2021

Assessing How Understory Plant and Pollinator Interactions are Affected by Differing Canopy Phenologies

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Award date:
2021

Awarding institution:
University of Plymouth

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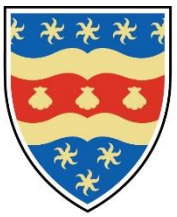

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Assessing How Understory Plant and Pollinator Interactions are Affected by Differing Canopy Phenologies

by

Jack Everatt

A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

RESEARCH MASTERS

School of Biological and Marine Sciences

March 2021

Acknowledgements

I want to thank the following people for helping with this research project: Firstly, I would like to thank my supervisor, Dr Paul Ramsay, for his guidance and knowledge both throughout this project. Plymouth University, for giving me the opportunity to undertake this research degree. Thirdly, Jess Tatton-Brown and the management team within Plymbridge woods, for allowing this project to be conducted within the woodland. Finally, I would like to thank my friends and family, for their continual support throughout both the survey period and write up periods over the last 18 months.

Author's declaration

At no time during the registration for the degree of Research Masters 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.

Word count of the main body of thesis: 6288

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Date: 12/03/2021

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Abstract

Advancements in springtime phenologies of plants and their pollinators have been widely observed within the northern hemisphere due to climate change. The observed advancements have led to concern over potential mismatching occurring between plant-pollinator interactions. The effect of forest canopies on understory phenological interactions has scarcely been investigated. We studied the effect of differing canopy closure parameters on understory phenological interactions within Plymbridge woods, Devon, UK, over a 6-month study period. The temporal overlap between canopy, understory flower and pollinators were investigated using Pianka overlap indices. Canopy phenology was modelled using NLSTIMEDIST package of R, giving three canopy parameters, canopy r (maximum rate of canopy closure), canopy c (temporal concentration) and canopy t (canopy closure duration). All temporal overlap values were as expected within the woodland, suggesting no mismatching has occurred within the woodland to date. Supporting previous literature, suggesting plants and their pollinators are shifting phenologies at similar rates. Canopy r was seen to have a significant positive relationship with the overlap between canopy and understory flowers, suggesting as canopy closure rate increased, the temporal overlap between canopy and flowers also increased. However, Canopy c contradicted this with a negative relationship with the overlap between canopy and understory flowers. The discrepancies seen between these

two canopy parameters are likely due to the low sample size due to limited resources within the study. Despite the low sample sizes within the study, the methodology used will likely be useful for future studies, investigating the effect of canopy closure on understory phenologies.

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1 Introduction

Insect pollinators play vital roles in terrestrial ecosystems providing worldwide ecosystem services (Bailey *et al.*, 2014; Klein *et al.*, 2007). One key ecosystem service provided by insect pollinators is acting as the primary pollinators for almost 90% of the worlds flower plant species (Bailey *et al.*, 2014; Ollerton, Winfree & Tarrant, 2011). In addition to this, insect pollinators benefit up to 75% of crops worldwide, increasing fruit and crop yields (Klein *et al.*, 2007). Natural pollination services are estimated at a yearly value of around $215 billion (Gallai *et al.*, 2009; Vanbergen & Initiative, 2013). Crop pollination - and thus fruit set - is enhanced by a greater pollinator diversity and abundance (Watson, Wolf & Ascher, 2011). As a result of this, crop fields adjacent to natural habitats – such as forest – have been shown to have increased crop yields (Bailey *et al.*, 2014; Watson, Wolf & Ascher, 2011). In addition to enhancing crop pollination, forest invertebrates play key roles in recreation, supporting and provisioning ecosystem services (Patterson & Coelho, 2009), as well as maintaining stable and healthy forest ecosystems (Burkle & Alarcón, 2011; Fontaine et al., 2005).

The ecological importance of insect pollinators and the ecosystem services they support are threatened by stressors linked to global climate changes (Bartomeus *et al.*, 2013; Kudo & Ida, 2013; Rafferty, 2017). Over the past 100 years, average global temperatures have risen by 0.6^{o}C and are expected to continue to rise (Root *et al.*, 2003). The increase in global temperature has caused springtime in the northern hemisphere to advance at a rate of 2.5 - 2.9 days per decade since the 1960s (Jentsch *et al.*, 2009; Menzel & Fabian, 1999; Menzel *et al.*, 2006; Parmesan, 2007). Advancements in springtime have been paralleled by

phenological advancements in plant and pollinator species, resulting in earlier flowering times and pollinator activity (Bartomeus *et al.*, 2011; Cole & Sheldon, 2017; Memmott *et al.*, 2007). All large-scale studies have indicated that climatic warming is the primary driver of the observed advancements (Bartomeus *et al.*, 2011; Cole & Sheldon, 2017).

As a result of ongoing climatic warming, future advancements in plant and pollinator phenologies are expected to occur (Hegland *et al.*, 2009), potentially leading to mismatches in phenologies of plants and their pollinators over a longer time scale. Mismatches in phenologies of plants and their pollinators would have detrimental effects on trophic interactions (Bartomeus *et al.*, 2011). In turn, mismatches would ultimately lead to extirpation and extinction events, and thus losses or reduction of key ecosystem services (Bartomeus *et al.*, 2011; Rafferty & Ives, 2011). Evidence to date has shown advancements of up to 4.5 and 7.7 days per decade for plant species and pollinators respectively (Fitter & Fitter, 2002; Forister & Shapiro, 2003; Roy & Sparks, 2000). However, studies of pollinator advancement have been conducted over much smaller spatial scales compared to the much larger-scale studies of advancements in plant species (Jentsch *et al.*, 2009; Parmesan & Yohe, 2003; Penuelas & Filella, 2001; Rafferty & Ives, 2011). Despite evidence for large scale advancements in phenology, there is little to no evidence for large scale mismatching events having occurred to this date (Bartomeus *et al.*, 2011). The lack of evidence for mismatching could be due to plant and pollinator species advancing their phenologies at similar rates, suggesting a shared response to climatic warming (Bartomeus *et al.*, 2011; Hegland *et al.*, 2009; Rafferty & Ives, 2011). Evidence for small-scale mismatching has been observed, between more specialised species (Kudo &

Ida, 2013; Kudo *et al.*, 2004), highlighting the need for further research in the area.

Phenological shifts within the canopy of temperate forests are well documented, with evidence for wide-scale lengthening of canopy growth seasons (Cole & Sheldon, 2017; Linderholm, 2006; Vitasse *et al.*, 2011). Observed lengthening has predominantly been observed within early springtime flushing (Cole & Sheldon, 2017; Vitasse *et al.*, 2009). Similarly to plants and pollinators, temperature appears to be the main driver for the observed advancements in phenology (Cole & Sheldon, 2017). However, unlike other phenological shifts, canopy phenologies have been seen over small spatial scales, and both between and within canopy species (Basler, 2016; Cleland *et al.*, 2007; Cole & Sheldon, 2017). Canopy phenologies have widespread implications on trophic interactions predominantly due to understory shading (Cole & Sheldon; Roberts *et al.*, 2015). Understanding how phenological shifts in the canopy may alter understory interactions is vital in understanding how forest habitats will react to ongoing climatic warming.

Despite widespread research on the effect of climatic warming on forest canopies, very little research has taken place on forest understory species. However, some of the only evidence indicating mismatching between plants and their pollinators has come from forest understories. Kudo et al. (2004) gave evidence for significant advancements - of up to 15 days - in the phenologies of two spring ephemeral species (*Corydalis ambigua* Cham. et Schlecht and *Gagea lutea* (L.) Ker Gawl), within a forest in Japan. The advancements in *C. ambigua* and *G. lutea's* phenologies were not mirrored by their bee pollinators (Kudo *et al.*, 2004). Consequently, the advancements observed caused mismatches between species, reducing seed set by up to 50% over the season (Kudo *et al.*, 2004). The observed

mismatch was recorded within a record high-temperature season, supporting previous evidence that extreme weather events can cause mismatches (Jentsch *et al.*, 2009). However, long-term studies in the same area have shown mismatches to occur over a longer study period of 10-14 years of *C. ambigua* and its pollinators (Kudo & Ida, 2013). These studies give some of the only evidence for temporal mismatching over a long time scale. However, both studies were focused on specific interactions in a small area in Japan, of which snowmelt events govern the growth and reproductive periods, and pollination was likely only carried out by overwintering queen bumblebees (Kudo & Ida, 2013; Kudo *et al.*, 2004). Consequently, it is pivotal to investigate mismatching events between understory flowers and pollinators over long time scales and under different canopy conditions to better understand these fundamental changes in phenologies, as the climate continues to warm, and springtime continues to advance.

