Among tree and habitat differences in the timing and abundance of spring caterpillars

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Abstract

1. Climate warming is causing many spring biological events to advance in timing and where the phenology of resource and consumer advance at different rates this can result in trophic asynchrony. While the temperate study system of deciduous tree – caterpillar – insectivorous passerine has been widely studied, little work has examined whether phenological distribution of caterpillars differ among tree taxa and habitats. If such differences exist they have the potential to underpin spatial variation in the trophic asynchrony in this food web.
2. Our first aim was to identify the effects of host tree versus local woodland composition on caterpillar abundance. Following this, the main aim was to examine the effects of tree taxon on the phenological distribution of caterpillar abundance and the trend in mass of individuals, with guild biomass the product of these two metrics.

3. We collected data on caterpillar abundance and mass throughout spring from 44 sites with varied woodland compositions across seven years. First, we analysed differences in caterpillar abundance among tree taxa and identified any additional effect of local woodland composition. Second, we explored differences in the phenological distribution of caterpillars among tree taxa, focusing on caterpillar i) abundance, ii) mass and iii) biomass.
4. We found substantial variation in the caterpillar abundance supported among tree taxa, including evidence that the density of oak foliage within a woodland can increase the abundance of caterpillars found on other trees. Some aspects of the phenological distribution of caterpillars differed among tree taxa, in particular the height of the peak, highest on oak. We show minimal, but significant, variation in timing and duration, whereas we did not find much evidence for variation in the shape of the phenological distribution or mass gain of caterpillars.
5. We show that the abundance and phenological distribution of caterpillars does differ between deciduous trees and that oak is distinct from most other common taxa. Woodland composition is likely to influence the site-level trend in caterpillar abundance and biomass; contributing to spatial variation in an important component of the woodland ecosystem and an ephemeral resource relied upon by many consumers species.

Introduction

Climate warming is driving species across multiple taxa and trophic levels to advance phenological traits (Cohen, Lajeunesse, & Rohr, 2018; Parmesan, 2006; Thackeray et al., 2016). The shifts in timing vary between species and trophic levels, with secondary consumers generally responding at a slower rate than producers and primary consumers (Thackeray et al., 2016, 2010). When a consumer is reliant upon an ephemeral resource with which it has become asynchronous this can be detrimental to fitness (Cushing, 1990; Durant, Hjermann, Ottersen, & Stenseth, 2007; Visser & Both, 2005) and the consumer is described as being ‘mismatched’ (Samplonius et al., 2020).

The temperate terrestrial tri-trophic food chain of deciduous tree – caterpillars – cavity nesting insectivorous passerine is perhaps the system in which asynchrony has been studied most (Both, van Asch, Bijlsma, van den Burg, & Visser, 2009; Charmantier et al., 2008; Shutt, Cabello, et al., 2019; Thomas, Blondel, Perret, Lambrechts, & Speakman, 2001; Visser, Holleman, & Gienapp, 2006). This system includes ephemeral resources at two trophic levels making it highly susceptible to trophic mismatch; young palatable leaves which the caterpillars require to grow to pupation (Feeny, 1970; Forkner, Marquis, Lill, & Corff, 2008; van Asch & Visser, 2007), and then the caterpillars are a key food source for many breeding birds (Bańbura, Blondel, de Wilde-Lambrechts, Galan, & Maistre, 1994; Betts, 1955; Sanz, 1998; Wilkin, King, & Sheldon, 2009). The temporally peaked distribution of caterpillar abundance/biomass is central to this woodland system (Gibb, 1950; Southwood, Wint, Kennedy, & Greenwood, 2004), with potential implications for breeding consumer species (Buse, Dury, Woodburn, Perrins, & Good, 1999; Reed, Jenouvrier, & Visser, 2013; Visser et al.,

2006) and herbivory damage to deciduous trees, possibly influencing tree growth, survival and forest productivity (Kulman, 1971; Marquis & Whelan, 1994; Whitham, Maschinski, Larson, & Paige, 1991; Whittaker & Warrington, 1985). If the phenological distribution differs among individual trees, species, areas within a woodland and more broadly between woodlands, this has the potential to result in a stabilising spatial portfolio effect (Schindler, Armstrong, & Reed, 2015) and buffering of the metapopulation from the negative effects of asynchrony, as some caterpillar consumer (e.g., birds) and resource (i.e., trees) populations are matched while others are mismatched. Extensions of the match-mismatch hypothesis recognise that if availability of the resource is important for consumer fitness then the height and width of the resource peak may matter in addition to its timing (Miller-Rushing et al. 2010).

The majority of studies within the woodland tri-trophic study system are focused on oak-dominated woodlands or mainly collect data about caterpillar abundance or biomass in relation to oak trees (Burgess et al., 2018; Hinks et al., 2015; Varley, Gradwell, & Hassell, 1974; Visser et al., 2006). Oak (*Quercus*) trees and woodlands are thought to be preferred by some breeding passerines, such as tits (Perrins, 1979), and are described as good resource for the development of caterpillars, at least for the winter moth, *Operophtera brumata*, although statistical comparison among tree taxa has been low powered (Feeny, 1970; Wint, 1983). Oak-dominated woodland, however, is not representative of the habitat present across all deciduous woodlands in these temperate environments. For instance, in Great Britain, although oak trees are the second most common broadleaf tree taxon, they make up just 16% of the area covered by broadleaf woodlands (Stagg & Ward, 2019), and many lepidopteran and passerine species in this system will feed, forage and nest in a variety of woodland habitats (Allan, 1979; Hagemeijer & Blair, 1997; Perrins, 1979; Skinner, 2009). The extent to which inferences about the caterpillar phenological distribution made in relation to oak can be generalised to other habitats is largely unknown (Shutt, Burgess, et al., 2019). Therefore, it is important to consider how the caterpillar peak varies among woodlands with different habitat compositions when aiming to understand the potential for trophic asynchrony across heterogenous temperate deciduous woodlands (Burger et al., 2012).

There are three main components that describe the phenological distribution of the spring caterpillar peak; peak date (timing), height (maximum abundance/biomass) and width (duration) (Shutt, Burgess, & Phillimore, 2019). Tree composition of woodland habitats may be an important determinant of spatial variation in the phenological distribution of the caterpillar peak, however relatively few studies have explored this topic. Most relevant work has focused on differences between deciduous, mixed and coniferous woodlands (Burger et al., 2012; Mägi et al., 2009; van Balen, 1973; Veen et al., 2010), with minimal focus on the differences among deciduous woodland compositions and specific tree taxa. Mägi et al. (2009) suggested that the phenological distribution of caterpillars in mixed birch and alder woodland in 2004 was more similar to that of coniferous woodlands than oak; characterised as having a low and wide peak, compared to the high but narrow peak in oak woodlands (van Balen, 1973; Veen et al., 2010; Visser et al., 2006). Birch and coniferous mixed woodlands were also found to host lower abundances of caterpillars (Burger et al., 2012). However, in a spatially replicated study of caterpillars on individual trees in Scotland, birch trees were found to host more caterpillars than many other deciduous species (Shutt, Burgess, & Phillimore, 2019). The same study also found that the height of the caterpillar peak differs among four deciduous tree taxa, with the peak on oak trees reaching much greater maximum abundances and some evidence of increased peak heights on willow trees as well (Shutt, Burgess, et al., 2019). Oak may not support the greatest abundance of all deciduous trees however; as in Białowieża Forest, Poland hornbeams, maples and limes were found to receive more herbivory damage than oak (Wesołowski & Rowiński, 2006).

There are a number of ways that woodland tree composition may influence the height, width and timing of the peak in caterpillar abundance and biomass. Tree species differ in leaf nutritional quality (Schultz, Nothnagle, & Baldwin, 1982; Yanar, Gömeç, Topkara, Solmaz, & Demir, 2017), which can affect Lepidopteran fecundity (Awmack & Leather, 2002), survival (Wint, 1983; Yanar et al., 2017) and growth (Loader & Damman, 1991). Preferential laying by females on specific hosts (Kakimoto, Fujisaki, & Miyatake, 2003; Thompson & Pellmyr, 1991), or dispersal by larvae (Forkner et al., 2008; van Asch & Visser, 2007) may also amplify differences in abundance among tree taxa, impacting biomass as the product of the abundance and size of caterpillars in the guild. Studies of spring caterpillars report differences in abundance and biomass between deciduous tree species, with oak and willow having the highest peaks (Shutt, Burgess, et al., 2019; Veen et al., 2010), however both studies had quite low power to detect among species differences and the sensitivity of biomass to changes in mass versus abundance is yet to be explored.

The width or duration of the peak may also vary through multiple mechanisms. For example, the diversity of the lepidopteran guild differs between tree species (Kennedy & Southwood, 1984), which may impact the peak width if lepidopteran species differ in their hatching phenology or growth rate. In addition, differences in nutritional quality or the phenology of the nutrition provided by different tree taxa (Kakimoto et al., 2003; Loader & Damman, 1991; Schultz et al., 1982) could generate among tree variation in the time caterpillars take to reach pupation. Finally the timing of peak abundance or biomass may vary among tree species as a result of differences in their leafing phenology (Murray, Cannell, & Smith, 1989; Roberts, Tansey, Smithers, & Phillimore, 2015). Such phenological differences among trees could select for adaptation of a caterpillar species' phenology or sort for caterpillar species that differ in their timing. However, the large variation in tree phenology within tree species (Cole & Sheldon, 2017; Murray et al., 1989), and even within individual trees, will reduce the strength of selection to coincide with the phenology of a particular tree species. Shutt, Burgess, et al., (2019) explored among tree species variation in peak timing in Scotland using three years of data with 6089 records of caterpillar presence/absence (575 caterpillars). They found no difference in peak timing between oak, willow, birch and sycamore, though credible intervals were broad, implying low power to detect a difference of a few days. Now with 7 years of data and 31215 samples we are able to analyse this topic using the abundance (rather than presence/absence) of caterpillars, providing more power to detect any differences.

In this study we use caterpillar data collected from 44 deciduous Scottish woodland sites that vary in their tree composition, to analyse tree and habitat-driven variations in the phenological distribution of caterpillar abundance and biomass throughout spring. First, we explore differences in the abundance of caterpillars supported by different tree taxa and identify any additional effect of differences in the local woodland density and composition. Second, we examine whether the phenological distribution of the caterpillar guild throughout spring differs among tree taxa for i) abundance and ii) mass, and how variation in each contributes to variation in their product iii) biomass. Throughout we compare each taxon to the average trend and to oak. Together this programme examines the capacity of woodland composition to provide a portfolio effect of herbivory pressure to trees, mismatch buffering for secondary consumers and tests the extent to which oak-dominated study systems are representative of other deciduous woodlands.

