Tree taxon effects on the phenology of caterpillar abundance and biomass

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Abstract

Phenological shifts are well documented biological responses to warming. While many studies have focused on the mean timing of an event, there is growing appreciation that the height and width of the phenological distribution will also impact on species interactions. A temperate deciduous forest food chain of oak trees – arboreal caterpillars – insectivorous passerines has become paradigmatic in research on phenological mismatch. This focus on oak-dominated woodlands means that we have limited insight into whether (i) caterpillar phenological distributions vary among tree taxa and habitats and (ii) oak is an exceptional host, which has implications for the potential for buffering of interactions on a local and landscape scale. Here, we survey caterpillar abundance and mass throughout spring on 10 tree taxa for 10 years across 44 Scottish woodland sites. We found substantial variation in caterpillar abundance among host taxa, with oak, birch and willow yielding similarly high numbers of caterpillars, and evidence that caterpillar abundance increases with the density of oak foliage within a woodland stand, but not with the density of other taxa. Considering variation in the phenological distribution of caterpillars on different host taxa, we found the main axis of variation to be the maximum abundance/total biomass reached, which was highest on oak. We found significant variation in the mean timing of abundance and duration of abundance and total biomass among hosts, though effect sizes were quite small, and little evidence for among host variation in the phenological distribution of individual caterpillar mass. In woodlands where oak is abundant, our findings are consistent with the presence of other tree taxa providing little local buffering of phenological mismatch. Whereas, in the absence of oak, birch and willow have the potential to support similarly substantial caterpillar abundances. These findings have implications for conservation, resilient forestry planting and management decisions.

Keywords

Abundance, biomass, caterpillar, deciduous forest, mass, match/mismatch hypothesis, phenology

Introduction

Climate warming is driving species across multiple taxa and trophic levels to advance the timing of seasonal events (Parmesan 2006; Thackeray *et al.* 2016; Cohen *et al.* 2018) and phenological shifts are one of the most highly documented biotic responses to climate change (Walther *et al.*, 2002; Parmesan and Yohe, 2003). The shifts in timing vary between species and trophic levels, with secondary consumers generally advancing less than producers and primary consumers (Thackeray *et al.* 2010, 2016).

Phenological synchrony of trophic interactions has become a concern under climate change due to trophic levels differing in their phenological reaction norms (Thackeray *et al.* 2016), which has the potential to generate shifts in the degree of (a)synchrony between a consumer and its resource, with potentially negative fitness consequences for the consumer (the match/mismatch hypothesis, MMH) (Cushing 1990; Visser & Both 2005; Durant *et al.* 2007; Samplonius *et al.* 2020). However, there has been a paucity of evidence that mismatch is leading to consumer population declines (Samplonius *et al.* 2020) or having positive effects for the producer, which may be explained if consumer-resource interactions are more 'buffered' than we have appreciated (Weir & Phillimore 2024). A major form that buffering of phenological interactions can take is where consumers are able to exploit alternative resources according to what is phenologically synchronous (Bartomeus *et al.* 2013), though to date there have been rather few studies examining the potential for this form of buffering.

A further factor that may contribute to phenological buffering being underappreciated is the tendency for research to focus on shifts in mean timing of populations/guilds (Thomas *et al.*, 2001; Charmantier *et al.*, 2008; Both *et al.*, 2009; Reed, Jenouvrier and Visser, 2013; Thackeray *et al.*, 2016; Burgess *et al.*, 2018; Roslin *et al.*, 2021) and to the neglect of the duration of events and the height of phenological peaks. We can describe the full phenological distribution of population (or guild) abundance or biomass with three parameters (Fig 1a): mean timing (Fig 1b), maximum height (Fig 1c) and width (Fig 1d; here defining the shape of the distribution independently of the height, similarly to a standard deviation) (Shutt *et al.* 2019a; Macphie *et al.* 2023). The duration of the distribution is determined by both the height and width (Fig 1c-d) and differs depending on the abundance or biomass at which is it measured. Extensions of the MMH recognise that if availability of the resource is important for consumer fitness then the height, width and resulting duration of the resource peak may matter in addition to the mean timing (Durant *et al.* 2005; Miller-Rushing *et al.* 2010; Macphie 2023). A consumer that is asynchronous with the mean timing of one resource may be buffered if the height and width of the resource phenological distribution result in adequate resource being present. Alternatively, if multiple resources are utilised locally, and these resources differ in their phenological distributions, this presents the potential for phenological buffering, where asynchrony with one resource is buffered by utilising an alternative synchronous resource.