To the best of our knowledge, no study to date has investigated how the phenological synchrony of understory plants and their pollinator species are affected by differing canopy phenologies within temperate forest habitats. Within this study, we aimed to fill in some gaps within this field by aiming to a) determine if, at present, it is likely that phenological mismatches have occurred within the sample site. b) determine the characteristics of a range of canopies, to investigate inter- and intra- specific variations in canopy phenologies. c) investigate how differing canopy parameters affect the phenologies and diversity of understory flowering and pollinator assemblages.

2 Methods

2.1 Site and survey period

The site chosen for the study was Plymbridge woods, Devon, UK. High levels of canopy and understory diversity compared to other local woodlands in the area was the determining factor in site selection. Due to higher levels of canopy heterogeneity than the rest of the woodland - which is predominantly monoculture blocks - two smaller plots were selected as the sampling sites (Figure 1). A total of 15 fixed sampling plots were selected within the two sampling areas, eight in the “hazel” area and seven in the “ruins” area. Each of the plots was marked with a 1m high post.

Due to this study's time constraints (1 year), we could not investigate phenological changes over a long temporal period. The sampling period ran from January 2019 until June 2019, allowing full canopy closure and peak flowering times within the sampling site. Sampling was stopped in June due to time constraints for the project. Ideally, sampling would have continued throughout the summer and autumn to allow for a full canopy cycle to occur and allow for later blooming flowers.

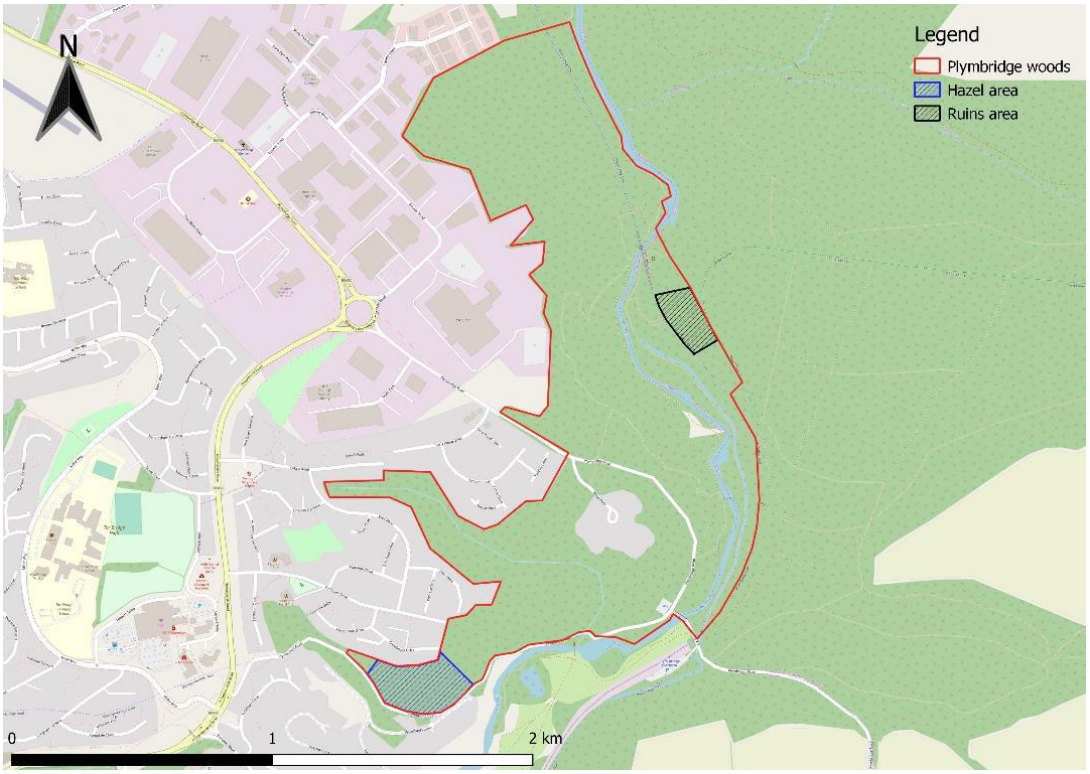


Figure 1. An overview map of the sample sites in Plymbridge woods, Devon, UK, showing both the hazel and ruins areas.

2.2 Field methods

2.2.1 Canopy photography

Hemispherical canopy photography was used to assess canopy closure. Photography was conducted using an Honor X8 smartphone with a clip-on fisheye lens attachment, giving almost a full 180^{o} angle of the canopy, following adapted methods of Smith and Ramsay (2018). Photos were taken at the highest possible resolution (3840 x 5120); this resolution was selected to give the highest level of accuracy for the photo analysis (Brusa & Bunker, 2014). The automatic phone camera settings were used, where photos were

overexposed manual exposure was selected, and the photo was retaken. Photos were taken either before 10:30 am or after 16:30 pm, to minimise overexposure and sun flares in the final photos. Photographs were stored as jpeg images.

Photos were taken every two-three days at each plot, for the full six-month survey period Plots were visited in the same order every visit, in order to take the photos at roughly the same time in each plot every sampling day. The phone was oriented on each visit using a removable guide platform, which was placed into the top of the marker posts.

2.2.2 Pollinator counts

Pollinator counts were undertaken using 2m x 2m quadrats. The quadrat was orientated by placing one corner over the fixed camera post and then a compass used to orient the quadrat in the same direction every time the plot was sampled. Adapted flower insect timed counts (FIT) were used (CEH, 2018). 10-minute counts were undertaken per plot, every two-three days between the hours of 11.30 and 14.30, allowing for maximum pollinator activity. The counts were not undertaken on days with temperatures of less than 13^0C, rainfall or high winds. Due to the fast-paced nature of pollination, identification down to species level was deemed to be impossible, for this reason, pollinators were classified into the following pollinator groups: bumblebees, bees, flies, hoverflies, beetles, wasps and butterflies. Each visitation to a fully open flower was recorded along with the flower species. A visitation was classified by an individual pollinator landing on or going into an open flower.

Videos cameras on tripods were going to be used in order to guarantee every pollinator

visit was recorded. However, due to the low pollination events throughout the sampling period, they were deemed unnecessary.

2.2.3 Flower counts

Flower counts were undertaken every two-three days using the same 2m x 2m quadrat; these counts were done last in the day due to flowers being the least time-sensitive to sample. Every fully open flower in the quadrat was counted. Later into the sampling period "blanket" coverage of *Hyacinthoides non-scripta* (L.) Chouard was observed, making it almost impossible to count every flower accurately. When this occurred, an average of flowers per inflorescence was taken from 20 individual plants. The number of inflorescences was then counted, and an estimation of total flower numbers was calculated from this.

2.3 Photo analysis

Image analysis of hemispherical photos was undertaken using ImageJ (Rueden et al., 2017). As hemispherical photos are a circular image inside a rectangular frame, each image was first cropped using the elliptical selection tool, and the outside was then cleared using the "clear outside" function, allowing for accurate estimation of gap fraction (sky within the picture).

Thresholding, as described by Brusa & Bunker (2014), separates the pixels of an image into groups based on each pixel's intensity. By thresholding canopy photographs, the pixels within the image can be split into sky and canopy groups. Thresholding for each

image was undertaken manually. Automated plugins - such as hemispherical 2.0 (Beckschäfer, 2015) within the Fiji package (Schindelin *et al.*, 2012) - could not be used due to slight variations in the placement of the fisheye lens each time, although these were very minimal accurate automation could not be achieved. Each image type was changed to RGB split, splitting the red, green and blue channels within each image. Thresholding was then undertaken using the blue light channel, which has been shown to give the highest levels of accuracy, as a result of low blue reflectance in the canopy, and high blue light transmittance in the sky (Brusa & Bunker, 2014). Canopy openness or the gap fraction was recorded for each image, along with the overall cover and canopy closure. The gap fraction within the canopy is the amount of sky visible between the canopies.