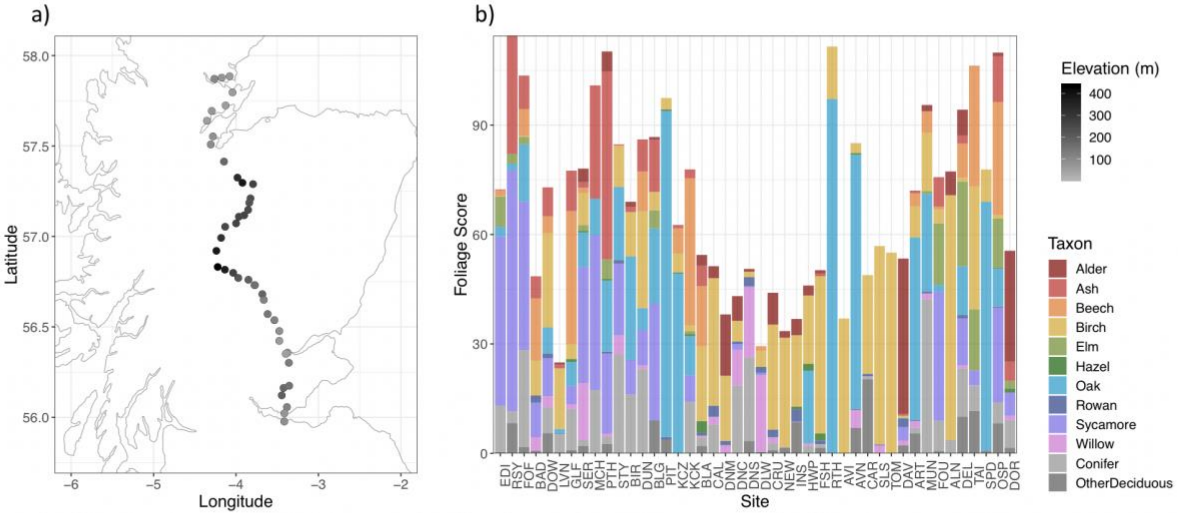

Figure 1: a) Map of site locations in Scotland, the darkness of the points indicates the site elevation and b) shows the woodland habitat composition at each site displayed as a foliage score that accounts for tree size, 1 unit of foliage score = 1 small tree (circumference at chest height 0.4-0.99m), sites are ordered by increasing latitude from left to right.

Methods

Study System

This study was carried out using 44 woodland sites along a 220 km transect between Edinburgh (55°980 N, 3°400 W) and Dornoch (57°890 N, 4°080 W) (Fig. 1a). This includes the 40 sites monitored between 2014-16 in Shutt, Bolton, Cabello, Burgess, & Phillimore (2018) with an additional four sites monitored from 2017 onwards. During spring 2020 the field season was restricted to the 22 most southern sites due to the Covid-19 pandemic. Woodland habitat composition has been surveyed at a 15m radius around each nest box installed at sites (n = 334 since 2017), including all trees with a trunk circumference of ≥40cm at chest height or a 'stand' with ≥6 branches within 20cm of each other at the base. Trees were identified to the genus level with the exception of some conifers, for full details of survey methods and site foliage score calculations see Shutt et al. (2018). The foliage scores for each tree taxon at each site are representative of the mean number of 'small' trees of each taxon within a circular area with a 15m radius (Fig. 1b).

Caterpillar Sampling

Caterpillar sampling followed the branch beating methodology described in Shutt, Burgess, & Phillimore (2019). A selection of trees at each site, representative of the site's woodland composition, are monitored for leafing phenology (Shutt, Cabello, et al., 2019); and those that had a branch of minimum length 1m and between 0.5-1.5m above the ground were also beaten. The tree taxa sampled include alder (*Alnus* sp.), ash (*Fraxinus* sp.), beech (*Fagus* sp.), birch (*Betula* sp.), elm (*Ulmus* sp.), hazel (*Corylus* sp.), oak (*Quercus* sp.), rowan (*Sorbus* sp.), sycamore (*Acer* sp.) and willow (*Salix* sp.). A branch, meeting the height and length criteria, was marked and beaten every four days to allow some recolonization between beatings. The trees sampled at each site were divided in two groups and each group was beaten alternately at two days intervals. The branch was held consistent between years unless damaged, broken or dead. The average number of trees sampled at each site in each year was 3, 6, 6, 14, 14, 15 and 14 respectively; with a total of 31215 beating samples recorded across the 7 years. Sampling began each year when 45% of the monitored trees across all sites had reached the 'first leaf' stage and continued until the end of the blue tit breeding season (Shutt, Burgess, et al., 2019); sampling periods extended between ordinal dates 120-166, 125-175, 130-173, 123-167, 129-172, 117-168 and 130-170 for 2014-20 respectively.

Branch beating was carried out using a clear plastic rubble sack measuring 76cm x 51cm. The bag was fully extended over the branch's foliage and closed with one hand at the maximum length, keeping the open end facing upwards. The bag was then beaten 30 times at a consistent impact and rate (roughly two per second) to dislodge any free-living invertebrates on the branch. After careful removal from the branch, all caterpillars (larvae of Lepidoptera (>90%), Hymenoptera, Diptera and Coleoptera; Shutt, Burgess, et al., 2019) with an estimated diameter of ≥1mm were counted and collected. We chose this threshold due to an assumption that the smallest caterpillars would be of minimal value to avian consumers, and as they are hard to see and collect, excluding them increases the consistency between samples and recorders. From 2017 onwards, the biomass of each sample was recorded to 0.01g using a Myweigh Triton T3R-500 Digital Scale. We found that some samples were of insufficient mass (< 0.02g) to show a read on the balance.

Statistical analysis

All analyses used Bayesian generalized linear mixed models (GLMM) in the MCMCglmm package (Hadfield, 2010) in R version 3.5.3 (R Core Team, 2019) and we present full models (Tables S1-5). Poisson GLMMs were used for all models looking at variations in caterpillar abundance and 1000 *a posteriori* simulations under each model were used to confirm that the data were not zero-inflated as compared with model expectation. Gaussian GLMMs were used to model caterpillar mass. Fixed effects parameters and random effects are consistent with a significant effect where the 95% credible intervals (CIs) do not overlap zero. As variances are bounded at zero we infer a random term to be significant where the lower credible interval is removed from 0. We used the mean of the posterior distribution when calculating parameter estimates based on the fixed effects, and the median when random effects were included. All models were run with sufficient iterations to ensure an effective sample size of >1000 for each focal parameter and convergence was assessed by visual inspection of the trace plots. Parameter-expanded priors were used for all models, with the residual variance treated as inverse-wishart with nu = 0.002. Default flat priors were used for the fixed effects.

Some structural random terms were included in all models (Table 1). These were site, year (as a factor), each site in each year (site-year), and day at each site in each year (day-site-year) to allow for spatio-temporal differences in caterpillar abundance and mass. We also included the tree ID and recorder of each beating sample. All results comparing caterpillar abundance, mass or biomass among tree taxa are presented as deviations from (i) the fixed effect prediction, which represents an average tree taxon, and (ii) the prediction for oak, described fully in Supplementary Information.

Table 1: Model compositions. Date refers to ordinal date which was scaled (mean = 146.77, SD =14.04), year was included as a factor and woodland composition refers to multi-membership component explained in the text. Int = intercept, abund = abundance, VCV = variances and covariances.

Model	Abundance decomposition (Table S1)	Habitat abundance (Table S2)	Abundance phenology model (Table S3)	Mass phenology model (Table S4)
Motivation	Decomposition of variance in abundance	Differences in the abundance of caterpillars among tree taxa and effect of woodland density and composition	Differences in phenological distribution of caterpillar abundance among tree taxa	Differences in phenological distribution of caterpillar mass among tree taxa
Response	Caterpillar abundance	Caterpillar abundance	Caterpillar abundance	log(Mean mass per caterpillar)
Fixed effects	Date Date^2	Total foliage score	Date Date^2	Date Date^2
Random terms	Site Tree taxa Tree ID Site-year Day-site-year Year Year-day Recorder	Tree taxa Woodland-composition Site Year Site-year Day-site-year Tree ID Recorder	Int, Date and Date^2 VCV across Tree taxa Int, Date and Date^2 VCV across Site Int, Date and Date^2 VCV across Year Site-year Day-site-year Tree ID Recorder	Int and Date VCV across Tree taxa Int and Date VCV across Site Year Site-year Sqrt(1/abund) VCV across units Day-site-year TreeID Recorder
Family	Poisson	Poisson	Poisson	Censored-Gaussian
Iterations (thin)	2500000 (500)	4500000 (800)	1050000 (100)	5500000 (500)
Burnin	50000	500000	50000	500000
Sample Size	4900	5000	10000	10000

Abundance

Variance decomposition of caterpillar abundance

We decomposed the variance in caterpillar abundance throughout spring to gauge to the relative contributions of spatial and temporal factors to the total variance observed in our data (abundance decomposition model, Table 1). The number of caterpillars recorded in each beating sample was the response variable with date and date^2 included in the fixed effects to account for the peaked temporal distribution. Date refers to ordinal date and was scaled in all models (prior to scaling: mean = 146.77, SD = 14.04). The variance explained by date (x) and date^2 (y) was calculated using the quadratic equation:

$$\text{Equation 1:} \qquad [\beta_x \quad \beta_y] * \begin{bmatrix} \sigma_x^2 & \sigma_{x,y} \\ \sigma_{x,y} & \sigma_y^2 \end{bmatrix} * [\beta_x \quad \beta_y]^T$$

The random terms included each day in each year (day-year) and the tree taxon sampled (tree taxa) in addition to the consistent terms listed above. We calculated the mean percentage of variance on the log scale that is attributable to the date and date^2 fixed effects and each random term across the posterior distribution.

Habitat variation in caterpillar abundance

We assessed differences in the abundance of caterpillars supported by different tree taxa, the influence of local foliage density and whether the amount of foliage of each tree taxon contributing to local woodland composition, from the habitat surveys, has any additional effect (habitat abundance model, Table 1). To calculate the site-level foliage scores for non-focal tree taxa, we combined all of the coniferous tree taxa into a ‘conifer’ group and all deciduous tree taxa, that are less common and not sampled in the branch beating, were grouped as ‘other deciduous’. Composition foliage scores for each tree taxon at each site were globally mean centred. The ‘total’ foliage score for each site was then calculated by summing the mean centred foliage scores for each taxon across each site, meaning that the total foliage scores among sites were distributed around a mean of zero. The site level total foliage score was included as a fixed effect to account for any effect of general site foliage density on abundance. We included tree taxon and the woodland composition foliage scores as focal random terms. We assessed the difference in abundance supported by different tree taxa using the posterior distributions of the tree taxon (sampled) random effects. The woodland composition component used a multi-membership approach, whereby the random effect for each tree taxon corresponded to the deviations from the fixed effect slope for total foliage score. The taxon-specific composition slopes intersect at the average amount of any tree taxon present at any site, and random effects were drawn from a distribution with a single variance estimated by the model. This allowed us to test for an effect of the amount of foliage of each tree taxon at a site, regardless of which tree taxon the sample was collected from.

