.045	0.36	0.133	2.69	0.046	96.62	0.98
	3	5	-34.56	12.85	-2.69	0.045	0.36	0.133	2.69	0.046	96.62	0.98
	4	6	-26.25	7.40	-3.50	0.012	0.26	0.074	3.53	0.012	100.07	0.99
	5	6	-63.31	34.79	-1.82	0.210	0.67	0.370	1.82	0.210	94.00	0.85
	6	6	-39.84	20.49	-1.94	0.147	0.42	0.216	1.94	0.147	95.00	1.14
	7	7	-12.85	3.83	-3.36	0.008	0.13	0.038	3.34	0.009	102.58	1.70
	8	7	-16.24	7.38	-2.20	0.040	0.17	0.075	2.20	0.040	98.00	1.90
	9	8	-34.52	10.70	-3.23	0.023	0.35	0.108	3.22	0.024	99.07	0.87
	10	8	-50.63	18.75	-2.70	0.074	0.53	0.196	2.69	0.074	95.61	0.72
	11	9	Model reached maximum 50 iterations									
	12	9	-20.83	9.75	-2.14	0.050	0.22	0.100	2.14	0.050	97.00	1.64
	13	9	-38.43	9.53	-4.04	0.007	0.38	0.094	4.02	0.007	101.19	0.66
	14	9	-44.39	14.22	-3.12	0.021	0.44	0.140	3.11	0.021	102.00	0.74
	15	9	-34.53	10.70	-3.23	0.023	0.35	0.108	3.22	0.024	99.07	0.87
	16	10	-50.63	18.75	-2.70	0.074	0.53	0.196	2.70	0.074	95.61	0.72
	17	10	-214.76	307.33	-0.70	0.535	2.20	3.167	0.70	0.537	97.47	0.76
	18	10	-55.73	16.36	-3.41	0.019	0.56	0.164	3.40	0.019	99.79	0.56

Table A5.3. Statistics from logistic growth models of canopy closure phenology data from hemispherical photography, smartphone fisheye photography and visual estimates using different temporal grains

Method	**Temporal Grain**	**ɵ2**	**SE**	**t**	**p**	**ɵ3**	**SE**	**t**	**p**	**DOY**	**SE**
Hemispherical photos	2	-13.12	0.67	-19.63	<0.001	0.11	0.006	19.63	<0.001	119.15	0.49
	4	-13.92	1.01	-13.79	<0.001	0.12	0.008	13.82	<0.001	118.96	0.67
	6	-14.95	1.24	-12.04	<0.001	0.13	0.010	12.07	<0.001	119.45	0.74
	8	-14.29	0.78	-18.41	<0.001	0.12	0.006	18.46	<0.001	119.84	0.51
	10	-12.95	1.55	-8.36	<0.001	0.11	0.013	8.40	<0.001	119.53	1.23
	12	-13.88	0.95	-14.65	<0.001	0.11	0.008	14.69	<0.001	121.35	0.67
	14	-15.33	1.07	-14.37	0.001	0.13	0.009	14.42	<0.001	117.80	0.59
Smartphone fisheye photos	2	-13.79	0.53	-26.14	<0.001	0.12	0.004	26.21	<0.001	118.42	0.36
	4	-14.17	0.69	-20.41	<0.001	0.12	0.006	20.46	<0.001	118.32	0.45
	6	-15.09	1.02	-14.72	<0.001	0.13	0.009	14.76	<0.001	118.57	0.59
	8	-14.16	0.75	-18.85	<0.001	0.12	0.006	19.01	<0.001	118.78	0.49
	10	-13.77	1.38	-10.52	<0.001	0.12	0.011	10.56	<0.001	118.78	0.92
	12	-14.06	0.93	-15.09	<0.001	0.12	0.008	15.14	<0.001	119.13	0.63
	14	-15.33	1.40	-10.96	0.002	0.13	0.012	11.00	<0.001	117.55	0.77
Visual estimates	2	-10.62	0.50	-21.29	<0.001	0.10	0.005	21.59	<0.001	109.17	0.47
	4	-11.04	0.72	-15.30	<0.001	0.10	0.007	15.48	<0.001	109.30	0.64
	6	-11.02	1.13	-9.75	<0.001	0.10	0.010	9.85	<0.001	109.48	1.03
	8	-11.54	1.21	-9.57	<0.001	0.11	0.011	9.65	<0.001	109.27	1.03
	10	-11.54	1.21	-9.57	<0.001	0.11	0.011	9.65	<0.001	109.27	1.03
	12	-12.00	1.60	-7.52	0.005	0.11	0.014	7.76	<0.001	109.72	1.31
	14	-12.31	1.83	-6.74	0.007	0.11	0.017	6.77	0.01	110.18	1.47