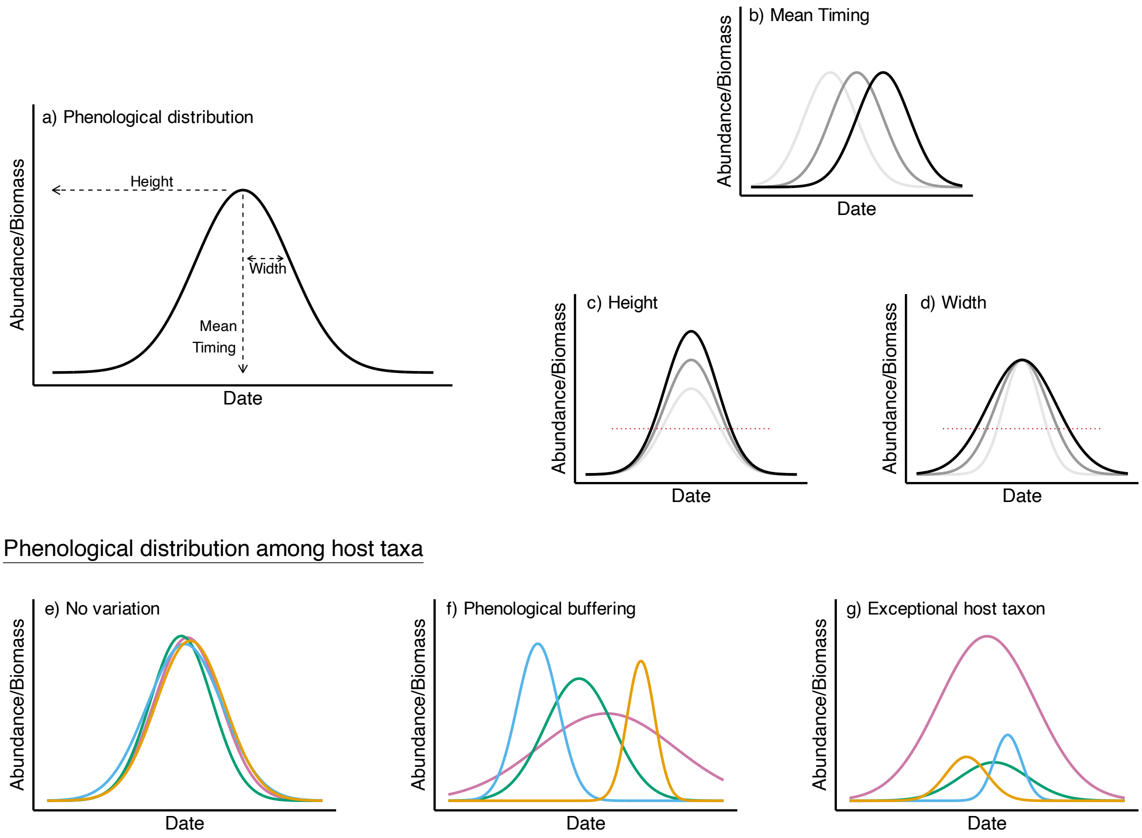

Figure 1: The parameters describing the phenological distribution and examples of how the distribution of a guild's abundance or biomass could differ among hosts. a) Shows the three main parameters describing the phenological distribution. b-d) Show the effect of changing each parameter: the parameter value increases moving from light grey to black. The red dotted line in c and d illustrate how differences in both the height (c) and width (d) of the phenological distribution influence the duration at a given abundance or biomass. e-g) Show four phenological distributions representing the guild phenological distribution on four different host taxa; e) shows no variation among taxa, f) shows variation the mean timing, height and width of the distribution that results in different taxa hosting the highest abundance or biomass over time, g) shows one exceptional taxon hosting more of the guild at all points in time despite differences in the phenological distribution among the other hosts.