Phenological Distributions

Abundance

To quantify differences in the phenological distribution of caterpillar abundance throughout spring on different tree taxa we allowed each taxon to have a distinct temporal trend over the course of the spring (abundance phenology model, Table 1). The fixed effects included date and date^2, allowing for a peaked trend over time. The focal random terms were the tree taxa random intercepts and slopes for date and date^2. In addition to the core random terms, we also included date and date^2 random slopes for site and year to account for spatio-temporal differences in the peak timing and shape. As adjustments to date and date^2 coefficients both influence the resulting height and timing of the peak, interpretation of the effects on the phenology of abundance is best understood through calculations of the model predictions for the specific metrics of interest. We used the posterior distributions for the fixed effects and the random effects (intercept, date and date^2) for each tree taxon to quantify the timing (peak date) of the maximum peak in abundance, the maximum abundance reached (height), and the width of the peak relative to height (calculated at half the height of the peak)- referred to as peak width- as well as the relative width of the peak among tree taxa, calculated at a consistent height (set at roughly half the height of the lowest curve)- referred to as peak duration. We primarily present peak width as an independent parameter governing the peak shape, but also discuss peak duration (which includes an effect of peak height) due to its relevance to phenological synchrony of consumers.

We assessed the adequacy of the quadratic function in describing the shape of the phenological distribution of caterpillar abundance by also modelling the peak including a cubic date term; allowing an asymmetrical trend over time (Table S5). Details of the analysis can be found in Supplementary Information.

Mass

To obtain the mean mass per caterpillar in a sample we divided the mass for each sample by the number of caterpillars weighed. We included a weighting variable ($\sqrt{1/\text{abundance}}$) to account for the number of caterpillars contributing towards each mass measurement. Due to restrictions in measuring small masses in the field, we have uncertainty in the accuracy of measurements ≤0.02g. All samples meeting this criterion were interval censored to a lower bound of 0.001g, the minimum mass viable for a caterpillar sampled in-line with the methodology (J. C. Weir, unpublished data), and an upper bound of 0.02g divided by the number of caterpillars. The mass measurements were log transformed and modelled as interval-censored Gaussian.

The mass model included date and date^2 in the fixed effects, allowing a curved trend if appropriate (mass phenology model, Table 1). The focal random terms were the tree taxa random intercepts and date slope. In addition to the core random terms, we included a date random slope for sites, allowing for spatial variation. Year was solely included as a random intercept to improve model convergence as there were just 4 years of mass data. To assess differences in the ultimate mass of a caterpillar on different tree taxa during our sampling period, the posterior distributions of the fixed effects and tree taxa random intercepts and slopes were used to calculate the predicted mass at day 168 (16th June), the latest date at which a caterpillar has been sampled from all tree taxa.

Biomass

We combined the model outputs for the phenological distribution of caterpillar abundance and mass to calculate the distribution of biomass. As abundance and mass were both estimated on the log scale, equations describing the change in caterpillar abundance and mass over time, for each tree taxon and the fixed effect mean trend, can be summed across each iteration of the posterior distribution to convert to a temporal prediction of biomass. Ideally this would be analysed using a bivariate model to allow for covariance between abundance and mass across random terms, however due to the interval censoring required for the mass data this could not be implemented. The coefficients for biomass have been used to calculate the same peak metrics as discussed for the abundance results.

Results

Within our dataset, 11% of branch beating yielded at least one caterpillar. Where a caterpillar was present, in 68% of cases there was just 1 and in 16% there were 2, with a maximum abundance of 107, recorded during an outbreak at one of our sites during 2019.

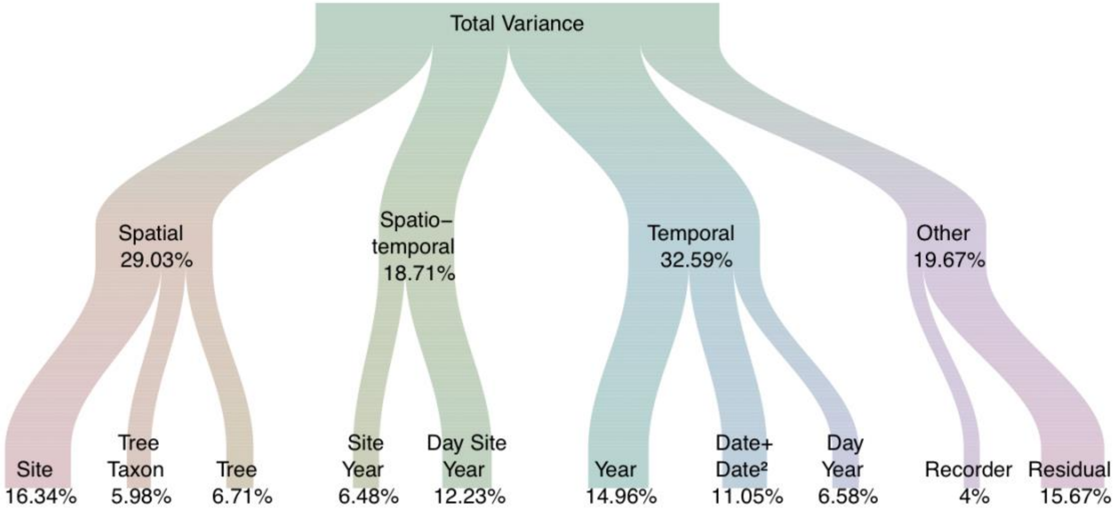

Figure 2: Riverplot depicting the percentage variance composition of caterpillar abundance estimated from terms in a Poisson GLMM (Table S1). All variables were included as random terms except for Date+Date^2 which were continuous variables included as fixed effects accounting for the peaked shape of the phenological distribution.

Abundance

Caterpillar abundance variance decomposition

The posterior distributions of variance (on log scale) for all terms included in the abundance decomposition model (Table 1, S1), including the calculated variance for the fixed effects, were removed from zero, indicating that each variable contributes to the variance in caterpillar abundance observed. The environmental components (all excluding 'Other') explained 80.33% (CIs: 73.76 - 86.78%) of the variance, with temporal and spatial components explaining similar amounts of 32.59% (CIs: 20.21 - 49.42%) and 29.03% (CIs: 18.02 - 41.10%) respectively (Fig. 2). The tree taxon sampled explained 5.98% (CIs: 1.24 - 14.08%) of the variance (Fig. 2).

Habitat variations in caterpillar abundance

We estimated substantial variance in the abundance of caterpillars sampled among tree taxa in the habitat abundance model (Table S2). Alder and ash support significantly fewer caterpillars than average and birch, oak and willow support more (Fig. 3a). Alder hosts 0.64 (CIs: 0.41 - 0.95) times as many caterpillars as an average taxon, ash hosts 0.52 (CIs: 0.32 - 0.81), birch hosts 1.43 (CIs: 1.01 - 2.03), oak hosts 1.53 (CIs: 1.09 - 2.22) and willow hosts 1.65 (CIs: 1.10 - 2.46). We found that alder, ash, beech, elm, rowan and sycamore all support significantly fewer caterpillars than oak (Fig. S1).

We found no relationship between the total habitat foliage score and the number of caterpillars recorded and the posterior for the variance in the slope predictions for the woodland composition- tree taxon foliage scores- was not removed from zero (Table S2). However, when we looked at the foliage score taxon random effects we found that an increase in the amount of oak at a site was predicted to significantly increase the abundance of caterpillars found on the branches of any tree at a site (Fig. 3b, Fig. 3c). Exponentiating the coefficient shows that a branch will have 1.02 (CIs: 1.001 - 1.03) times as many caterpillars on it for every additional unit of oak foliage (equivalent to one small tree). Within the woodland compositions across our sites, branches of any tree taxon within mature oak-dominated woodlands can reach 5.19 (CIs: 1.73 – 17.45) times the caterpillar abundance of a woodland without oak, purely attributed to the local habitat composition (Fig. 3c).

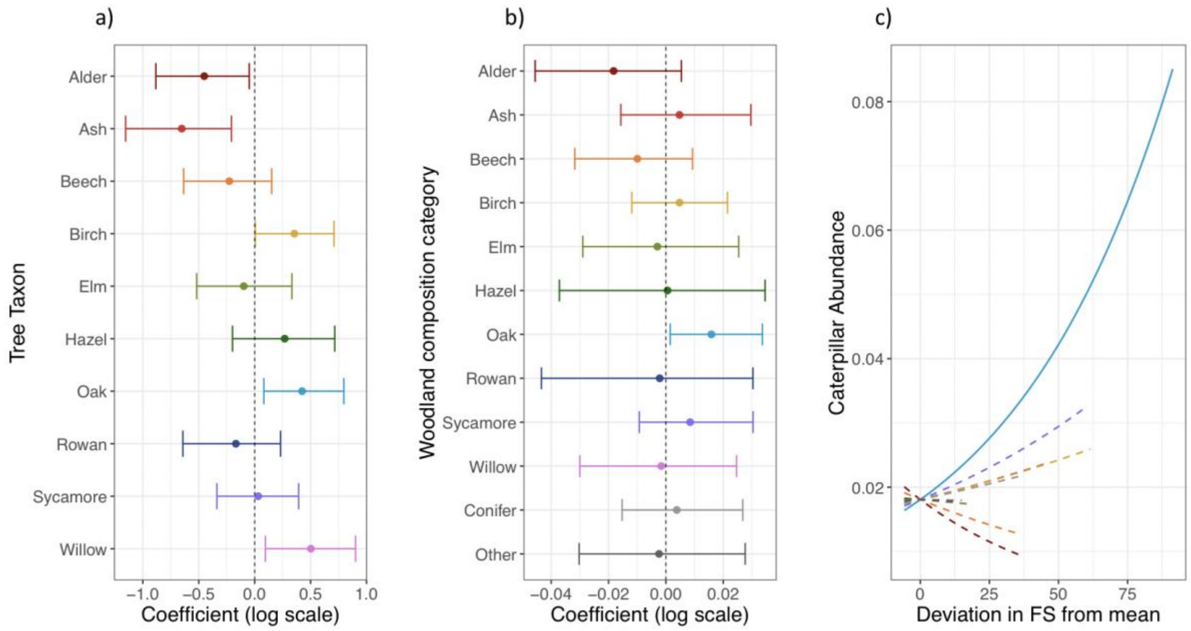

Figure 3: a-b) Posterior median and 95% credible intervals for random effects in a Poisson GLMM (Table S2). Predicted coefficients for a) the log difference in abundance of caterpillars sampled from each tree taxon and b) the log change in caterpillar abundance on an average branch with an increase in the amount of foliage of the tree taxon within the local woodland composition (globally mean centred foliage scores). c) Slope predictions from a Poisson GLMM (Table S2) analyzing the change in caterpillar abundance with change in the amount of foliage of each tree taxon present at each site (globally mean centered). The intercept falls at the mean foliage score (FS) of each taxon at any site and mean total FS across all sites. Dashed lines indicate an insignificant difference in slope from zero, the solid line indicates a significant result. All lines represent the range of foliage scores of each taxon present across all sites.