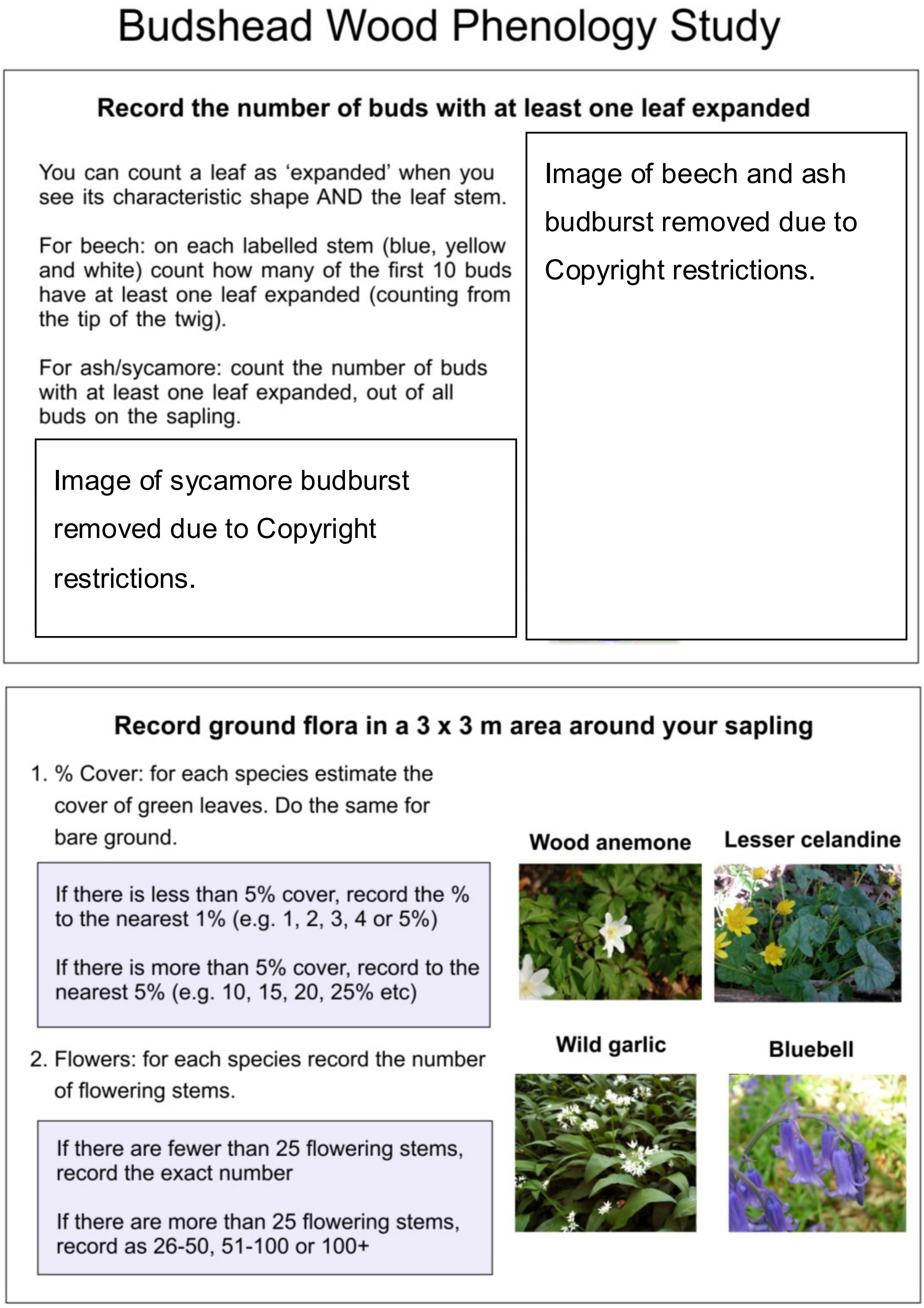
Table A5.4. Statistics from logistic growth models of canopy closure phenology data from smartphone fisheye photography with a 14-day temporal gain and varying start dates