Nowhere have the impacts of climate change on phenology and the MMH been more intensively studied than the temperate terrestrial tri-trophic food chain of deciduous tree – caterpillars – cavity nesting insectivorous passerine system (Thomas *et al.* 2001; Visser *et al.* 2006; Charmantier *et al.* 2008; Both *et al.* 2009; Samplonius *et al.* 2016; Cole *et al.* 2021). This system includes ephemeral resources at two trophic levels, which is expected to make it more susceptible to climate-mediated asynchrony; caterpillars rely on young palatable leaves while they grow to pupation (Feeny 1970; van Asch & Visser 2007; Forkner *et al.* 2008), and a short-lived peak in caterpillars serves as a key food source for many breeding birds (Betts 1955; Bańbura *et al.* 1994; Sanz 1998; Wilkin *et al.* 2009; García-Navas & Sanz 2011; Samplonius *et al.* 2016). The phenological distribution of abundance and biomass of caterpillars has potential top-down implications for herbivory damage to deciduous trees, which can affect tree growth, survival and forest productivity (Crawley, 1985; Kulman 1971; Whittaker & Warrington 1985; Whitham *et al.* 1991; Marquis & Whelan 1994) and bottom-up implications for the fitness of consumer species (Buse *et al.* 1999; Visser *et al.* 2006; Reed *et al.* 2013).

Most work on the woodland tri-trophic system has focused on oak-dominated (*Quercus* spp.) woodlands or mainly collect data on caterpillar abundance (or biomass) on oak trees (Varley *et al.* 1974; Visser *et al.* 2006; Hinks *et al.* 2015; Burgess *et al.* 2018). This taxonomic bias may have arisen due to tit and flycatcher species appearing to prefer oak habitats (Perrins 1979; Simms 1971) and experimental work showing evidence that oak provides a good resource for developing caterpillars, including the winter moth *Operophtera brumata* (Feeny 1970; Wint 1983; but see Weir 2023). Whilst there is evidence that oaks support an especially diverse range of Lepidopteran species (Narango et al., 2020), many temperate woodland lepidopteran species (and the passerine species that prey on them) will feed, forage and breed across a variety of woodland habitats (Allan 1979; Perrins 1979; Hagemeijer & Blair 1997; Simms 1971; Skinner 2009) and oak-dominated woodland represents just a fraction of the arboreal habitat present.

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). The extent to which inferences about the caterpillar phenological distributions on oak trees can be generalised to other tree species is largely unknown (Shutt *et al.* 2019a). If oak is exceptional as a resource (Fig 1g), as judged by the abundance and biomass of caterpillars, then framing the MMH with respect to this single primary producer taxon in oak-dominated woodlands may be a reasonable simplification of the food web, with other tree taxa contributing little to the size of the caterpillar guild on a local scale. However, oak represents a small proportion of the available woodland habitat in which many lepidopteran and passerine species are found (Allan 1979; Perrins 1979; Hagemeijer & Blair 1997; Simms 1971; Skinner 2009; Stagg & Ward 2019).