2.4 Data analysis

All statistical analysis was carried out using R v.3.6.1 (R Core Team, 2019), with the exception of the Pianka overlap null models, which used the TimeOverlap program (Castro-Arellano *et al.*, 2010).

2.4.1 Pollinator preference

Due to a low pollinator sample size, the preference data was first collated. *Digitalis purpurea* (L.), *Glechoma hederacea* (L.), *Potentilla sterilis* (L.) Garcke and *Veronica chamaedrys* (L.) were all removed from the data set due to receiving no pollinators throughout the sampling period. Three other species (*Geranium robertianum* (L.),

Taraxacum officinale (L.) Weber and *Viola riviniana* Rchb.) had very low pollination rates throughout the surveying period and were collated into "others" groups. Within the pollinator groups, both the butterfly group and the wasp group were removed due to no pollination and very low pollination respectively. Although collating the data reduced the sample size of species, it was necessary to meet assumptions of statistical tests used.

In order to test for flower preference, Fisher's exact test (Fisher, 1992) was used in place of chi-square, due to more than 20% of observations being less than five. As a result of the low sample size, *p* values were calculated using a Monte Carlo simulation, with 2000 replicants, the Monte Carlo simulation was run within the Fisher's exact test within R. Preference between specific plant and pollinator species was visualised using the Corrplot r package (Wei & Simko, 2017), these plots visualise the Pearson residuals, showing preference between groups. The circles' size and colour indicate the strength of preference between groups—dark red large circles indicate a strong preference.

2.4.2 Canopy modelling

The phenological characteristics of the canopy were investigated using the R package NLSTIMEDIST (Steer, Ramsay & Franco, 2019). Canopy closure data were fit to the model using the timedist() function, and accuracy of fit was assessed using summary() and a pseudo R^2 produced with the $m$rss() function. Both cumulative distribution function plots (CDF) and probability density function plots (PDF) were then produced using the tdCfdplot() and tdPdfplot() functions respectively in order to visualise the modelled data per plot over the sampling period.

This analysis produces three statistically meaningful parameters, r, c and t, within this

study, these are; canopy r, canopy c and canopy t. Canopy r is the maximum rate of canopy closure, units: none. Canopy c is the measure of temporal concentration, i.e. how quickly canopy closure occurs, units: $time^{-1}$. Canopy t is a measure of canopy closure duration, i.e. how many days it took from the first leaf to grow until full canopy closure, units: time (Steer, Ramsay & Franco, 2019).

2.4.3 Interspecies canopy phenology

Significant variation within each plot's phenological characteristics was observed after fitting the canopy data to the NLSTIMEDIST model. Due to this, variation within the phenological parameters (canopy r, canopy c and canopy t) - between the dominant canopy species - was investigated. Levene's test of homogeneity was used in order to determine heterogeneity within the groups. A one-way ANOVA was then used to determine the variance between the differing canopy species present within the sampling plots.

2.4.4 Temporal niche overlap

The temporal overlap between canopy, understory flowers and pollinators were estimated using the Timeoverlap program. The Timeoverlap program was used to calculate Pianka indices per plot. In order to assess the significance of the Pianka indices the ROSARIO algorithm (n = 10000) is used, to create null distributions (Castro-Arellano *et al.*, 2010), ROSARIO is used due to its ability to maintain autocorrelation through a continuous distribution of activity. In contrast, other algorithms, such as RA3 and RA3, are designed for nominal data (Castro-Arellano *et al.*, 2010). Two-tailed p values were calculated – as a result of no prior directional expectation – following the methods of

(Castro-Arellano *et al.*, 2010)

3 Results

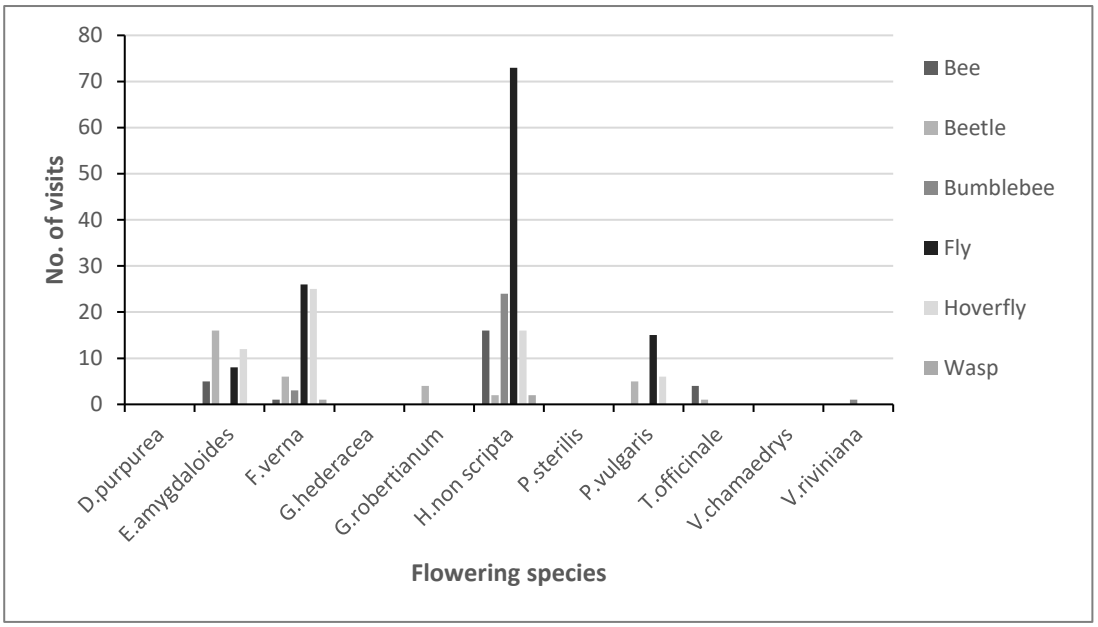
3.1 Flower and pollinator groups

A total of 272 pollinators were recorded visiting 11 understory flowering species (Figure 2a). The fly and hoverfly groups had the highest visitation frequency, with 122 (44.4%) and 59 (21.69%) visits respectively. The beetle group showed the highest visitation diversity, visiting six plant species. No pollinator group visited all 11 plant species. *Hyacinthoides non-scripta* and *Ficaria verna* received the most visitations with 133 (48.8%) and 62 (22.7%) visits respectively (Figure 2a).

Plots R1 and R4 were seen to receive the highest number of visits (Figure 2b), with 89 (31.9%) and 51 (18.75%) of visits, respectively. Plot R4 was the only plot which received all six pollinator groups, R1 and R3 both received visits from five pollinator groups. Plots H6, R3 and R5 all received no pollinators, in correspondence to having either no flowers present or very low abundance of flowers present (Table 1).

Hyacinthoides non-scripta was the most common flowering species. It was present in 12 of the 15 plots and had the highest peak flower abundance within every plot in which it was present (Table 1). The highest abundance of *H. non-scripta* was seen in plot H3 with 745 flowers, and an average peak flower abundance of 260 across all plots. Plots H6 and R3 had no flowering species present in the sampling period.

a)



b)