Phenological distributions

Abundance

Annual peaks in the temporal distribution of caterpillar abundance in our data are clear (Fig. S2), and supported by the significant negative quadratic term from the abundance phenology model (-0.84, CIs: -1.18 - -0.52, Table S3). We found substantial variance in the tree taxon intercepts and date slopes effects of the abundance phenology model (Table 1), but not the date^2 effects (Table S3). The fixed effects indicated the phenological distribution of abundance on an average tree taxon, in an average site and year, and predicted a mean peak date of 154.03 (CIs: 146.96 - 161.31), 3rd June, peak height of 0.06 (CIs: 0.02 - 0.14) caterpillars per branch, peak width of 25.91 days (CIs: 21.14 – 31.47 days) and duration of 40.43 days (CIs: 26.08 – 54.79 days), calculated at a threshold of 0.01 caterpillars per branch. In calculating peak width and duration a small proportion (< 1%) of the posterior samples yielded NAs due to some iterations either not predicting a negative quadratic term or predicting a peak height beneath the threshold for peak duration. These iterations were excluded which will make the median and CIs underestimates. The low peak height value was likely due to the large variance among sites and years and 89% of the beating samples recording zero caterpillars.

Investigating tree taxon specific peaks showed differences in the phenological distributions of caterpillar abundance (Fig. 4a). The peak timing on sycamore was significantly earlier than for the average taxon (-2.81 days, CIs: -6.33 - -0.29, Fig. 4b). The timing of the caterpillar abundance peak on hazel, oak, rowan and willow trees also showed trends towards deviating from the average taxon by 4.33 (CIs: -1.24 - 14.93), 1.92 (CIs: -1.13 - 5.00), -2.64 (CIs: -6.61 - 0.38) and 2.53 (CIs: -1.01 - 6.79) days respectively; however the CIs were not removed from zero (Fig. 4b). The height of the peak in caterpillar abundance was significantly different to an average taxon for alder, oak and willow trees, reaching 0.58 (CIs: 0.35 - 0.93), 1.87 (CIs: 1.25 - 2.87) and 1.61 (CIs: 1.02 - 2.61) times the peak height, respectively (Fig. 4c). As a proportional change, CI removal from one was the threshold for significance. The peak on ash and birch also showed trends towards deviating from the average taxon prediction, reaching 0.60 (CIs: 0.34 - 1.002) and 1.41 (CIs: 0.94 - 2.09) times the height respectively; however the CIs included one (Fig. 4c).

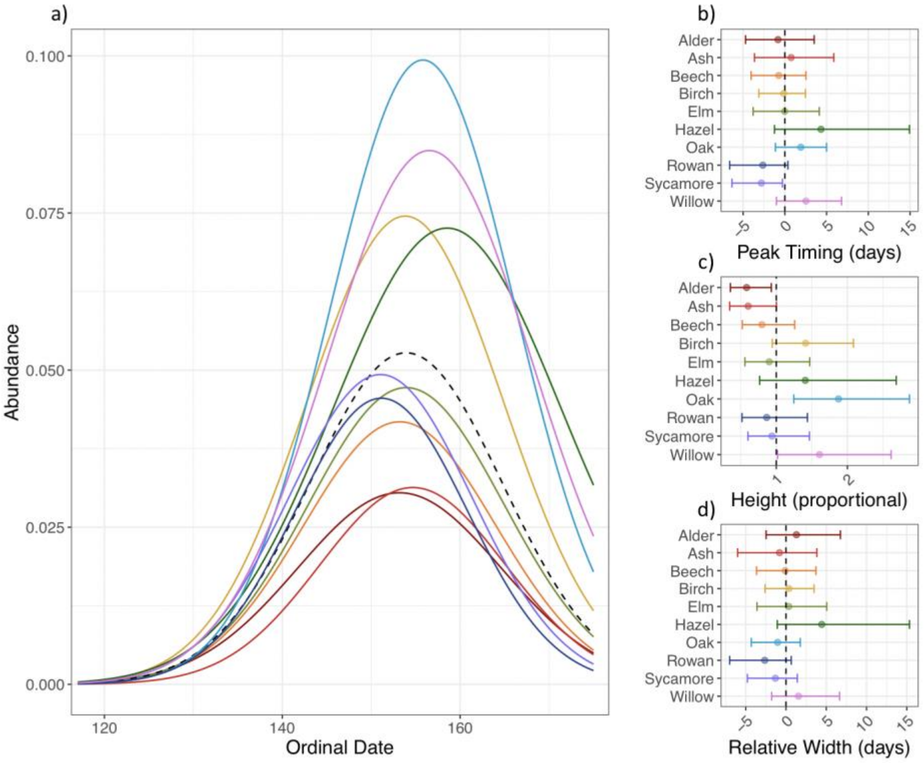

Figure 4: Model predictions for the phenological distribution of caterpillar abundance throughout spring on branches of different tree taxa (Table S3). a) shows the model predictions for the change in caterpillar abundance over time (ordinal date) for each tree taxon, the black dashed line depicts the curve prediction from the fixed effects. Plots b-d) show the difference between each tree taxon and the fixed effect prediction (indicated by a black dashed line at zero or one) for the b) timing of the peak in abundance, c) proportional height of the peak (maximum abundance) and d) width of the peak at half of the height. The median and 95% credible were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

The peak width, representing the relative shape of the peak, did not significantly differ between any taxon and the trend on an average tree (Fig. 4d). This suggests that the shape of the peak in caterpillar abundance was relatively consistent among tree taxa. However, the peak on oak, rowan and sycamore showed non-significant trends towards a narrower, more strongly peaked, distribution with a width difference of -1.04 (CIs: -4.31 - 1.77), -2.64 (CIs: -7.00 - 0.65) and -1.32 (CIs: -4.80 - 1.40) days relative to the trend on an average taxon and the peak on hazel and willow showed trends towards a broader peak by 4.44 (CIs: -1.08 - 15.33) and 1.56 (CIs: -1.78 - 6.65) days respectively (Fig. 4d). Due to relatively consistent shape but variable peak height, the peak duration showed more variation among taxa with the peak on willow lasting for a significantly longer duration, by 8.17 days (CIs: 0.33 - 19.01 days), than the average trend (Fig. S3). The abundance peak on ash, birch, hazel and rowan showed non-significant trends towards differing in duration to an average taxon, differing by -7.79 (CIs: -19.12 - 1.63), 4.57 (CIs: -2.16 - 12.07), 11.61 (CIs: -1.42 - 34.41) and -5.82 (CIs: -14.99 - 1.75) days respectively (Fig. S3). Whilst the peak on oak was suggested to have a narrower shape, due to the increased relative peak height the duration was suggested to be longer (4.83 days, CIs: -3.09 – 12.34), albeit non-significantly. The peak on oak was found to be significantly later than rowan and sycamore, higher than all tree taxa tested except hazel and willow and lasting for a longer duration than peaks on alder, ash, beech, rowan and sycamore (Fig. S4).

In the peak asymmetry model (Table S5), we found that although the cubic term was significant (Table S6), the resulting asymmetry in the peak estimate was low (Fig. S8) and therefore the use of a quadratic function adequately described the shape of the peak.

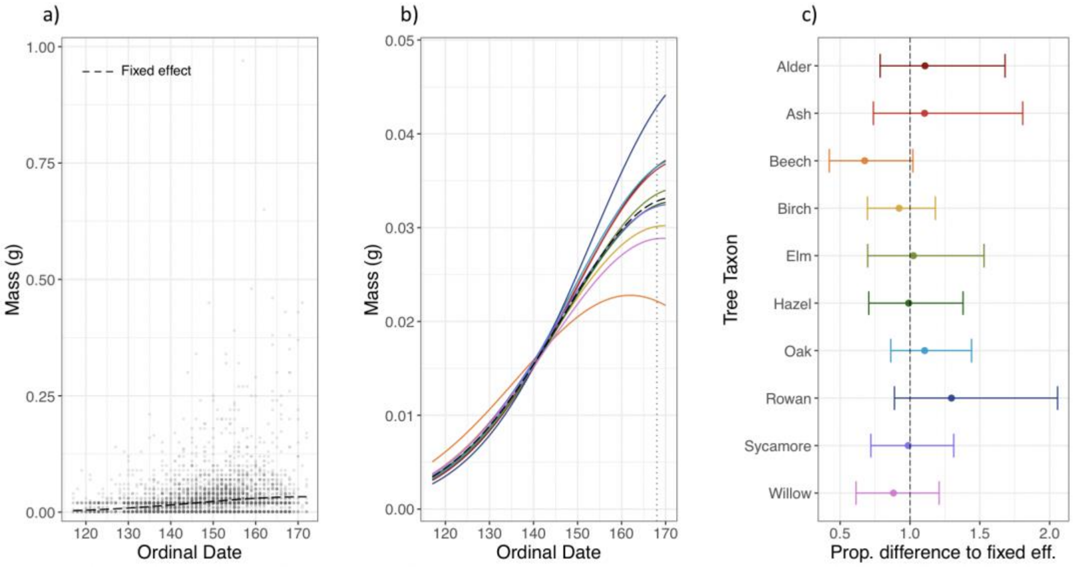

Figure 5: Slope predictions from a model analyzing the change in caterpillar mass throughout spring (Table S4). a) The black dashed line indicates the change in mass over time from the fixed effects. The points show the mass data, with transparency indicating the frequency of the point. The two bolder lines of points highlight the two levels of interval censored samples making up 4.9% of all samples. b) shows the model predictions for the change in mass over time for caterpillars on each tree taxon with the black dashed line showing the fixed effect trend from plot a). The grey dotted vertical line indicates the day 168 (16th June), the latest date with caterpillar mass data for all tree taxa. c) shows the posterior median and 95% credible intervals for the proportional difference in day 168 mass between each tree taxon and the fixed effect prediction.