The potential for the composition of woodlands to contribute to phenological buffering depends on how phenological distributions of caterpillars vary among host trees. For instance, if all tree taxa host a similar phenological distribution of caterpillars, there would be very limited scope for a mixed woodland composition to provide phenological buffering for either caterpillars or birds(Fig 1e), as being asynchronous with the resource on one tree taxon means being asynchronous with all. Where there are differences among tree taxa in the timing, width and duration of the caterpillar peak, but peak heights are similar, this can give rise to the potential for phenological buffering for generalist caterpillars or birds (Fig 1f);if resource levels are low due to being asynchronous with one tree taxon, the consequences for consumers may be buffered by asynchrony being less and/or resource levels being more plentiful on alternative taxa. . In addition, if multiple tree taxa support similar numbers of caterpillars (i.e. one tree taxon is not exceptional) this enhances the potential for spatial heterogeneity in woodland composition to facilitate buffering via spatial portfolio effects, whereby consumer-resource asynchrony at one location is buffered by synchronous interactions elsewhere (Burgess *et al.* 2018; Schindler et al., 2015; Weir & Phillimore 2024).

A wide variety of mechanisms exist that could give rise to among host taxon variation in the timing, height and width of the peak in the abundance and biomass of the caterpillar guild. For instance, timing differences in the abundance of caterpillars could reflect adaptation of different populations or species to the leaf out times of different host species (Murray *et al.* 1989; Roberts *et al.* 2015; Cole & Sheldon 2017) or dominant hosts in a stand. Differences in leaf nutritional quality (Schultz *et al.* 1982; Yanar *et al.* 2017), could affect Lepidopteran abundance and biomass through effects on fecundity (Awmack & Leather 2002), survival (Wint 1983; Yanar *et al.* 2017), and growth (Loader & Damman 1991). Preferential laying by females on specific hosts (Thompson & Pellmyr 1991; Kakimoto *et al.* 2003), or dispersal by larvae (van Asch & Visser 2007; Forkner *et al.* 2008) could amplify differences in abundance and biomass among tree taxa. Where host tree species differ in their ability to support an abundance of caterpillars this could have secondary effects at the tree stand-level, via local source-sink dynamics; arising via dispersal of caterpillars between trees or via indiscriminate host-choice by females during egg-laying. Among tree taxon variation in caterpillar growth rates, time to pupation and the caterpillar species supported could all generate differences in the width of the phenological distribution of biomass.

Field comparisons of caterpillar phenological distributions among woodland types have been few in number, particularly in relation to differences among deciduous taxa, with more focus given to comparing oak to coniferous or other deciduous habitats (van Balen 1973; Mägi *et al.* 2009; Veen *et al.* 2010; Burger *et al.* 2012). Evidence that oak may not be the sole key resource comes from field studies in Białowieża Forest, Poland – where hornbeams (*Carpinus betulus*), maples (*Acer platanoides*) and limes (*Tilia cordata*) were all found to receive more herbivory damage than pedunculate oak (*Q. robur*) (Wesołowski & Rowiński 2006) – and in Scotland – where willow (*Salix* spp.) and birch (*Betula* spp.) hosted quite similar caterpillar abundances to oak (Shutt *et al.* 2019a). In addition, experimental work finds that the growth and survival of a dominant European forest species, the winter moth (*Operophtera brumata*), is higher on a range of other host taxa than on oak (Weir 2024). The only work that we are aware of that compares phenological distributions of caterpillars across multiple deciduous taxa is Shutt et al.'s (2019a) study in Scotland, which reported no difference in peak timing between oak, willow, birch and sycamore (*Acer pseudoplatanus*), though estimates had broad credible intervals.

Here we build on Shutt et al.'s (2019a) study on the effects of tree taxa on the phenological distribution of caterpillars, using 7.5x the number of caterpillar samples (48466 records), collected over 10 years from 44 deciduous Scottish woodland sites and incorporating an additional six tree taxa. We have two main aims that are directed at establishing the potential for caterpillar host-breadth to generate phenological buffering in this system. First, we test the general hypothesis that abundance varies among tree taxa, and the more specific hypothesis that oak trees and oak woodlands host exceptional abundances of caterpillars. Second, we assess the degree to which the full phenological distribution (timing, height, width and duration) of abundance, mass and biomass varies among host tree taxa. These tests allow us to examine the potential for woodland composition to provide a source of phenological buffering in this system. Gaining answers to these questions has implications for climate resilient management of forests and the food webs that they host.