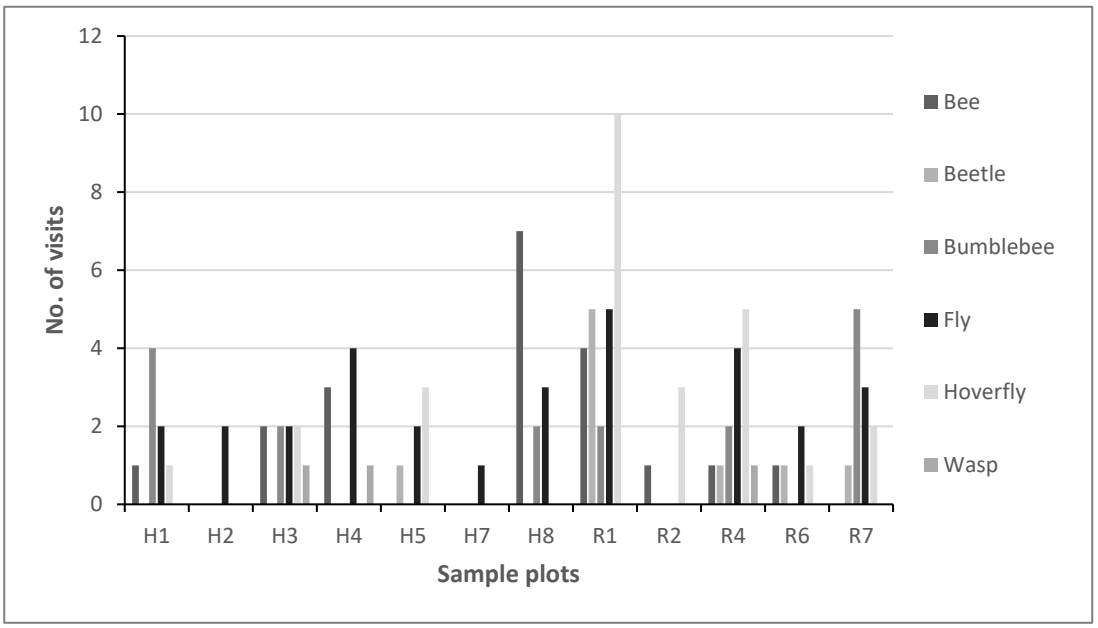


Figure 2. a) Total number of pollinator visitations to understory flowering species. b) Total number of pollinator visits per survey plot. Plymbridge woods, Devon, UK.

Table 1. Peak number of flowers per species for each plot. Plymbridge woods, Devon, UK.

Flowering species	Plot														
	H1	H2	H3	H4	H5	H6	H7	H8	R1	R2	R3	R4	R5	R6	R7
D.purpurea													2		
E.amygdaloides									66						
F.verna	1		1		6			4	5			15			
G.hederacea									12						
G.robertianum									6						
H.non scripta	498	35	745	724	37		26	705	103	76		147		95	706
P.sterilis									7						
P.vulgaris									37					18	
V.chamaedrys									6						
V.riviniana									4			1			
T.officinale									5						

3.2 Pollinator preference

Fisher's exact test, investigating pollinator preference, showed a simulated *p* value of <0.001 based on 2000 replicate samples, indicating a significant preference within the data. The strongest preference was seen between the beetle group and *Euphorbia amygdaloides* (L.) (Figure 3). A strong preference was also observed between beetles and the "others" groups. High levels of preference were seen toward *H. non-scripta* by both bumblebees and flies. Hoverflies showed a preference for *F. verna*. Interactions between all other flower and pollinator groups were shown to be of little to no preference. The bee group was shown to have the least specific preference, suggesting them to be the most generalist pollinator group.

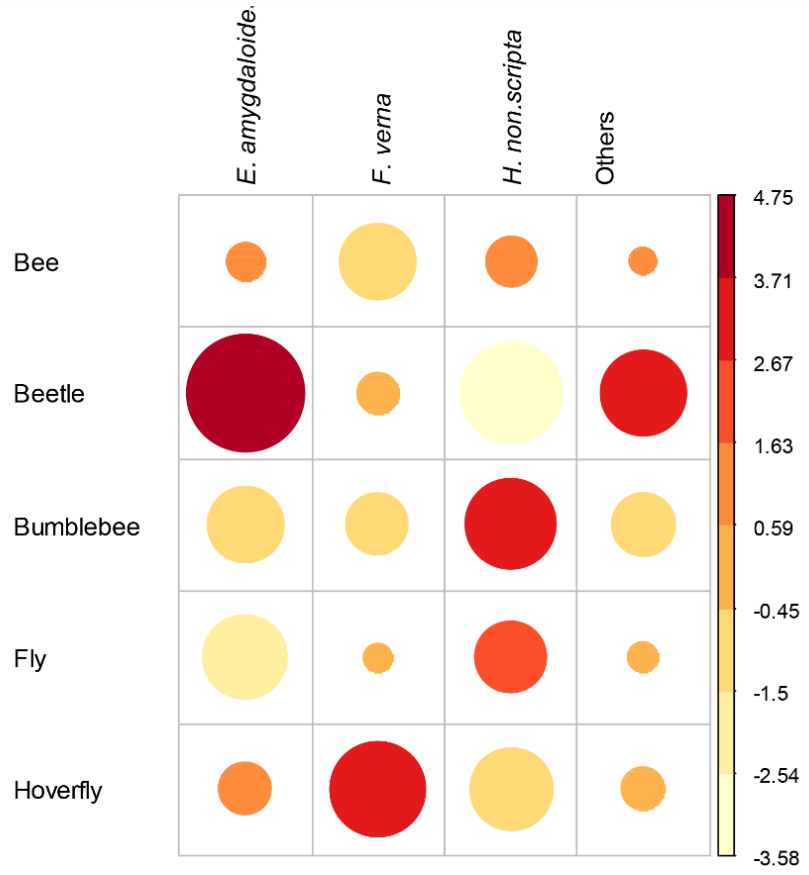


Figure 3. Correlation between pollinator groups and flowering plant species. Indicating the preference of flowers for each pollinator group. The size and colour of each circle indicates the strength of the correlation. Dark red indicating a strong positive correlation. Strong positive correlations indicate a high level of preference towards that flower. Plymbridge woods, Devon, UK.

3.3 Canopy closure

The highest canopy cover was observed within plot R2, with a maximum canopy cover of 84.66% and a gap fraction of 15.34% (Table 2). The lowest overall canopy cover was seen in plot R1 with a maximum coverage of just 68.83% and a gap fraction of 31.17% (Table 2). *Quercus robur* (L.) and *Fagus sylvatica* (L.) were both the dominant canopy species in four plots. *Corylus avellana* (L.) and *Acer pseudoplatanus* (L.) were the dominant species within one plot each (Table 2). Five of the plots showed no dominance and were deemed to be of mixed dominance.

Table 2. Final canopy closure percentages. Overall cover combines the canopy cover, tree trunk and branch cover. Gap fraction indicates the sky gaps within the canopy. Plymbridge woods, Devon, UK.

Plot	Dominant Canopy species	Canopy %	Overall cover %	Gap fraction %
H1	*F. sylvatica*	39.47	84.19	15.81
H2	*A. pseudoplatanus*	40.97	82.68	17.32
H3	*C. avellana*	31.01	78.14	21.86
H4	*Q. robur*	32.57	74.39	25.61
H5	*Mixed*	31.42	73.72	26.28
H6	*Mixed*	39.75	79.24	20.76
H7	*Q. robur*	29.52	74.27	25.73
H8	*Mixed*	31.20	75.89	24.11
R1	*Mixed*	29.26	68.83	31.17
R2	*F. sylvatica*	35.34	84.66	15.34
R3	*Q. robur*	32.72	78.72	21.28
R4	*Q. robur*	27.11	80.65	19.35
R5	*Mixed*	21.66	75.83	24.17
R6	*F. sylvatica*	31.40	82.66	17.34
R7	*F. sylvatica*	32.00	83.57	16.43

3.3.1 Canopy modelling

The canopy closure data was fit to the NLSTIMEDIST model in R (R Core Team, 2019). The majority of model parameters were fit successfully, showing very low standard errors, with high significance values ($p < 0.01$; Appendix 1). However, the canopy r parameter for plots H4 and H5, both showed higher standard errors (around 0.03) and significantly lower significance value ($p < 0.1$; Appendix 1). Despite this, pseudo R^2 values for plots H4 and H5 were both shown to be high ($R^2 > 0.99$; Appendix 1) suggesting the model was fit to both plots. R^2 values for every other plot were also high ($R^2 > 0.98$; Appendix 1).

Cumulative distribution function plot (CDF) (Figure 4a) and probability density function plot (PDF) (Figure 4b) were produced, in order to summarise canopy parameters visually. Canopy closure for all plots started between days 92 and 113 (Figure 4a) and all plots had

finished canopy closure by day 150. CDF plot showed a relatively uniform pattern in canopy completion, with all plots showing a similar distribution. Plot R7 was shown to have the highest realisation of r (canopy c) indicated by the sharp early peak in Figure 4b, resulting in the earliest canopy closure (canopy t) on day 116 (Figure 4a). Plot H5 had the lowest realisation of r (canopy c) (Figure 4b), resulting in the latest canopy closure day of 150 (Figure 4a). Four of the top 5 fastest closing plots were plots dominated by *F.sylvatica* (R7, H1, R2 and R6). The five plots with the slowest closing canopies were a mix of *Q.robur* and mixed plots (*Q.robur* – H7 and H4, Mixed – H5, H6 and R5).