Start DOY	ө2	SE	t	p	ө3	SE	t	p	DOY	SE
79	-15.39	1.92	-8.02	0.001	0.13	0.016	8.05	0.001	119.00	1.07
81	-14.79	1.09	-13.61	<0.001	0.12	0.009	13.67	<0.001	118.72	0.67
83	-12.83	1.24	-10.37	<0.001	0.11	0.010	10.41	<0.001	119.52	1.02
85	-13.07	1.18	-11.10	<0.001	0.11	0.010	11.14	<0.001	117.82	0.92
87	-13.90	1.35	-10.29	<0.001	0.12	0.011	10.31	<0.001	118.39	0.93
89	-14.19	0.70	-20.26	<0.001	0.12	0.006	20.32	<0.001	118.23	0.46
91	-15.33	1.40	-10.96	0.002	0.13	0.012	11.00	0.002	117.55	0.77

Appendix 6.1

Pilot citizen science project to monitor canopy closure phenology in relation to understorey phenology

Example instruction sheet page 1



Budshead Wood Phenology Study

Record the number of buds with at least one leaf expanded

You can count a leaf as 'expanded' when you see its characteristic shape AND the leaf stem.

For beech: on each labelled stem (blue, yellow and white) count how many of the first 10 buds have at least one leaf expanded (counting from the tip of the twig).

For ash/sycamore: count the number of buds with at least one leaf expanded, out of all buds on the sapling.

Image of sycamore budburst removed due to Copyright restrictions.

Image of beech and ash budburst removed due to Copyright restrictions.

Record ground flora in a 3 x 3 m area around your sapling

1. % Cover: for each species estimate the cover of green leaves. Do the same for bare ground.

If there is less than 5% cover, record the % to the nearest 1% (e.g. 1, 2, 3, 4 or 5%)

If there is more than 5% cover, record to the nearest 5% (e.g. 10, 15, 20, 25% etc)