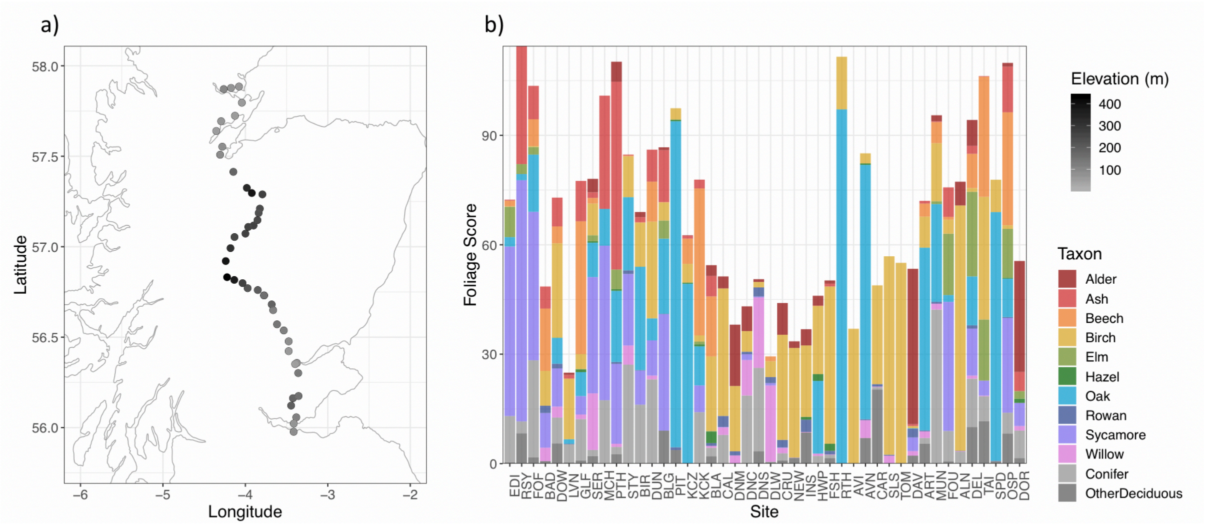

Figure 2: a) Map of site locations in Scotland, the darkness of the points indicates the site elevation and b) shows the woodland habitat composition at each site displayed as a foliage score which accounts for tree size (Shutt *et al.* 2018, see methods), sites are ordered by increasing latitude from left to right.

Materials and Methods

Study System

This study was carried out at 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. 2a). This includes the 40 sites monitored between 2014-16 (Shutt *et al.* 2018) and four additional sites monitored from 2017 onwards (Macphie *et al.* 2023). Since 2020 the number of sites monitored for caterpillars has varied, with some, predominantly northern, sites excluded in some years: the number of sites monitored were 2020=22, 2021=37, 2022=43, 2023=22. Woodland habitat composition has been surveyed at a 15m radius around each nest box installed at the sites (6-8 nest boxes per site, with one site limited to 4), 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, categorised by three sizes: small (circumference at chest height [cch]: 0.4-0.99m), medium (cch: 1.0-2.49m) and large (cch: >2.50m). 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 intended to approximate the relative contribution of different taxa to the local foliage in a metric equivalent to the mean number of 'small' trees of each taxon within a 15m radius circular area (Fig. 2b). One 'medium' tree contributes 6.25 units and one 'large' tree contributes 39.06 units.

Across all sites and species, the percentage of woodland composed of any taxon ranges from 0-100% and each tree taxa was absent from at least 4 of the sites (Fig 2b). The range of site tree compositions includes 11 birch dominated sites, six oak dominated, two alder dominated, two sycamore dominated, one beech dominated and one willow dominated (with dominance defined by a threshold of 50%). The remaining 21 sites were of various mixed compositions, only one is dominated by 100% birch."