Mass

Most caterpillars throughout spring weighed less than 0.1g, although caterpillars of up to 0.96g (n=1) have been recorded (Fig. 5a). There was a significant and pronounced trend for mass to increase over the course of the spring and for the rate of increase to decline (Fig. 5b, Table S4). There was no significant variance among tree taxa in the intercept or date slope, however there was slightly more variance estimated in the slope estimates than intercept which is why the predicted trends intersect at a central date (Fig. 5b, Table S4). The day 168 mass of caterpillars (in mid-June) predicted from the fixed effects, representing an average tree taxon, was 0.033g (CIs: 0.023 - 0.047g). Whilst the curves and day 168 masses do not differ significantly between any tree taxon and the fixed effect trend (Fig. 5b-c), caterpillars sampled from beech showed a strong trend towards a lower mass, reaching 0.68 (CIs: 0.42 - 1.02) of the mass of caterpillars from the average trend. Caterpillars from oak and rowan showed non-significant trends towards a greater mass, reaching 1.11 (CIs: 0.86 – 1.44) and 1.30 (CIs: 0.89 - 2.06) times that of the average, respectively (Fig. 5c). In comparison to oak, we found the ultimate mass of caterpillars was significantly less for those sampled from beech, with negative trends also suggested for birch and willow (Fig. S5).

Biomass

The combined fixed effects from the abundance and mass phenology models (Tables 1, S3, S4) predicted a peak date for the distribution of biomass on an average taxon of 156.84 (CIs: 150.94 - 163.39), 5th June; two days later than the peak in abundance. The maximal biomass peak height was predicted to be 0.0015g (CIs: 0.0006 - 0.0037g) per branch, a peak width of 23.80 days (CIs: 20.00 - 28.13), suggesting a more strongly peaked shape than the distribution of abundance, and a duration of 30.90 days (CIs: 16.68 - 45.45) at a threshold of 0.35mg of caterpillars per branch. Similarly to the abundance peaks, some iterations (<2% in general, but 5-7% for alder, ash and beech peak duration) produced NAs in the calculations of peak width and duration so the median and CIs are underestimates.

The most noticeable differences between the phenological distributions of caterpillar abundance and biomass were the increased relative height of the caterpillar peak on oak compared to other taxa and decreased relative height on beech, becoming more similar to the peaks on alder and ash (Fig. 4a, 6a). Unlike in abundance, the biomass peak on sycamore was not significantly earlier than an average taxon, however the CIs fell very close to zero, predicting a peak -2.82 (CIs: -6.22 - 0.04) days earlier (Fig. 6b). Similarly to the abundance peaks; hazel, oak, rowan and willow showed trends towards deviating in timing by 4.39 (CIs: -1.08 - 13.01), 1.74 (CIs: -1.52 - 4.69), -1.96 (CIs: -5.97 - 1.68) and 1.93 (CIs: -1.52 - 6.25) days, respectively, with the addition of beech also now showing trends towards peaking earlier by -2.15 (CIs: -6.25 – 1.17) days (Fig 6b).

The height of the peak in caterpillar biomass remained significantly different to an average taxon on oak trees, reaching 2.10 (CIs: 1.33 - 3.37) times the maximum mass (Fig. 6c) and whilst the biomass peak height on alder remained lower than the average trend (0.61, CIs:

0.36 – 1.11), the CIs include one. Due to the reduced mass of caterpillars on beech trees, the biomass peak height was predicted to be 0.64 (CIs: 0.38 - 1.09) times the height predicted for an average taxon, albeit non-significantly (Fig. 6c). The biomass peak on birch and willow branches continued to tend towards deviating non-significantly from an average taxon, reaching 1.34 (CIs: 0.85 - 2.08), and 1.55 (CIs: 0.90 - 2.61) times the height respectively, with the hazel biomass peak also showing trends towards an increased height of 1.54 (CIs: 0.81 – 3.24) times the average (Fig. 6c).

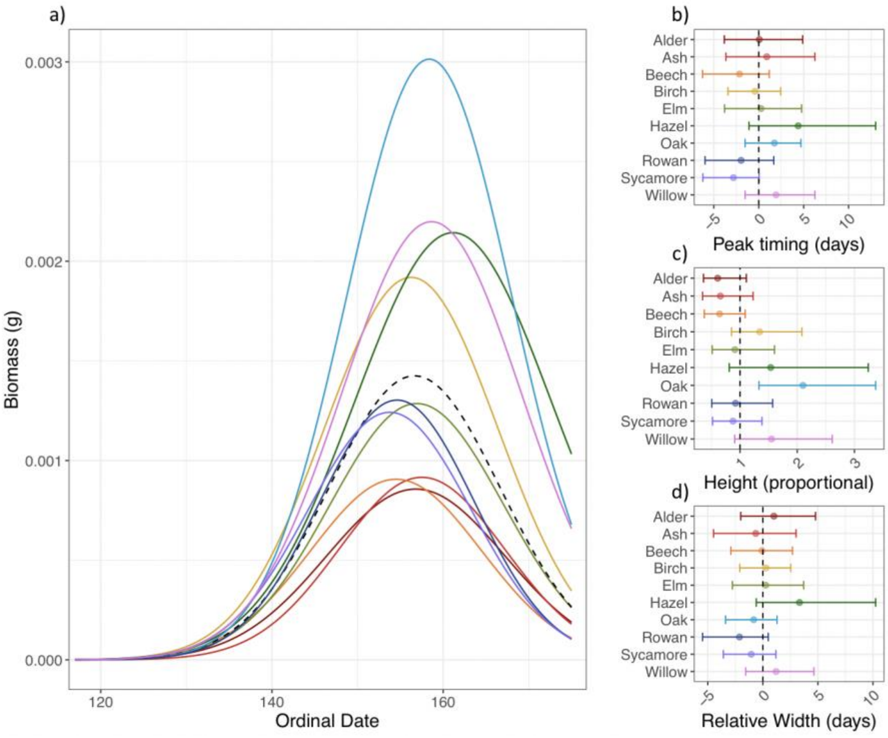

Figure 6: Predictions for the phenological distribution of caterpillar biomass throughout spring on branches of different tree taxa (based on models in Table S3+4). a) shows the model predictions for the change in caterpillar biomass over time (ordinal date) for each tree taxon, the black dashed line depicts the curve prediction from the fixed effects. Plots b-d) show the difference between each tree taxon and the fixed effect prediction (indicated by a black dashed line at zero or one) for the b) timing of the peak in biomass, c) proportional height of the peak (maximum biomass) and d) width of the peak at half of the height. The median and 95% credible were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

The biomass peak width, representing the relative shape of the peak, continued not to differ significantly between any taxon and the average trend (Fig. 6d), however, similarly to in the abundance results, the peaks on hazel, oak, rowan and sycamore showed strong trends towards deviating from average by -3.33 (CIs: -0.60 - 10.24), -0.82 (CIs: -3.39 - 1.29), -2.12 (CIs: -5.47 - 0.49) and -1.05 (CIs: -3.59 - 1.19) days respectively (Fig. 6d). Consequently, the peak duration at a consistent height again showed more variation, yet did not significantly differ between any taxon and the average trend (Fig. S6) because there were no distinct variations in the phenological distribution of mass. Nevertheless, the caterpillar biomass peak on beech, hazel, oak and willow showed strong trends towards differing in duration to an average taxon, differing by -6.53 (CIs: -16.89 – 1.57), 10.40 (CIs: -1.72 - 27.50), 7.05 (CIs: -0.87 - 15.53) and 7.22 (CIs: -0.53 - 17.48) days respectively (Fig. S6). The biomass peak timing, height and duration on oak differed to other taxa similarly to the peaks in abundance, with the addition of the peak on beech now also falling significantly earlier than on oak (Fig. S7).

Discussion

We find that several aspects of the phenological distributions of abundance and biomass are sensitive to tree taxon (Fig. 4, 6). The major difference was in the peak height, and like earlier work (Mägi et al., 2009; Shutt, Burgess, et al., 2019; Veen et al., 2010) we find that caterpillars are most abundant on oak and willow, with alder and ash especially poor (Fig. 3a, 4c, 6c). In agreement with Shutt et al. 2019, we find timing differences between tree taxa to be quite slight, though peak caterpillar phenology on sycamore trees falls earlier than on an average taxon, with deviating trends also suggested in multiple other taxa (Fig. 4b, 6b). Whilst the shape of the peak is generally consistent (Fig 4d, 6d), we show the peak in abundance lasts for a significantly longer period of time on willow than average (Fig. S3), with some suggestion that the peak duration also varies among other taxa (Fig S3, S6). We suggest among taxa differences in biomass are more attributable to abundance than mass, as we find no evidence for caterpillar mass gain differing among tree taxa compared to average (Fig. 5), although caterpillars on beech reach a significantly lower mass than those on oak (Fig. S5). In addition, we also found the prevalence of oak within the local woodland composition increases the number of caterpillars hosted by any tree, regardless of taxon (Fig. 3c).

Our results strongly support previous work that finds the phenological distribution of caterpillar abundance on oak trees reaches a high abundance but is present for a relatively brief duration (van Balen, 1973; Varley et al., 1974; Veen et al., 2010; Visser et al., 2006). The very high abundance and biomass of caterpillars observed in oak woodlands appears not to be representative of other woodland types that are more common across the UK (Stagg & Ward, 2019), despite its use as a baseline for comparison when the distribution in other woodland compositions has been studied (Mägi et al., 2009). On the contrary, our results suggest the phenological distribution of caterpillars on elm, rowan and sycamore are most representative of an average deciduous tree, particularly in relation to peak height as there are fewer distinctive differences in timing and duration. Generally speaking, oak, hazel, willow and to some extent birch deviate towards hosting larger caterpillar abundances than average, whilst alder, ash and to some extent beech deviate in hosting smaller abundances. These differences in the phenological distribution of spring caterpillar abundance provide evidence for biotic drivers of divergent caterpillar prevalence among tree taxa; though the causes remain to be established.

We find that the phenological distribution of the mass of the sampled caterpillar guild increases rapidly in early spring before asymptoting (Fig. 5). Our main results show minimal difference in caterpillar growth rate and the mass of caterpillars at the end of spring when comparing each taxon to an average tree; although caterpillars from beech weighed significantly less than those sampled from oak, with mass also lower on birch and willow (Fig. S5). Our results are consistent with rearing experiments using winter moth (*O. brumata*) that found more successful growth and mass at pupation from feeding on oak compared to hazel and beech (Feeny, 1970; Wint, 1983). Given our findings of greater abundance on oak and these experimental findings, it is perhaps surprising that the caterpillars sampled do not reach a higher mass or asymptote earlier than on other trees. However, as the budburst of oak falls later than may taxa (Cole & Sheldon, 2017), the asymptote in caterpillar mass on oak relative to the duration of food availability may well fall earlier than on other taxa. Our measure of mass will capture various processes including individual growth, and the appearance and disappearance of species from the guild through both varied phenologies among caterpillar species and beta diversity between locations.

When we combine the minimal among tree difference in caterpillar mass with abundance estimates we do see some effect on the phenological distribution of biomass, primarily through adjustments to peak height (Fig. 4, 6). The greatest difference in peak dimensions between the distributions of abundance and biomass among tree taxa is the increase in oak peak height, and decrease in beech, relative to the other trees (Fig. 6, S7). As most studies use frass fall or half-fall to quantify the peak in biomass (Charmantier et al., 2008; Hinks et al., 2015; Smith et al., 2011; Visser, Noordwijk, Tinbergen, & Lessells, 1998), the contribution of abundance and mass phenology to the biomass peak timing is unexplored. With just a two-day difference in peak phenology between abundance and mass, our results suggest that the trend in abundance is more prominent than mass in dictating the timing of the biomass peak. Therefore, factors impacting caterpillar abundance differentially between locations are likely to have a greater impact on spatial variation in caterpillar phenology than those impacting mass.