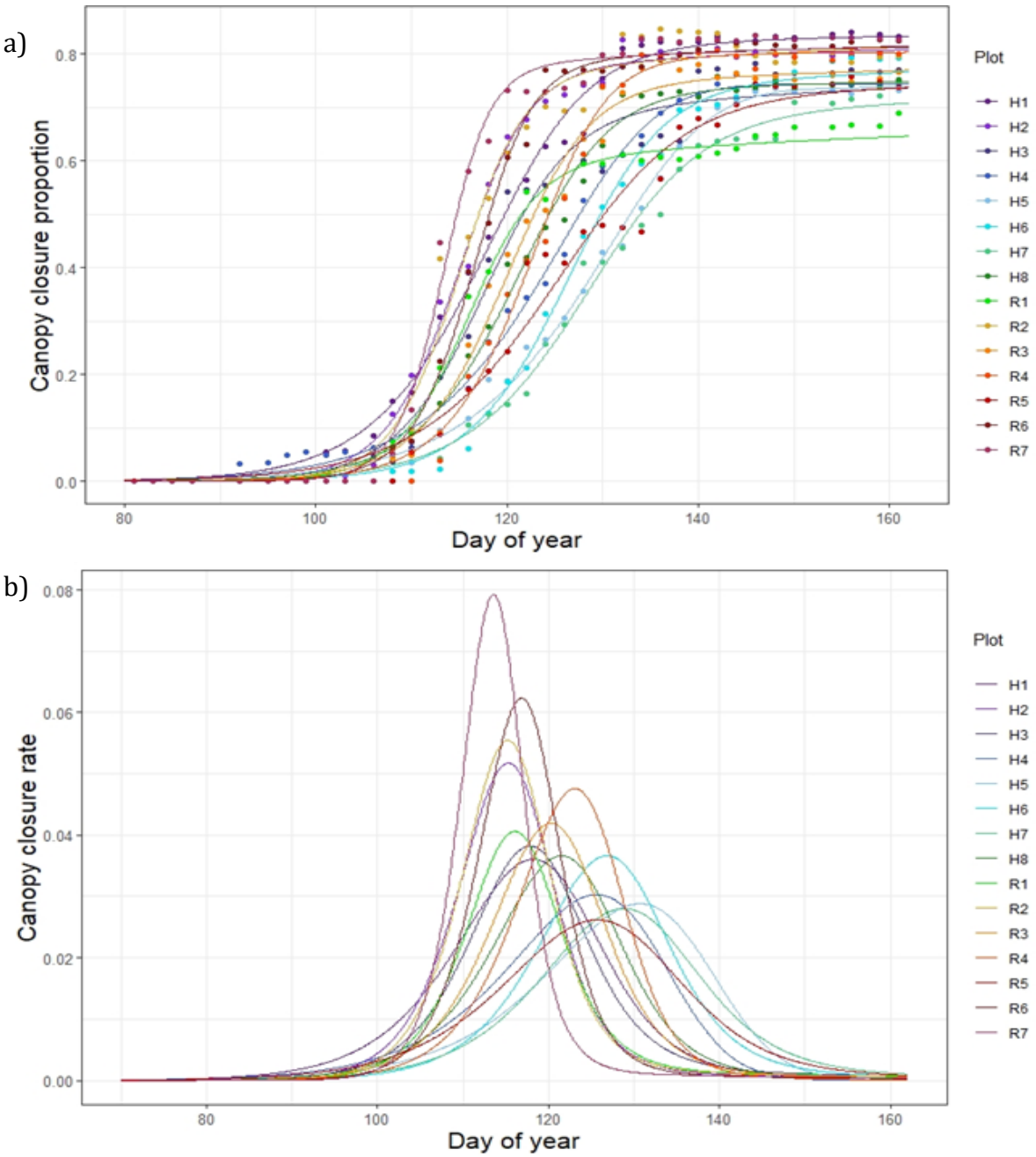


Figure 4. a) Cumulative distribution function (CDF) and b) corresponding probability density functions (PDF), for canopy closure events within 15 plots in Plymbridge woods, Devon, UK. Probability density function describes the rate of canopy closure completion, where the area under the curve is equal to 100% canopy closure.

3.3.2 Interspecies canopy variation

Due to the variation observed between canopy species in figure 4, inter-species variation was investigated to determine if canopy closure rates or duration were significantly different between canopy species. Plots were divided into groups based on dominant canopy species (Table 2). Variation in the canopy parameters between dominant species was investigated (canopy r, canopy c, canopy t). Levene's test for homogeneity indicated homogeneity within all canopy parameters ($F > 0.05$, *p value* > 0.05). One- way ANOVA indicated there to be no significant differences in the canopy parameters (canopy r, canopy c and canopy t) between any of the canopy species groups (canopy r, f= 0.55, *p value* = 0.66, canopy c, f = 2.51, *p value* = 0.11, canopy t, f = 2.91, *p value* = 0.08). These results indicate no significant differences between the canopy closure rates or durations of the dominant canopy species tested.

3.4 Overlap indices

The analysis of temporal niche overlap between the canopy and the flowers (Table 3) showed a significantly greater than the expected overlap in plot R4, with a Pianka overlap of 0.784, compared to the expected value of 0.187. The same results were observed within the temporal niche overlap between the canopy and *H. non-scripta*. Very little variation within the observed Pianka values was shown when comparing overall flower – canopy overlap and *H. non-scripta* – canopy overlap, suggesting that the majority of overlap can be attributed to the presence of *H. non-scripta*. This observation is concurrent with *H. non-scripta* being the dominant and most abundant species within every plot (Table 1).

Table 3. Pianka index overlap values between the canopy, understory flowering plants and pollinator groups. Can = Canopy, Fl = Overall flower, Hns = *H. non-scripta*, Pol = Overall pollinators, *p* values are shown in brackets.

Plot	Can - Fl	Can - Hns	Pol - Fl	Pol - Hns	Can - Pol
H1	0.726 (0.136)	0.726 (0.12)	0.629 (**0.033**)	0.628 (**0.033**)	0.546 (0.100)
H2	0.689 (0.157)	0.689 (0.16)	0.141 (0.409)	0.141 (0.401)	0.075 (0.342)
H3	0.568 (0.109)	0.568 (0.12)	0.546 (0.285)	0.546 (0.278)	0.147 (0.715)
H4	0.772 (0.108)	0.772 (0.104)	0.432 (0.153)	0.432 (0.153)	0.197 (0.561)
H5	0.594 (0.383)	0.606 (0.355)	0.204 (0.561)	0.116 (0.657)	0 (0.909)
H6	-	-	-	-	-
H7	0.627 (0.165)	0.627 (0.17)	0.367 (0.133)	0.367 (0.128)	0.429 (0.067)
H8	0.747 (0.125)	0.747 (0.124)	0.504 (0.107)	0.504 (0.118)	0.614 (**0.016**)
R1	0.531 (0.264)	0.306 (0.421)	0.512 (0.366)	0.134 (0.769)	0.225 (0.422)
R2	0.435 (0.292)	0.435 (0.302)	0.454 (**0.022**)	0.454 (**0.026**)	0.371 (**0.046**)
R3	-	-	-	-	-
R4	0.784 (**0.042**)	0.784 (**0.042**)	0.181 (0.944)	0.127 (0.872)	0.079 (0.932)
R5	-	-	-	-	-
R6	0.635 (0.176)	0.605 (0.21)	0.322 (0.406)	0.278 (0.498)	0.184 (0.456)
R7	0.491 (0.223)	0.491 (0.22)	0.566 (**0.088**)	0.566 (**0.089**)	0.676 (**0.006**)

Temporal niche overlap between pollinator groups and flowers was shown to be significantly higher than expected in plots H1, R2 and R7. Similar results were observed between *H. non-scripta* and pollinator groups' niche overlap, further suggesting that *H. non-scripta* contributes to the majority of the overlap within the flowering groups. Plot R1 showed the largest variation between overall flowers and *H. non-scripta* likely due to the high flowering diversity within the plot (Table 1).