Caterpillar Sampling

Caterpillar sampling followed the branch beating methodology described in Shutt *et al.* (2019a). A selection of trees at each site, approximately representative of the site's tree composition (Fig S1), were monitored for leafing phenology (Shutt *et al.* 2019b) and those that had a branch of minimum length 1m and between 0.5-1.5m above the ground were also beaten. The focal tree taxa sampled were alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), birch (*Betula* spp.), elm (*Ulmus glabra*), hazel (*Corylus avellana*), oak (*Quercus* spp.), rowan (*Sorbus aucuparia*), sycamore (*Acer pseudoplatanus*) and willow (*Salix* spp.). One branch per tree meeting the height and length criteria was marked and beaten every four days. 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 total individual trees sampled at each site in each year was 2014=3, 2015-16=6, 2017-18=14, 2019=15 and 2020-23=14, with a total of 48466 beating samples recorded across the 10 years. Sampling began each year when approximately 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 *et al.* 2019a), with the exception of 2020 in which sampling began when we were able to begin field work and tree phenology was not recorded due to the Covid-19 pandemic. Sampling periods extended between the following ordinal dates in each year: 2014=120-166, 2015=125-175, 2016=130-173, 2017=123-167, 2018=129-172, 2019=117-168, 2020=130-170, 2021=133-175, 2022=119-170 and 2023=127-171.

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 *et al.* 2019a) 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 total biomass of each sample was recorded to 0.01g using a Myweigh Triton T3R-500 Digital Scale. We recorded the cases where 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 S2-5). Poisson GLMMs were used for all models looking at variation in caterpillar abundance and posterior predictive checks were used to confirm that the data were not zero-inflated as compared with model expectation. Gaussian GLMMs were used to model individual caterpillar mass.

All models included the following structural random terms to allow for spatio-temporal differences in caterpillar abundance and individual mass (Table S1): site, year (as a factor), site-by-year and day-by-site-by-year. We also included the unique tree ID and recorder of each beating sample as random terms.

Abundance

Variance decomposition of caterpillar abundance

To quantify the relative contributions of spatial and temporal factors to variation in caterpillar abundance we decomposed the variance (abundance decomposition model, Table S1). The response variable was the number of caterpillars recorded in each beating sample with date and date^2 included in the fixed effects to account for the humped temporal distribution. Date refers to ordinal date and was z-transformed in all models (prior to scaling: mean = 146.77 [27th May, 26th in leap years], SD = 14.04). The variance explained by date (a) and date^2 (b) was calculated by matrix multiplication between the parameter estimates and covariance matrix of the two variables using the quadratic equation:

Equation 1: $$[\beta_a \quad \beta_b]\begin{bmatrix}\sigma_a^2 & \sigma_{a,b}\\ \sigma_{a,b} & \sigma_b^2\end{bmatrix}[\beta_a \quad \beta_b]^T$$

In addition to the structural random terms that were included in all models, this model included each day in each year and the host tree taxon. We calculated the mean percentage of latent scale variance that is attributable to the date and date^2 fixed effects and each random term.

Tree taxon and habitat variation in caterpillar abundance

We assessed differences in the abundance of caterpillars supported by different tree taxa (host-level), the effect of local foliage density and whether the foliage score of each tree taxon (stand-level) contributing to local woodland composition has any additional effect (habitat abundance model, Table S1). To calculate the site stand-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 at the host-level were grouped as 'other deciduous'. The *i*th observation of caterpillar abundance on host taxon *j* at site *k* was modelled as:

Equation 2:

$$y_{ijk} = b_0 + u_j^{(h)} + \sum_s (b_1 + u_s^{(g)}) f_{sk} = b_0 + u_j^{(h)} + b_1 f_k + \sum_s u_s^{(g)} f_{sk}$$

Here b_0 is the intercept, $u_j^{(h)}$ is the effect of host taxon *j*, f_{sk} is the (globally mean-centered) foliage score for each stand taxon *s* at site *k and* $f_k = \sum_s f_{sk}$ *is* the total foliage score at site *k*. b_1 is the average effect of foliage score on *y* (irrespective of stand composition) and $u_s^{(g)}$ is the deviation from this average for taxon *s* in the tree stand. $u_j^{(h)}$ and $u_s^{(g)}$ are random effects with estimated variance.