2. Flowers: for each species record the number of flowering stems.

If there are fewer than 25 flowering stems, record the exact number

If there are more than 25 flowering stems, record as 26-50, 51-100 or 100+

Wood anemone

Lesser celandine

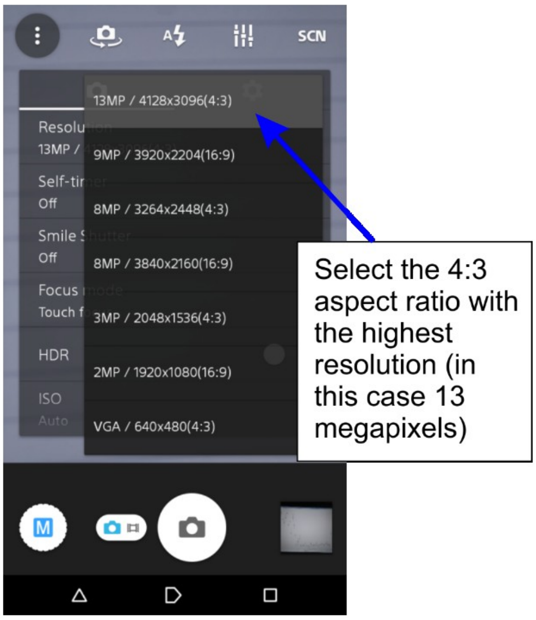
Wild garlic

Bluebell

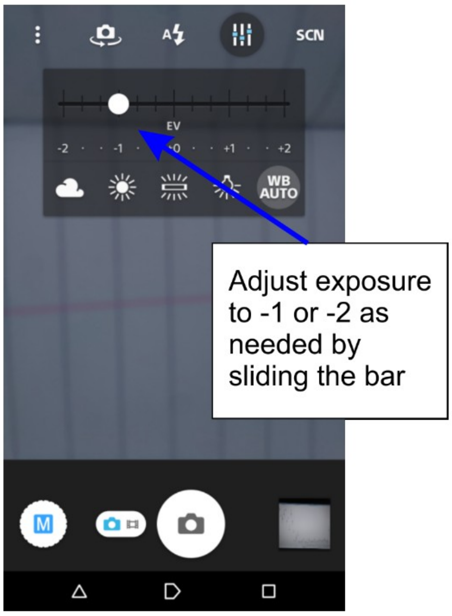
Example instruction sheet page 2

Taking smartphone fisheye photos of the forest canopy

1. Attach the fisheye lens and open your camera app
2. Set the aspect ratio to 4:3 (to do this go into settings > resolution > select '4:3' option). This will maximise the field of view of the camera.
3. Stand in the same place each time you take a photograph (e.g. immediately in front of the sapling, facing downhill).
4. Always hold the camera lengthways when you take the canopy photo, and try to hold the camera as flat as possible, so it is pointing directly towards the sky.
5. To reduce the problem of lens flare, try to take photos early or late in the day.
   If the sky is bright, adjust the exposure settings (go to settings > slide the dial down to -1.0 or -2.0 EV so that there is good contrast between trees and the sky).



Select the 4:3 aspect ratio with the highest resolution (in this case 13 megapixels)



Adjust exposure to -1 or -2 as needed by sliding the bar

NB: The appearance of camera settings may vary with different smartphone models. On the training day we will help you find the right settings on your phone.

Example data sheet

Surveyor name:

Sapling number:

Date	Photo taken (✓)	Leaf expansion out of/__	Lesser celandine		Bluebells		Wild garlic		Wood anemone		Bare ground
			% Cover	✿	% Cover	✿	% Cover	✿	% Cover	✿	% Cover
12/3	✓	3	15	10	50	0	5	0	0	0	10

Copy of the guidance notes written by the Active Neighbourhoods project

Plymouth Phenology Study – Budshead Wood

Thank you for taking the time to be part of this citizen science survey at Budshead Wood. Your observations will be important in determining how we can monitor climate change in British woodlands.

Time you'll need

Trees can be checked twice a week, starting from now (March 2018) as flowers are starting to appear, and finishing in a couple of months' time when the tree canopy has fully closed. It only takes a few minutes to check each tree sapling - the time you spend in the woodland each time will depend on how many trees you would like to monitor. The tree saplings for this project are marked with a green number tag, as shown in the photo above.

Equipment

Clipboard, smart phone (with camera), fish-eye lens (contact us if you would like one), pen/ pencil, recording sheet for each tree, locations of trees and instructions sheet.

Photographs

For every sapling you monitor, a photo should be taken of the canopy above from now (March 2018) until it is fully in leaf. Photos can be taken using the fish-eye lens clipped onto your smart phone. The best time to take photos is during earlier morning or later afternoon, to reduce the likelihood of lens flare. Name each photo with the date and tree tag number of the sapling you're stood by.