The overlap between canopy and pollinator groups was significantly higher than expected within plots H8, R2 and R7, suggesting higher than expected advancement within the canopy or a prolonged pollinator activity period.

The canopy parameters were plotted against the overlap values to determine how an increased rate of canopy closure and duration of canopy closure affected the overlap

between groups (Figure 5). Two significant relationships were observed between overlap and the canopy parameters. Canopy r was seen to have a significant positive relationship with the overlap between the canopy and flowering species (Figure 5b) (R^2 = 0.6, *p* value = 0.009. Indicating that as canopy r (maximum rate of canopy closure) increases, the overlap between canopy and flowering also increases. Canopy c was seen to have the opposite relationship with the overlap between the canopy and understory flowering species (figure 5c) (R^2 = 0.35, *p* value = 0.0436). Indicating that as canopy c (canopy closure rate) increases, the overlap between the canopy and understory flowering plants decreases. Despite the significance of this interaction, the R^2 value was relatively low (R^2 = 0.35). All of the other interactions between the canopy parameters and the overlap indices were seen to be insignificant (very low R^2, *p* value = > 0.05).

Despite lack of significance, the overlap between pollinators and canopy and the overlap between pollinator and flowers were both seen to have a very similar response to increased canopy closure rate and duration (Figures 5a, 5b and 5c). This suggests that pollinators may have a similar response to both canopy closure and flowering. However, despite some slight trends being observed, most of the data is relatively flat across all canopy parameters. Suggesting, that canopy closure duration, and canopy closure rate have little effect on the overlap values recorded, thus suggesting that the phenologies of understory flowers and pollinators are shifting alongside the phenology of the canopy itself.

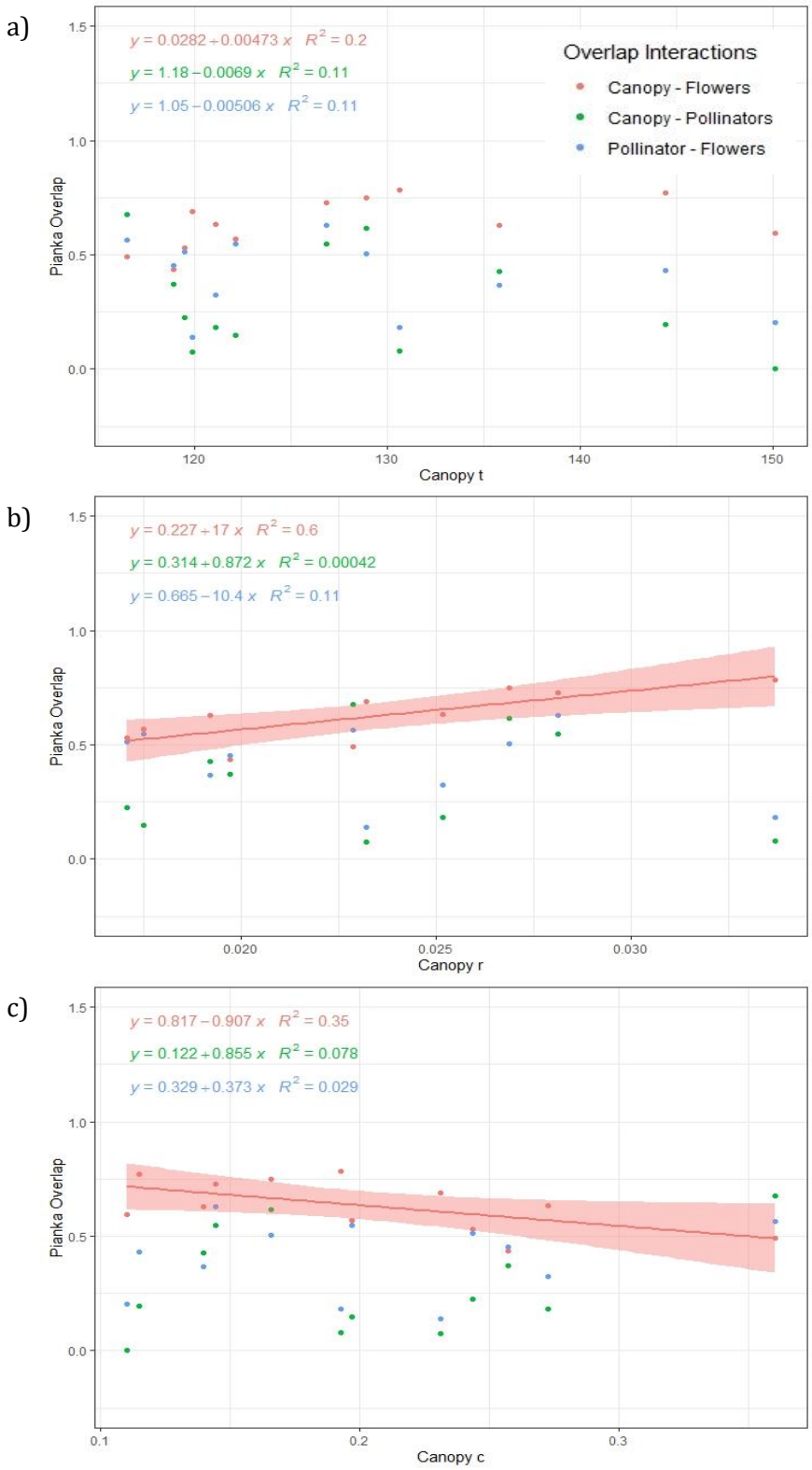


Figure 5. The relationship between the Pianka overlap between canopy, pollinators and flowering plant species and canopy closure parameters produced within the NLSTIMEDIST package a) Canopy t, b) Canopy r and c) Canopy c. Two significant relationships were found, canopy – flower overlap and canopy r, p = 0.0009, R^2 = 0.6 and canopy – flower overlap with canopy c, p = 0.0436, R^2 = 0.35.

4 Discussion

4.1 Pollinators' flower preference

The obtained pollinator preference results provide: (1) A baseline study of expected pollinator preferences within temperate forests within the UK, supporting potential future studies. (2) Evidence of specific flower preferences by pollinator groups, supporting previous literature within this field (de Camargo et al., 2019; Lunau & Maier, 1995; Shrestha et al., 2013). (3) Indicates that expected species interactions remained intact within the site.

Pollinator attracting traits within flowers, such as colour, scent and morphology, is thought to have developed due to selection pressures by insect pollinators (Streinzer et al., 2019; Van der Niet & Johnson, 2012; Weiss, 1997). However, among these traits, colour is the predominant factor in flower detection and discrimination for the majority of insect pollinators (de Camargo et al., 2019; Shrestha et al., 2013). Studies have observed that innate colour preferences and reward-based learning determine colour preference in most insect pollinators (Ings, Raine & Chittka, 2009; Lunau & Maier, 1995; Streinzer et al., 2019). The observed distributions within our site are consistent with specific flower preferences observed in the literature (Arnold, Savolainen & Chittka, 2009; Doering et al., 2012; Ings, Raine & Chittka, 2009; Sutherland, Sullivan & Poppy, 1999).

Bumblebee groups indicated a strong preference for *H. non-scripta*. This finding is consistent with described visitation preferences within other UK woodlands, indicating queen bumblebees as the predominant pollinators of *H. non-scripta* (Corbet & Tiley, 1999). Bumblebee preference towards *H. non-scripta* is likely due to their well-

documented preference towards the UV-blue spectrum of flowers (Chittka et al., 2004; Ings, Raine & Chittka, 2009; Raine et al., 2006). This strong innate preference towards blue flowers by bumblebees was observed even when blue flowers were less rewarding, suggesting that innate choices are a stronger determining factor in colour choice than learnt behaviour (Ings, Raine & Chittka, 2009).

The bee group showed little to no preference towards any of the plots' flowering species, but rather indicated a more uniform preference across all flowering species, suggesting them to be a more generalist group. This finding is consistent with current literature, bee species have been shown to have a range of preferences, from the blue-green spectrum (Arnold, Savolainen & Chittka, 2009; Rao & Ostroverkhova, 2015) and also towards white – yellow flowers (Leleji, 1973) have also been observed. The polylectic characteristics observed across populations, both within this study and previous literature, is likely to be due to high levels of bee diversity, ultimately displayed as a broader range of preferences (Rao & Ostroverkhova, 2015). Bee species have also been shown, in conjunction with innate behaviour, to use reward-based learnt behaviour. The use of reward-based behaviour allows bees to quickly learn to associate flower colours with the highest reward flowers, giving them a distinct advantage over pollinators which rely predominantly on innate colour preference (Ings, Raine & Chittka, 2009).