Phenological Distributions of Abundance, Mass and Biomass

Caterpillar abundance

To quantify how the phenological distribution of caterpillar abundance throughout spring differs among tree taxa, we allowed each taxon to have a distinct temporal trend in abundance over the course of the spring (abundance phenology model, Table S1). Date and date^2 were included as fixed effects, to allow for a humped phenological distribution over time (Shutt *et al.* 2019a). We included tree taxon random effects on the intercept, date and date^2 slopes to capture among taxon variation in phenological abundance distributions. We included date and date^2 random slopes for site and year as additional structural terms. For each tree taxon we used model posteriors to derive estimates of the mean timing, height (maximum abundance), and width, calculated at half the peak height. We also calculated how the duration of the peak varied among tree taxa (peak duration) at a consistent abundance of 0.01 caterpillars per branch. We primarily present peak width as a metric that describes the shape of the peak and rate of change in abundance whilst being unaffected by peak height. We also discuss peak duration (which includes an effect of peak height, Fig 1 c-d) due to its implications for top-down and bottom-up trophic impacts, describing the length of time for herbivory of young leaves and key food availability for many breeding birds.

We assessed the adequacy of the quadratic function in describing the shape of the phenological distribution of caterpillar abundance by including a cubic date term. The additional cubic term allows for the phenological distribution to take an asymmetric form (Table S6). Details of the analysis can be found in Supplementary Information.

Caterpillar Mass

To obtain the mean mass per caterpillar in a sample we divided the mass for each sample by the number of caterpillars weighed. 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 between 0.001g and (0.02/n)g, where 0.001g is the minimum mass viable for an individual caterpillar sampled in-line with the methodology (J. C. Weir, unpublished data) and n is the number of caterpillars in the sample. Average individual mass observations were log transformed and modelled as interval-censored Gaussian.

The individual mass model included date and date^2 in the fixed effects, which would allow for a curved trend in proportional growth if appropriate (mass phenology model, Table S1). The focal random terms were the tree taxa random intercepts and date slope. In addition to the structural random terms, we included a date random slope for sites, allowing for spatial variation in phenology. Year was included as a random intercept but not as a random slope in order to aid model convergence, as mass data were only recorded since 2017. The residual variance for each observation was modelled as $\frac{1}{n}VAR(u) + VAR(e)$ where n is the number of caterpillars in the sample, $VAR(u)$ is the variance in individual caterpillar mass after accounting for all other terms in the model, $VAR(e)$ is the residual variance which includes variability in the true mean individual mass across samples and measurement error; thus weighting the confidence in each sample by the number of caterpillar from which the mean per caterpillar was calculated. 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 of an individual caterpillar at day 168 (16th June), which corresponds to the latest date on which a caterpillar has been sampled on each of the tree taxa.

Caterpillar biomass

Total biomass, the product of abundance and average individual mass, can be obtained by exponentiating the sum of the linear predictors from the abundance and individual mass models, since both were modelled on the log scale. Ideally a bivariate model would have been used to allow for covariance between abundance and individual mass across random terms, however due to the interval censoring required for the mass data this could not be implemented. Instead, we used the posterior distributions of the two models to generate a posterior distribution for the phenological distribution of total biomass. The same peak metrics as discussed for the abundance results were calculated, with peak duration estimated at a total biomass of 0.25mg.