The impact of oak foliage density, increasing caterpillar abundance throughout the local area (Fig. 3c), suggests that oak-dominated woodlands may be unique in spring caterpillar prevalence when compared to other woodland compositions. Whether the increased abundance throughout areas with increasing oak is driven by increased survival rates or successful pupation remains unknown, however increased fecundity is unlikely (Honěk, 1993) to have a wide-spread impact as caterpillars from oak show no significant increase in mass compared to those on an average tree. Fecundity may, however, influence the differences in abundance between oak and specific taxa, such as beech, as the divergence in mass is more substantial; however this difference could be driven by differing lepidopteran guild compositions. The increased abundance on oak also appears not be driven by the general density of foliage, as the site foliage density effect was close to zero and non-significant (Table S1). The tall and broad crown of a mature oak tree may make dispersal of caterpillars to other trees more successful than from other typically smaller tree taxa such as willow and birch. An implication of these findings is that the common practice of monitoring caterpillar prevalence purely on oak (Burgess et al., 2018; Hinks et al., 2015; Visser et al., 2006) may miss spatial-heterogeneity in caterpillar abundance both between locations and within larger sites. However, the increased caterpillar abundance on oak could make these habitats the most important to consumers; acting as a source that contributes to the repopulation of areas with lower consumer breeding success, as the prevalence of oak within an area has been shown to increase fledging success (Shutt et al., 2018).

The tree composition within a woodland seems likely to influence mismatch buffering through the variation it drives in dimensions of the site-level caterpillar peak. Our study suggests the habitat-driven buffering potential may be stronger than previously suggested (Shutt, Burgess, et al., 2019), as we have identified further differences in the caterpillar peak among tree taxa, particularly in peak height but also in timing and duration. The differences in peak height between tree taxa could impact mismatch between different areas within a similar region or more broadly between woodlands and geographical locations as the tree composition present is likely to influence the maximum caterpillar density reached, potentially altering the negative consequences of trophic asynchrony for the consumer. The peak on willow lasts for eight days longer than average, providing a food source for over a third of the time many consumers spend in the nest. The peaks on alder, ash, beech, rowan and sycamore were all shorter than on oak (Fig. S4), implying that the peak may vary substantially in duration between an oak-dominated woodland and one with a mixed composition. There is also potential for within site peak duration to be influenced by tree composition through deviations in peak phenology, as the peak falls three days earlier on sycamore than on average tree taxa (Fig. 4) and three-five days earlier on beech, rowan and sycamore than on oak (Fig. S4).

Habitat composition is manipulatable by foresters and land managers and here we examine the implications of our findings in this context. First, in general increased defoliation negatively impacts on tree health and productivity (Kulman, 1971; Marquis & Whelan, 1994; Whitham et al., 1991; Whittaker & Warrington, 1985). Defoliation may be minimised if there is a lower density of oak, thereby preventing the additive effect it has on the abundance of caterpillars overall. However, with the exception of oak, caterpillar abundance appeared to be insensitive to the amount of other tree taxa present. The second implication relates to the conservation of consumer populations for whom more resource is expected to be beneficial, though the importance of resource abundance versus resource timing relative to breeding is relatively underexplored (but see Naef-Daenzer & Keller, 1999; Ramakers, Gienapp, & Visser, 2019). The high density of prey in oak woodlands is thought to be a driver of preference for this habitat by some breeding passerines (Perrins, 1979). However, mixed woodlands containing trees with more varied caterpillar peak timings may extend the period of caterpillar availability and total abundance across spring, also potentially of benefit to consumer species. In addition our study reveals substantial site effects in the phenological distribution of caterpillar abundance (Table S3), and some site effect on mass (Table S4), which implies that factors in addition to habitat play an important role (Fig. 2).

We have shown new detailed insights into habitat-driven variations in caterpillar abundance and the phenological distribution of caterpillar abundance and biomass among tree taxa. Our results highlight the spatio-temporal differences in caterpillar phenology, abundance and trophic interactions between different woodland compositions. We show that the phenological distribution of spring invertebrates in oak-dominated study systems are not representative of the distributions present across the broader range of deciduous woodland compositions also at risk of temperature-mediated trophic mismatch. Our findings have applications in woodland management and reforesting for the conservation of woodland lepidopteran and insectivore communities.

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Supplementary Information

We found that alder, ash, beech, elm, rowan and sycamore all support significantly fewer caterpillars than oak (Fig. S1), hosting 0.42 (CIs: 0.29 - 0.58), 0.34 (CIs: 0.22 - 0.54), 0.52 (CIs: 0.39 - 0.69), 0.60 (CIs: 0.41 - 0.84), 0.55 (CIs: 0.39 - 0.78) and 0.67 (CIs: 0.53 - 0.84) times as many caterpillars respectively.

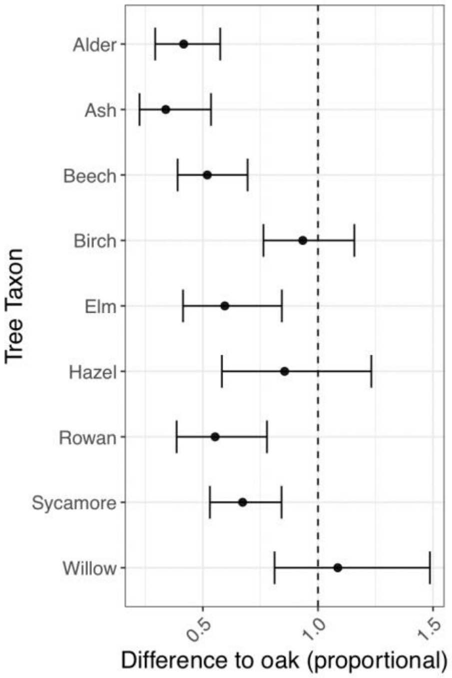

Figure S1: Posterior median and 95% credible intervals of the model prediction for the proportional difference in caterpillar abundance between each tree taxon and oak. Calculated from tree taxa random effects in a Poisson GLMM (Table S1). Black dashed line at 1.0 indicates no difference to oak/significance threshold.

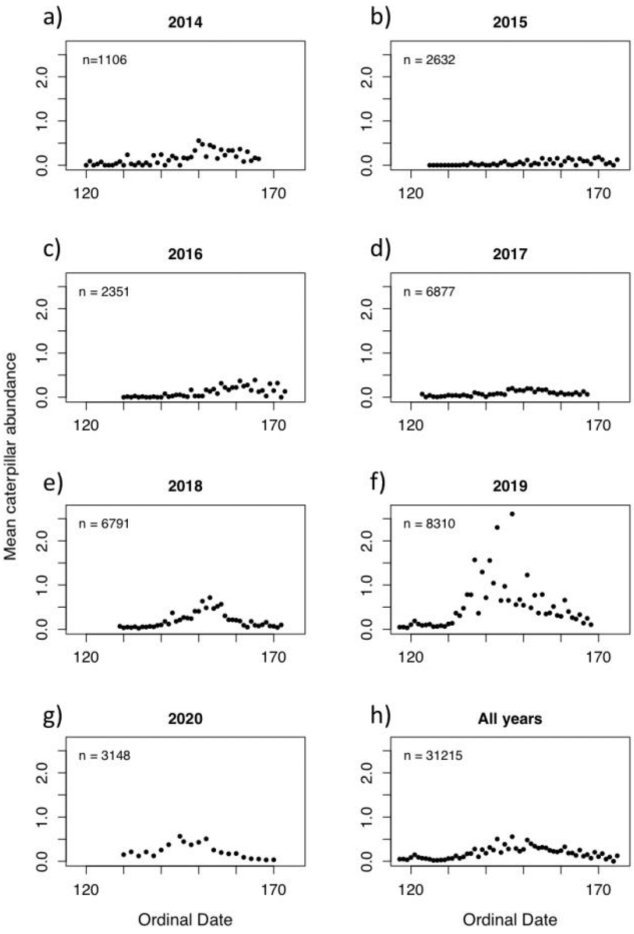

Figure S2: Plots a-g show the mean abundance of caterpillars sampled on each day of each year and plot h shows the mean abundance on each day across all years, calculated from the mean at each site on each day, n indicates the total number of beating samples within each year or the total for all years.

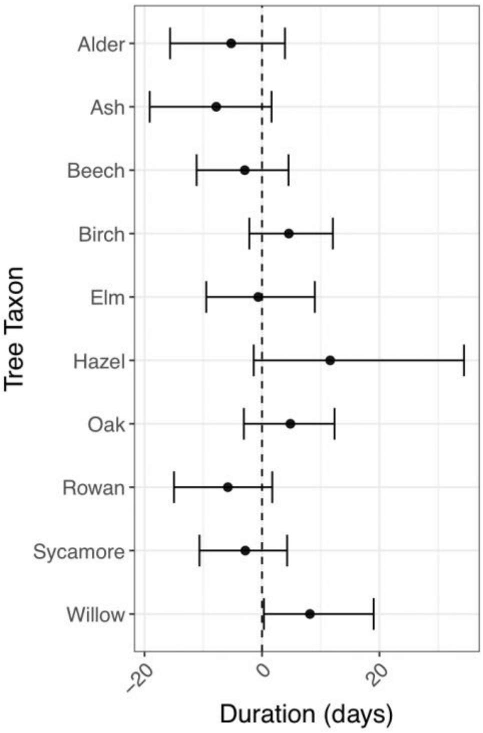

Figure S3: Posterior median and 95% credible intervals for model prediction of the difference in peak duration (at an abundance of 0.01 caterpillars) for each taxon compared to the fixed effect trend. Calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions in a Poisson GLMM (Table S4).