The beetles' group, which was predominantly observed to be pollen beetles throughout the sampling, showed a very strong preference towards *E. amygdaloides*. Strong pollination by pollen beetles on *E. amygdaloides* has been observed previously (Marshall, 2014), likely due to strong colour preference towards yellow flowers (Doering et al., 2012).

Hoverflies indicated a preference towards *F. verna* and *E. amygdaloides*, both of which have yellow flowers, to which hoverflies are strongly attracted (Primante & Dötterl, 2010; Sajjad & Saeed, 2010; Sutherland, Sullivan & Poppy, 1999). Flower preference in hoverflies' has also been shown to be driven by olfactory cues (Primante & Dötterl, 2010). The fly group indicated a strong preference for *H. non-scripta*; however, no literature was found to support the observed preference. Observing other pollinator groups, this is likely to be due to a combination of colour and olfactory cues (de Camargo et al., 2019; Primante & Dötterl, 2010; Shrestha et al., 2013). Although specific flower preferences were seen within most pollinator groups, the majority of pollinators were also shown to visit other flower species within the site (figure 2a). These findings support previous literature that suggests that most pollinator groups are generalist species (Bartomeus et al., 2011; Rafferty & Ives, 2011).

The consistencies between the observed data and previous literature suggest that the phenological interactions between the pollinator groups and plant species are still intact, supporting evidence for generalist species shifting phenologies at similar rates (Bartomeus et al., 2011; Rafferty & Ives, 2011). Despite the majority of pollinator groups being generalists, more specialised pollinators may be more vulnerable to mismatching events if phenological rates start to shift at differing rates in the future (Memmott et al., 2007). Previous literature within UK woodlands has shown queen bumblebees to be the major pollinator for *H. non- scripta* (Corbet & Tiley, 1999). This is potentially a cause for concern due to previous literature indicating long term mismatching of queen bumblebees within forest habitats (Kudo & Ida, 2013; Kudo et al., 2004). However, within

these cases, ephemeral flower species with very short flower periods were studied (Kudo & Ida, 2013; Kudo et al., 2004). Short flowering periods are known to be a major factor in increasing the chances of mismatching (McKinney et al., 2012; Miller-Rushing et al., 2010); thus, mismatching is unlikely to occur in between bumblebees and *H. non-scripta* due to longer flowering period. Despite this, further monitoring of more specialised interactions within forest habitats in the UK is advised, as sudden increases in temperatures are likely to cause variable responses between species interactions (Jentsch et al., 2009).

4.2 Canopy phenology

The phenological modelling of the canopy within this study was predominantly used to view its effect on understory relationships. Although clear variation within the modelled data and between the individual plots can be observed (Figures 4a, 4b), no significant differences were seen when comparing inter-species variation of canopy parameters. The findings from this study are not consistent with previous literature within this field (Chuine, Cambon & Comtois, 2000; Cole & Sheldon, 2017; Vitasse et al., 2009), the majority of which indicated significant variation between and within canopy species. The observed results within the present study are likely due to the low sample size of just 15 plots. Denéchère et al. (2019) suggested that a minimum of 28 individual trees is a sufficient sample size to determine phenological differences between individuals. Phenological rank has been described in the past to classify trees into distinct phenological categories: early, average and late trees (Chesnoiu et al., 2009; Delpierre et al., 2017; Denéchère et al., 2019). Despite a few fringe trees displaying early or late

phenologies, the vast majority of canopy trees are ranked within the average category, displaying little variation within their phenologies (Chesnoiu et al., 2009). Due to this study's sample size, very low numbers of these fringe trees would be expected, suggesting why no inter-species variation was observed. Despite being statistically insignificant, potential trends can be observed within the data, showing that *Q. robur* had the highest canopy variability and overall phenological characteristics than other canopy species. The phenological plasticity observed with *Q. robur* is consistent with previous literature within woodlands in the UK (Cole & Sheldon, 2017). *Quercus robur* had the largest range of phenological characteristics as compared to all other species. Suggesting that phenology of *Q. robur* has the highest sensitivity to temperature cues of any of the studied species.

4.3 Relationship between canopy, understory flowers and pollinator species

The previous indication of synchrony between plants and pollinators (Figure 3) was supported by the Pianka overlap indices (Table 3). These indicated all overlap values to be either as expected or higher than expected, in the case of plots R2 and R7. This study's observed results indicate simultaneous shifts within phenologies of generalist understory species, supporting previous literature (Bartomeus *et al.*, 2011; Hegland *et al.*, 2009; Rafferty & Ives, 2011). This would suggest that phenologies of canopy species had little to no effect on understory interactions. The resulting patterns are likely to be due to shared temperature responses which govern phenological timing (Bartomeus *et al.*, 2011; Hegland *et al.*, 2009).

When comparing the Pianka overlap values to the canopy closure parameters, a slight

positive relationship was seen between canopy closure rate (canopy r) and the overlap between the canopy and flowering plants (Figure 5). This relationship suggests that as the maximum canopy growth rate increases, overlap between the two groups would also increase. Although this study indicated no significant reduction in plant-pollinator overlap due to increased canopy closure rates, there is potential for a detrimental effect to occur within early flowering species if canopy closure rate increases in the future. With an increased frequency of early spring heatwave events (IPCC, 2007), canopy closure rates are likely to advance in the coming years (Cole & Sheldon, 2017). An advancement in canopy closure rate will reduce light availability on the canopy floor for early spring flowering species. Reduction in light availability has been shown to cause delays within flowering periods (Hou *et al.*), which in turn has the potential to cause a reduction in the synchrony between understory plant species and their pollinators. A lack of phenological synchrony would likely lead to a reduction in seed set and food resources for pollinator species, ultimately leading to reductions in population abundance (Kudo & Ida, 2013; Kudo *et al.*, 2004).

In addition to the potential reduction in understory flowering, increased rates of canopy closure could also directly affect pollinator groups. Most pollinators have been shown to prefer more open areas and tend to spread out from forest habitats in order to forage for floral resources (Bailey *et al.*, 2014; Watson, Wolf & Ascher, 2011). This is likely due to considerably better thermoregulation whilst in open areas (Cao *et al.*, 2017; Herrera, 1997; Kilkenny & Galloway, 2008). Therefore, an extension of the canopy period during early spring could reduce the pollinator presence within this time.

A slight negative relationship between canopy rate concentration (canopy c) and the

overlap between the canopy and flowering species was also observed. This relationship was unexpected, as a similar result to canopy r would be expected. However, despite the significant relationship, the R^2 value was relatively low (Figure 5c), suggesting a weak relationship between the two variables. Further studies are needed in order to understand this relationship fully. All other interactions between the canopy parameters and overlap indices were seen to be insignificant (Figures 5a, 5b, 5c). The lack of significance within these interactions is most likely due to the low sample sizes within the project.

While not conclusive, overall patterns suggest that the interactions between understory species are still intact within this woodland, suggesting that phenologies are shifting at similar rates. These findings support previous literature, which indicates generalist species to simultaneously shift phenologies as a shared response to the environmental cues that govern phenology (Bartomeus *et al.*, 2011; Hegland *et al.*, 2009; Rafferty & Ives, 2011). However, further research is needed to confirm this over a longer period.

4.4 Evaluation and revision of the methodology

The abundance of non-significant results within this study is likely due to the low sample sizes of primarily canopy plots and pollinator abundance. In order to assess the differences in canopy phenologies, Denéchère et al. (2019) suggested a minimum sample size of 28 individual plots; this would allow for variation within and between canopy species to be observed. The low number of plots within this study was due to a lack of time and resources. Despite the low sample size, the analysis of canopy closure using hemispherical phone photography developed by Smith and Ramsay (2018), in

conjunction with phenological modelling using the R package NLSTIMEDIST (Steer, Ramsay & Franco, 2019), provided extremely useful information on how canopies closed within the site. The usage of these two techniques proved to be useful tools in predicting phenological interactions. Low abundance in pollinator abundance throughout the sample period was also an issue within this project. The aforementioned increase in sampling plots is likely to increase the overall pollinator abundance within the sampling period. On top of increasing the number of plots, increasing the plot area is would also increase overall pollinator abundance, i.e. using a 3m x 3m quadrat instead of 2m x2m quadrat. With larger sample sizes, NLSTIMEDIST (Steer, Ramsay & Franco, 2019) could also be utilised in assessing the phenological characteristics of understory plant and pollinator species. Thus, allowing for in-depth assessment between the relationships of canopy closure and understory plants and pollinators by allowing for comparisons to be made between the r, c and t parameters produced.