Observations

For each tree sapling, record the number of buds in leaf - the method for doing this will vary depending on whether you are monitoring beech, ash or sycamore. The numbers of flowers surrounding each sapling should also be recorded on the sheets provided.

Health and Safety

When working in the woodland, be aware of other users such as dog walkers and take care when walking on uneven ground with exposed tree roots, especially after wet weather. If monitoring trees on your own, ensure somebody knows what you're doing and how long you intend to be out for.

Where to send your observations and photographs

Keep all of your recording sheets for each tree, as well as your photographs. These can be scanned/ saved to a USB stick and transferred to Alison Smith in person at the end of the project, or you can email these to alison.smith@plymouth.ac.uk each week or at the end of the project.

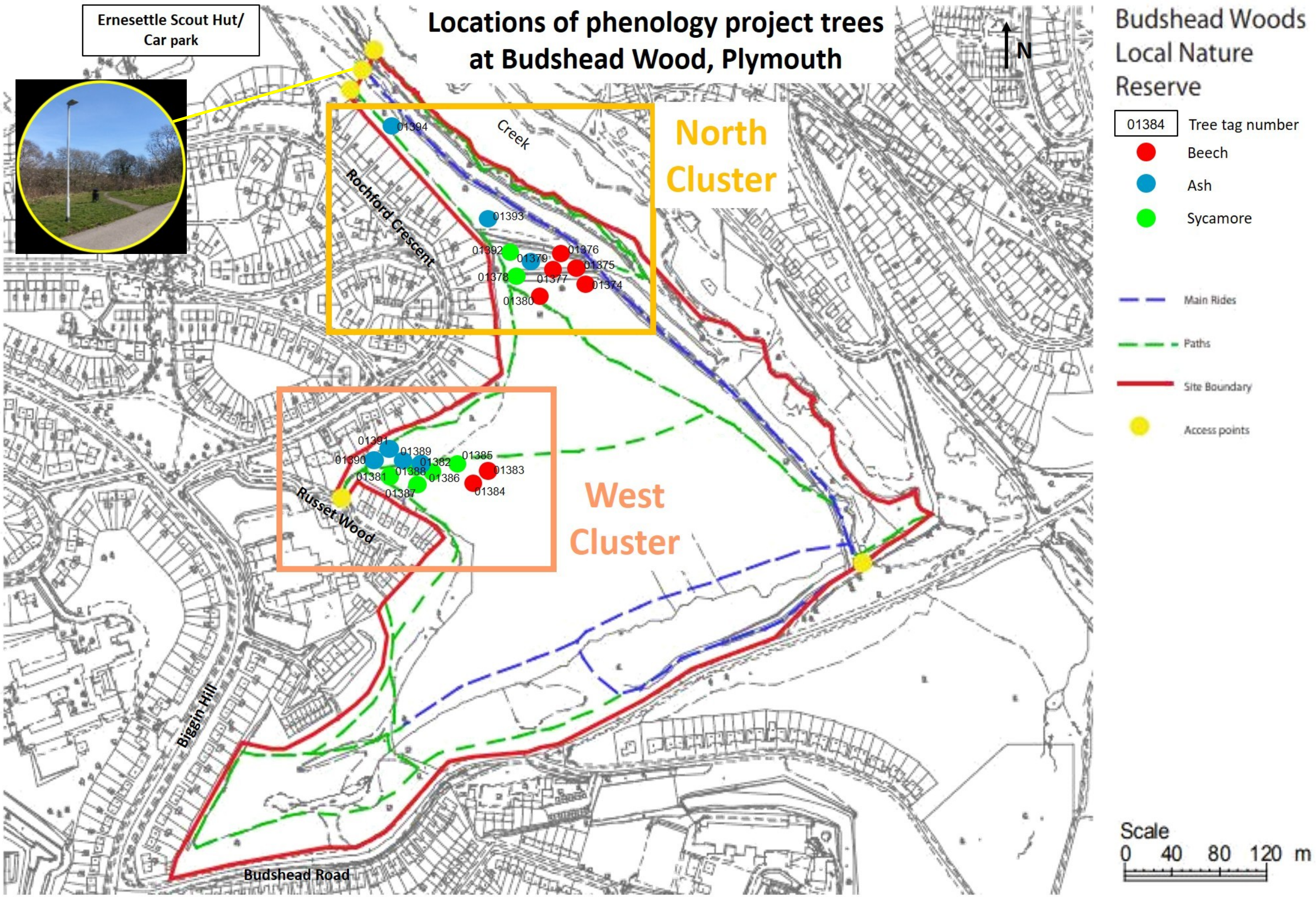
Any queries? To find out more, contact:

Alison Smith at alison.smith@plymouth.ac.uk

or Hayley and Tim at Active Neighbourhoods:

Hayley Partridge hayley.partridge@plymouth.gov.uk

Tim Russell tim.russell@plymouth.gov.uk


Locations of phenology project trees at Budshead Wood, Plymouth

Appendix 7.1

List of abbreviations used in the thesis

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
ART	Aligned Rank Transform (method for transforming non-normal data-sets to allow use of parametric statistical analyses)
ASNW	Ancient semi-natural woodland
BB	Budburst
CO	Canopy openness (percentage of the sky hemisphere not obstructed by canopy elements, within a given field of view—if calculated from hemispherical photography in HemiView, CO is weighted according to the gap fraction zenith angle)
DBH	Diameter at breast-height
DCP	Digital Cover Photography (method used to calculate LAI from non-hemispherical photographs)
DOY	Day of year (referring to the day of the year in the Julian calendar)
DN	Digital number (represents the intensity of green, red and blue colour channels in a photograph)
EVI	Enhanced Vegetation Index (in satellite remote sensing, a measure of surface reflectance of near infra-red, red and blue waveband radiation used to detect canopy greening— EVI is a newer and more sensitive measure than NDVI)
EV	Exposure value (usually ranging from -2 to +2 in a camera's exposure compensation settings)
GPS	Global Positioning Satellite

GSF	Global site factor (a measure of the proportion of solar radiation penetrating below the forest canopy relative to solar radiation at a nearby position in the open—calculated from hemispherical photographs based on the size and position of canopy gaps, and knowledge of site latitude and longitude)
HP	Hemispherical photography
HV	HemiView (software for analyzing hemispherical photographs)
ICP	International Cooperative Programme (European programme for monitoring air pollution effects on forests)
IJ	ImageJ (open-access image analysis software)
LAI	Leaf area index (a widely-used measure of canopy structure, representing one half the total green leaf area per unit ground surface area)
LE	Leaf expansion
LiDAR	Light Detection and Ranging (method using sensors to detect reflection of laser pulses, used in satellite and near-surface remote sensing to estimate canopy structural attributes)
MDS	Multi-dimensional scaling
MODIS	Moderate Resolution Imaging Spectroradiometer (product providing daily surface coverage of satellite imagery)
MP	Mega-pixels
NDVI	Normalised Difference Vegetation Index (in satellite remote sensing, measures surface reflectance of near infra-red, red and blue waveband radiation to used to detect canopy greening)
NFIs	National Forest Inventories
NPP	Net primary productivity
NVC	National Vegetation Classification
PAR	Photosynthetically active radiation

PAWS	Plantation on an ancient woodland site
PCA	Plant canopy analyser
PERMANOVA	Permutational multivariate analysis of variance
ROI	Region of Interest (in relation to selecting an area if a photograph to analyse in ImageJ image analysis software)
SP	Smartphone fisheye photography
UAV	Unmanned aerial vehicle
USA-NPN	United States of America National Phenology Network
VE	Visual estimation (of canopy leaf expansion)