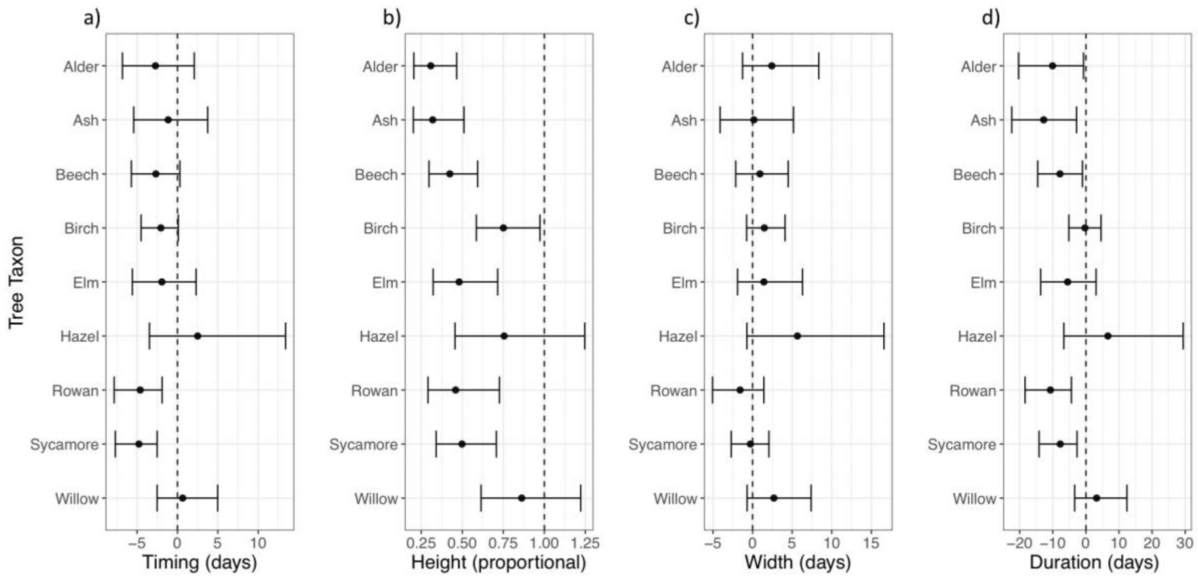

Figure S4: Posterior median and 95% credible intervals for (Table S4) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar abundance in spring, calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions. Plots show a) the difference in the timing of the peak in abundance, b) the proportional difference in the height of the peak (maximum abundance), c) the difference in the peak width at half of the peak height and d) the difference in the duration of the peak (at a set abundance of 0.01 caterpillars).

When comparing the abundance peak metrics of each taxon to the peak on oak we saw a greater number of significant differences than compared to the average trend. The peak on rowan and sycamore trees was significantly earlier than on oak by -4.61 (CIs: -7.84 - -1.90) and -4.78 (CIs: -7.70 - -2.52) days respectively (Fig. S4). The peak on alder, ash, beech, birch, elm, rowan and sycamore were all found to have a significantly lower height, reaching 0.31 (CIs: 0.20 - 0.47), 0.32 (CIs: 0.20 - 0.51), 0.42 (CIs: 0.30 - 0.59), 0.75 (CIs: 0.59 - 0.97), 0.48 (CIs: 0.32 - 0.72), 0.46 (CIs: 0.29 - 0.73) and 0.50 (CIs: 0.34 - 0.71) times the height of the peak on oak trees, respectively. The width of the peak at half the height on birch, hazel and willow showed non-significant trends towards being broader than on oak by 1.48 (CIs: -0.75 - 4.10), 5.66 (CIs: -0.72 - 16.69) and 2.69 (CIs: -0.69 - 7.40) days respectively. The peaks on alder, ash, beech, rowan and sycamore last for a significantly shorter duration by -10.07 (CIs: -20.34 - -0.71), -12.76 (CIs: -22.40 - -2.82), -7.84 (CIs: -14.56 - -1.04), -10.72 (CIs: -18.39 - -4.38) and -7.75 (CIs: -14.15 - -2.98) days respectively (Fig. S4).

When comparing the day 168 mass of caterpillars on each tree taxa to those from oak we found caterpillars sampled from beech weighed significantly less at 0.60 (0.38 - 0.97) times the mass of those sampled from oak (Fig. S5). Birch and willow also show non-significant trends towards a lower mass, reaching 0.83 (CIs: 0.65 - 1.03) and 0.79 (CIs: 0.55 – 1.08) times the mass respectively (Fig. S5).

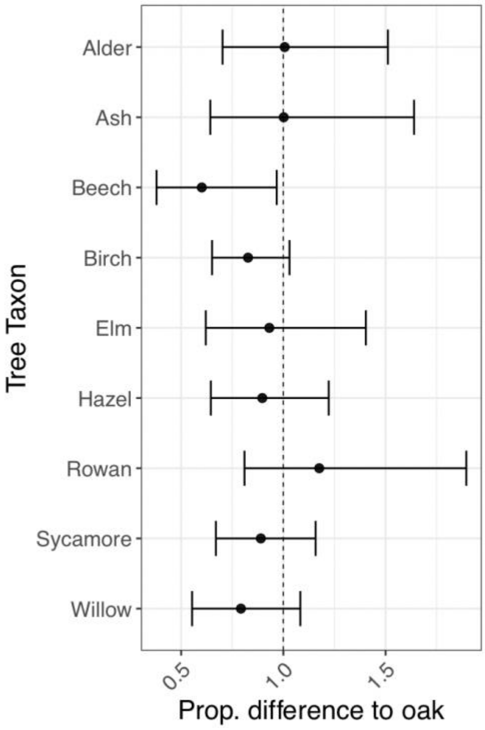

Figure S5: Posterior median and 95% credible intervals for model predictions of the proportional difference in caterpillar mass between each tree taxon and caterpillars sampled from oak (Table S5). Calculated for day 168 (16th June) for the average year and site, the latest date with caterpillar mass data for all tree taxa, using the posterior distributions for all fixed effect parameters and tree taxa random effects and interactions in a censored-gaussian GLMM.

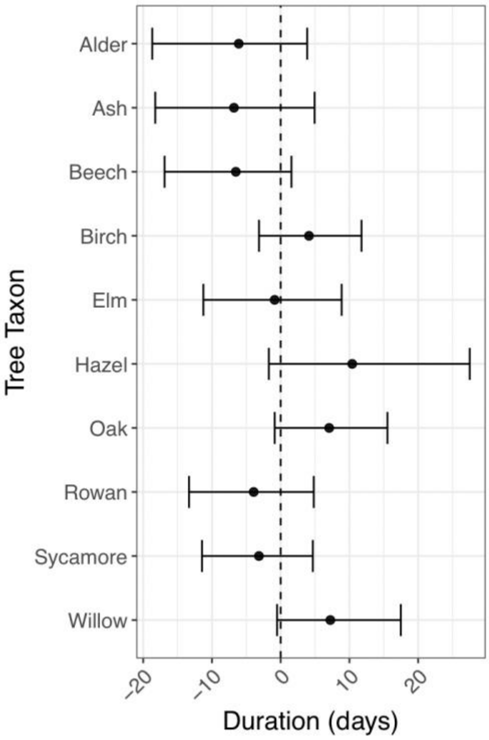

Figure S6: Posterior median and 95% credible intervals for model prediction of the difference in peak duration (at a biomass of 0.00035g of caterpillars) for each taxon compared to the fixed effect trend (Table S4+5). Calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions in a bivariate censored-gaussian (mass) and Poisson (abundance) GLMM.

As with the distributions of caterpillar abundance among tree taxa, there were multiple differences between each taxon and oak in the biomass peak metrics (Fig. S7). The peak on beech, rowan and sycamore trees was significantly earlier than on oak by -3.91 (CIs: -7.51 - -0.51), -3.73 (CIs: -7.15 - 0.42) and -4.58 (CIs: -7.31 - -1.99) days respectively (Fig. S7), and the peak timing on birch trees also showed a strong trend towards falling -2.14 (CIs: -4.46 - 0.20) days earlier. The biomass peaks on alder, ash, beech, birch, elm, rowan and sycamore were found to have a significantly lower height, reaching 0.29 (CIs: 0.18 - 0.47), 0.31 (CIs: 0.18 - 0.56), 0.31 (CIs: 0.18 - 0.47), 0.64 (CIs: 0.48 - 0.87), 0.43 (CIs: 0.27 - 0.71), 0.44 (CIs: 0.26 - 0.71) and 0.41 (CIs: 0.27 – 0.60) times the height of the peak on oak trees, respectively. The width of the peak at half the height on birch, hazel and willow showed non-significant trends towards being broader than on oak by 1.67 (CIs: -0.58 - 3.11), 4.31 (CIs: -0.18 - 11.43) and 2.12

(CIs: -0.37 - 5.56) days respectively. The peak duration on alder, ash, beech, rowan and sycamore lasted for a significantly shorter duration by -13.01(CIs: -25.47 - -3.16), -13.78 (CIs: -25.36 - -2.69), -13.48 (CIs: -23.74 - -5.69), -11.00 (CIs: -19.73 - -4.53) and -10.32 (CIs: -17.27 - -4.32) days respectively, and peaks on birch and elm also show strong non-significant trends towards a shorter duration by -2.98 (CIs: -7.91 - 1.39) and -7.98 (CIs: -17.40 - 1.34) days (Fig. S7).

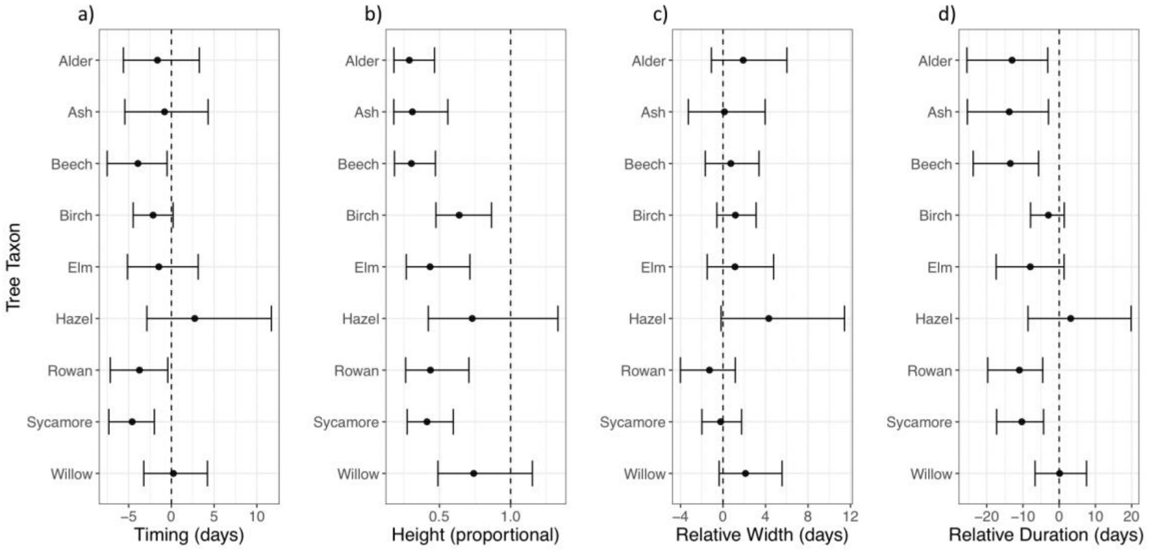

Figure S7: Posterior median and 95% credible intervals for combined censored-gaussian (mass) and Poisson (abundance) GLMM (Table S4+5) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar biomass in spring, calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions. Plots show a) the difference in the timing of the peak in biomass, b) the proportional difference in the height of the peak (maximum biomass), c) the difference in the peak width at half of the peak height and d) the difference in the duration of the peak (at a set biomass of 0.00035g of caterpillars).