As the phenologies of both canopy and understory species are governed by temperature (Bartomeus et al., 2011; Cole & Sheldon, 2017; Memmott et al., 2007), it would be beneficial to take air temperature readings throughout the sampling period. Recording temperature throughout the sampling period would help determine how different groups react to certain changes in temperatures.

5 Conclusion

This study used a novel combination of methods which allow for in-depth analysis of the effects of canopy closure on understory trophic systems; these methods need to be developed in future studies and in order to gather sufficiently large datasets.

Despite previous literature indicating phenological mismatching in forest habitats (Kudo & Ida, 2013; Kudo et al., 2004), this study indicated no mismatching within the study site. These findings suggest that understory plants and their pollinators are shifting phenologies at a similar rate alongside advancements within the canopy. However, it does suggest that an increased rate of canopy closure may result in a larger overlap between the canopy and early blooming understory flowering species, resulting in higher levels of shading in the early spring. This trend has the potential to lead to adverse effects on understory trophic systems in the future. The observed trends are likely to be more prominent in the presence of extreme weather events, such as heatwaves in early spring (Jentsch et al., 2009). The observed climatic warming has been shown to increase the frequency of these events (IPCC, 2007), which is a potential cause for concern.

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7 Appendices

Appendix 1. Maximum canopy % per plot estimate parameters from NLSTIMEDIST in R, with standard errors in brackets. *** $p < 0.001$, . $p > 0.1$, statistical moments for each predicted model. The proportion of variation explained by the model (R^2) and statistical moments for each modelled plot.

Plot	Canopy max %	r (SE)	sig.	c(SE)	sig.	t(SE)	sig.	R^2	M	SD	Skew	Kurtosis	Entropy
H1	84.19	0.028 (0.003063)	***	0.1446 (0.008721)	***	126.8 (1.515)	***	1.00	117.95	13.83	3.10	32.55	5.54
H2	82.68	0.023 (0.001243)	***	0.2313 (0.01296)	***	119.9 (0.5869)	***	1.00	117.53	16.82	6.08	59.74	5.17
H3	78.14	0.01751 (0.001472)	***	0.1968 (0.02464)	***	122.1 (1.238)	***	0.98	124.38	28.61	5.09	37.93	5.71
H4	74.39	0.06882 (0.03565)	.	0.1149 (0.007525)	***	144.4 (6.27)	***	1.00	121.97	11.18	-0.84	1.68	5.46
H5	73.72	0.06553 (0.03673)	.	0.1104 (0.007825)	***	150.1 (7.074)	***	1.00	126.87	11.65	-0.84	1.67	5.52
H6	79.24	0.02096 (0.001381)	***	0.1693 (0.009158)	***	133 (0.8986)	***	1.00	129.18	19.53	5.37	50.42	5.58
H7	74.27	0.01921 (0.001559)	***	0.1399 (0.009067)	***	135.8 (1.328)	***	0.99	132.06	23.37	4.83	41.14	5.89
H8	75.89	0.02688 (0.003121)	***	0.166 (0.01165)	***	128.9 (1.443)	***	0.99	121.65	13.48	4.18	45.88	5.39
R1	68.83	0.01708 (0.000644)	***	0.2437 (0.01663)	***	119.5 (0.5003)	***	0.99	123.56	29.94	5.14	37.33	5.53
R2	84.66	0.01971 (0.001439)	***	0.2573 (0.02818)	***	118.9 (0.8472)	***	0.99	119.87	22.92	5.76	48.06	5.26
R3	78.72	0.02306 (0.002107)	***	0.1931 (0.01565)	***	125.9 (1.109)	***	0.99	122.06	16.82	5.62	55.88	5.36
R4	80.65	0.03369 (0.006609)	***	0.1925 (0.01514)	***	130.6 (1.863)	***	1.00	122.13	9.19	2.59	36.40	5.03
R5	75.83	0.0226 (0.00404)	***	0.12084 (0.01375)	***	134.75351 (3.12827)	***	0.98	126.74	19.23	3.68	33.29	5.91
R6	82.66	0.02517 (0.001313)	***	0.2724 (0.01355)	***	121.1 (0.4595)	***	1.00	118.24	13.69	6.83	76.49	4.86
R7	83.57	0.02288 (0.001429)	***	0.3601 (0.03181)	***	116.5 (0.5258)	***	0.99	116.32	16.77	6.90	68.62	4.66

Appendix 2. Additional sampling carried out throughout the whole woodland site, showing canopy species, canopy cover percentage and understory species. Plymbridge woods, Devon, UK.

Plot_name	Canopy species	Canopy cover %	Understory species
E1	*A. pseudoplatanus, F.sylvatica*	82.32	*H.non-scripta*
E2	*F.sylvatica*	78.34	*H.non-scripta*
E3	*Quercus sp.*	73.28	*H.non-scripta*
E4	*Quercus sp.*	77.37	*H.non-scripta*
E5	*Quercus sp., A. pseudoplatanus*	73.93	Bare
E6	*Quercus sp., A. pseudoplatanus*	73.43	Bare
E7	*Quercus sp.*	71.26	*H.non-scripta*
E8	*Quercus sp., F.sylvatica*	70.89	*H.non-scripta, A.nemorosa*
E9	*Quercus sp., A. pseudoplatanus, F.sylvatica*	78.93	*H.non-scripta, A.nemorosa*
E10	*Quercus sp., F.sylvatica*	73.03	*H.non-scripta*
E11	*Quercus sp., F.sylvatica, Ilex sp.*	71.37	*H.non-scripta*
E12	*Quercus sp., F.sylvatica*	73.72	*H.non-scripta*
E13	*Quercus sp., F.sylvatica*	72.61	*H.non-scripta*
E14	*Quercus sp.*	73.92	Bare
E15	*Quercus sp., Ilex sp.*	73.27	Bare
E16	*Quercus sp., F.excelsior*	80.71	Bare
E17	*Quercus sp., F.sylvatica*	75.61	*A.nemorosa, F.verna*
E18	*C.sativa, A. pseudoplatanus*	69.21	*H.non-scripta, G.robertianum,F.verna*
E19	*C.sativa, A. pseudoplatanus*	69.73	*H.non-scripta,E.amygdaloides*
E20	*A. pseudoplatanus, F.excelsior*	65.27	*H.non-scripta,E.amygdaloides*
E21	*A. pseudoplatanus, F.excelsior*	67.06	Bare
E22	*C.sativa, F.sylvatica*	71.51	*H.non-scripta*
E23	*Quercus sp., F.sylvatica*	74.16	*H.non-scripta, A.nemorosa*
E24	*Quercus sp., F.sylvatica, C.sativa*	75.61	*H.non-scripta*
E25	*Quercus sp., A. pseudoplatanus*	69.97	*H.non-scripta*
E26	*Quercus sp., F.sylvatica, C.sativa*	71.32	*H.non-scripta*
E27	*Quercus sp.*	70.35	*H.non-scripta*
E28	*Quercus sp.*	73.32	Bare
E29	*Quercus sp.*	69.06	Bare
E30	*Quercus sp.*	68.97	Bare
E31	*F.sylvatica*	75.24	Bare
E32	*F.sylvatica*	73.15	*H.non-scripta*
E33	*F.sylvatica*	75.44	*A.nemorosa*
E34	*Quercus sp., F.sylvatica*	81.66	Bare
E35	*Quercus sp., F.sylvatica*	79.85	*A.nemorosa*
E36	*F.sylvatica*	82.33	Bare
E37	*F.sylvatica*	80.41	Bare
E38	*Quercus sp., F.sylvatica*	80.04	Bare
E39	*A. pseudoplatanus, F.sylvatica*	81.32	*H.non-scripta, A.ursinum, F.verna*