Model output tables

Table S1: Poisson GLMM for variance composition of caterpillar abundance. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.319 (-4.111 - -2.533)	4900
Date (scaled)	0.48 (0.388 - 0.57)	4655
Date² (scaled)	-0.442 (-0.528 - -0.355)	4482
Random Terms		
Site	0.667 (0.36 - 1.075)	1844
Tree ID	0.273 (0.222 - 0.34)	4900
Tree Taxa	0.146 (0.048 - 0.608)	1657
Site Day	0.491 (0.424 - 0.598)	4148
Day	0.272 (0.195 - 0.364)	4539
Site Year	0.258 (0.184 - 0.359)	3392
Year	0.278 (0.077 - 1.885)	1111
Recorder	0.103 (0.048 - 0.33)	2814
Residual	0.641 (0.563 - 0.739)	3885

Table S2: Poisson GLMM analysing differences in caterpillar abundance between the different tree taxa sampled, the effect of site foliage density and the effect of the amount of foliage of each tree taxon within the local woodland composition, included using multi-membership.

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-4.02 (-4.892 - -3.192)	4707
Total Foliage Score	0.001 (-0.019 - 0.018)	3842
Random Terms		
Sampled Tree Taxa	0.126 (0.038 - 0.594)	3146
Habitat Composition	0 (0 - 0.001)	1063
Site	0.388 (0.194 - 0.696)	3547
Year	0.288 (0.062 - 1.796)	816
Site Year	0.232 (0.158 - 0.336)	5000
Tree ID	0.269 (0.221 - 0.338)	5000
Site Day	1.032 (0.916 - 1.166)	5000
Recorder	0.166 (0.069 - 0.484)	3030
Residual	0.643 (0.57 - 0.746)	4589

Table S3: Poisson GLMM for analysing variations among tree taxa in the phenological distribution of caterpillar abundance throughout spring. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.164 (-4.191 - -2.225)	10000
Date (scaled)	0.864 (0.042 - 1.743)	8866
Date^2 (scaled)	-0.841 (-1.177 - -0.523)	7069
Random Terms		
TreeTaxa- Intercept var	0.154 (0.036 - 0.626)	1340
TreeTaxa- Intercept:Date slope covar	0.02 (-0.097 - 0.154)	8865
TreeTaxa- Intercept:Date^2 slope covar	0.002 (-0.102 - 0.081)	8750
TreeTaxa- Date slope var	0.046 (0.011 - 0.212)	3123
TreeTaxa- Date slope:Date^2 slope covar	0 (-0.04 - 0.068)	8719
TreeTaxa- Date^2 slope var	0.02 (0 - 0.129)	2586
Site- Intercept var	0.872 (0.553 - 1.548)	6973
Site- Intercept:Date slope covar	-0.104 (-0.337 - 0.056)	6315
Site- Intercept:Date^2 slope covar	-0.229 (-0.437 - -0.124)	5703
Site- Date slope var	0.243 (0.145 - 0.425)	3166
Site- Date slope:Date^2 slope covar	0.018 (-0.041 - 0.092)	6168
Site- Date^2 slope var	0.105 (0.057 - 0.186)	5096
Year- Intercept var	0.472 (0.159 - 3.22)	473
Year- Intercept:Date slope covar	-0.293 (-1.975 - 0.367)	7155
Year- Intercept:Date^2 slope covar	0.038 (-0.269 - 0.491)	5163
Year- Date slope var	0.501 (0.171 - 2.851)	578
Year- Date slope:Date^2 slope covar	-0.052 (-0.627 - 0.149)	5671
Year- Date^2 slope var	0.047 (0.005 - 0.339)	1302
Site-Year	0.259 (0.197 - 0.37)	5472
Recorder	0.146 (0.064 - 0.355)	2616
Site-Day	0.266 (0.204 - 0.333)	4355
Tree ID	0.263 (0.212 - 0.328)	6000
Residual	0.64 (0.555 - 0.727)	2203

Table S4: Censored-gaussian GLMM for analysing variations among tree taxa in the phenological distribution of log caterpillar mass throughout spring. Date refers to ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.884 (-4.131 - -3.651)	10446
Date scaled	0.533 (0.38 - 0.687)	3491
Date^2 scaled	-0.147 (-0.207 - -0.088)	1549
Random Terms		
TreeTaxa- Intercept var	0 (0 - 0.026)	2113
TreeTaxa- Intercept:Date slope covar	0 (-0.006 - 0.024)	3714
TreeTaxa- Date slope var	0.001 (0 - 0.086)	1011
Site- Intercept var	0.029 (0 - 0.078)	948
Site- Intercept:Date slope covar	-0.009 (-0.04 - 0.016)	2207
Site- Date slope var	0.044 (0.015 - 0.098)	1652
Year	0 (0 - 0.183)	1063
Site-Year	0.02 (0 - 0.052)	824
Recorder	0.006 (0 - 0.04)	2522
Site-Day	0.128 (0.087 - 0.184)	2677
Tree ID	0.041 (0.021 - 0.071)	2614
Weighting	0.97 (0.863 - 1.069)	1388
Residual	0.023 (0.002 - 0.055)	671

Asymmetry in the abundance peak

Methods

It is already established that there is a peaked phenological distribution of caterpillar abundance throughout spring in temperate deciduous woodlands (Gibb, 1950; Shutt, Burgess, et al., 2019; Southwood et al., 2004; van Balen, 1973), though the shape of peak has not been examined. We assessed the adequacy of the quadratic function in describing the shape of the phenological distribution of caterpillar abundance by also modelling the peak including a cubic date term; allowing an asymmetrical trend over time. The extent of asymmetry was quantified by comparing the percentage of the peak width predicted to fall before and after the vertex of the curve.

The peak asymmetry model included the caterpillar abundance per sample as the response variable with an intercept, date, date^2 and date^3 in the fixed effects, allowing an asymmetrical peak (Table S5). Date refers to ordinal date and was scaled (prior to scaling: mean = 146.77, SD =14.04). The random terms allowed for each site-year to have a separate intercept, date and date^2 slopes and for covariance among these terms. Separate site and year random intercepts and slopes were not included to aid model convergence. We do not anticipate this will pose an issue, as our aim was solely to identify the general phenological trend. We calculated the extent of asymmetry at each quartile of the peak height across the posterior distribution because the ratio of duration to the left and right of the peak is not necessarily constant.

Table S5: Model composition for the peak asymmetry model. Date refers to ordinal date which was scaled (mean = 146.77, SD =14.04). Int = intercept and VCV = variances and covariances.

Model	Peak asymmetry (Table S6)
Motivation	Evidence of asymmetry in peak shape
Response	Caterpillar abundance
Fixed effects	Date Date^2 Date^3
Random terms	Int, Date and Date^2 VCV across Site-year Day-site-year Tree ID Recorder
Family	Poisson
Iterations (thin)	2000000 (1000)
Burnin	50000
Sample Size	1950

Results

Annual peaks in the temporal distribution of caterpillar abundance in our data are clear (Fig. S2), and supported by the significant date^2 term (-0.666, CIs: -0.769 - -0.565, Table S6) in the peak asymmetry model. The cubic parameter was significant and negative (-0.193, CIs: -0.256 - -0.124), indicating a negatively skewed peak (Table S6), however the resulting asymmetry in the curve is quite small (Fig. S8). Each quartile shows 52-57% of the peak duration to the left and 43-48% to the right. On the basis of the quite minor asymmetry we conclude that inclusion of the quadratic date term, without cubic, is sufficient.

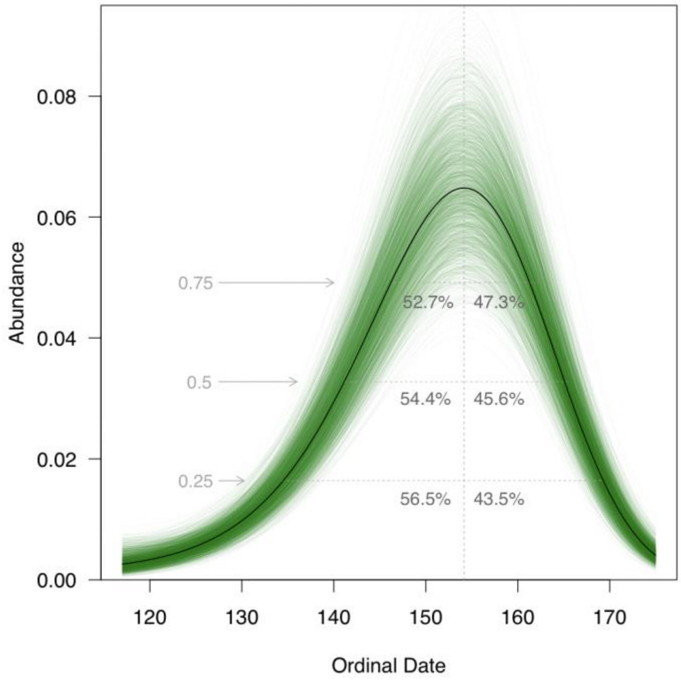

Figure S8: Posterior distribution for Poisson GLMM allowing a cubic (asymmetrical) relationship between caterpillar abundance and ordinal date (Table S3). Percentage of peak width falling before and after the peak date at 0.25, 0.5 and 0.75 of the peak height are shown in grey.

Table S6: Poisson GLMM using a cubic function to analyse possible skew in the distribution of caterpillar abundance across ordinal date (scaled: mean = 146.7727, SD =14.04083).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
<u>Fixed Terms</u>		
Intercept	-2.977 (-3.244 - -2.699)	1950
Date (scaled)	0.862 (0.703 - 1.024)	1684
Date^2 (scaled)	-0.666 (-0.769 - -0.565)	1506
Date^3 (scaled)	-0.193 (-0.256 - -0.124)	1589
<u>Random Terms</u>		
SiteYear- Intercept var	1.6 (1.3 - 2.059)	1950
SiteYear- Intercept:Date slope covar	-0.278 (-0.473 - -0.085)	2078
SiteYear- Intercept:Date^2 slope covar	-0.425 (-0.583 - -0.303)	1512
SiteYear- Date slope var	0.643 (0.489 - 0.851)	1659
SiteYear- Date slope:Date^2 slope covar	0.074 (-0.024 - 0.153)	1734
SiteYear- Date^2 slope var	0.202 (0.13 - 0.27)	2105
Recorder	0.164 (0.065 - 0.382)	1690
Site Day	0.232 (0.175 - 0.3)	1950
Tree ID	0.335 (0.274 - 0.402)	1950
Residual	0.632 (0.568 - 0.735)	1826