Fixed effects were considered significant if the 95% credible intervals (CIs) did not overlap zero. Random effects were considered significant if the lower credible interval for their variance was removed from 0. We used the mean of the posterior distribution when estimating effect sizes and the mode for reporting the random term variances. Where we present estimates on the data scale these correspond to the median rather than the mean expectation on the data scale. 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 random effect (co)variances such that the marginal priors for the variances were scaled $F_{1,1}$ with a scale of 100. An inverse gamma distribution with shape=scale=0.002 was used for the residual variance. Default flat priors were used for the fixed effects.

All results comparing caterpillar abundance, average individual mass or total biomass among host tree taxa are presented primarily as deviations from the fixed effect prediction, which represents an average tree taxon. In addition, to test the hypothesis that oak is exceptional as a caterpillar resource we also estimate taxon effects as deviations from the prediction for oak, described fully in Supplementary Information. The abundance and individual mass of caterpillars are both modelled on the log scale, meaning that the exponent of coefficients relating to differences in abundance, mass or peak height among tree taxa quantifies proportional differences.

Results

Overall, we found that 9.2% of branch beating yielded at least one caterpillar. Where a caterpillar was present, in 70.6% of cases there was just 1 and in 15.3% there were 2, with a maximum abundance of 107, recorded during an outbreak at one of our sites during 2019.

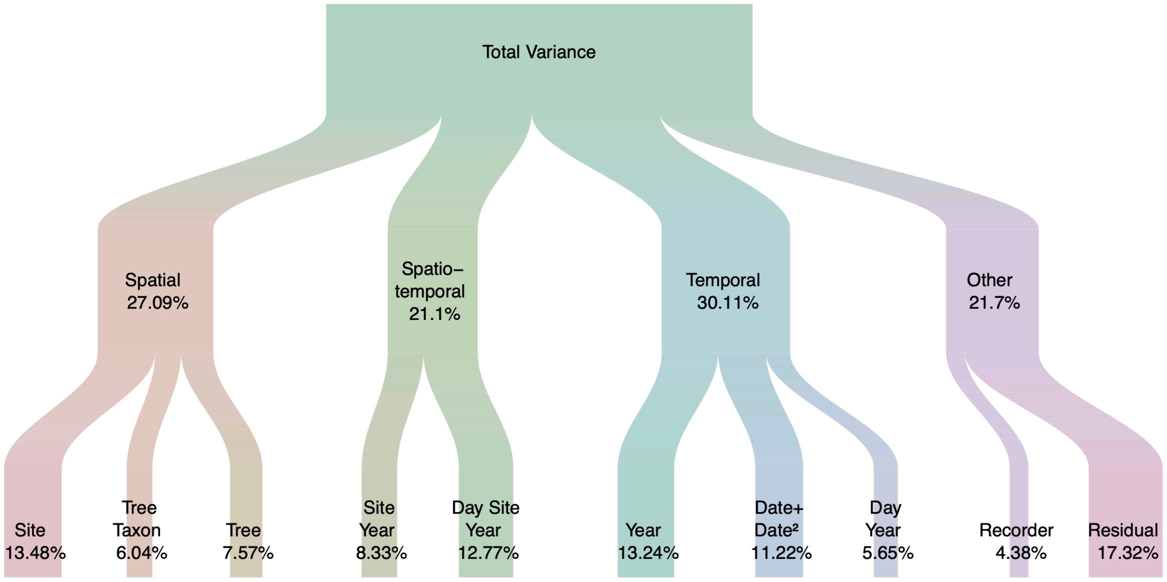

Figure 3: Riverplot of the percentage variance composition of caterpillar abundance estimated from terms in a Poisson GLMM (Table S2). All variables were included as random terms except for Date+Date^2 which were included as numeric fixed effects to model the humped shape of the phenological distribution.

Abundance

Partitioning variance in caterpillar abundance

All variance posterior distributions in the abundance decomposition model (Table S1, S2) were removed from zero, meaning that we have statistical support for each term. The spatial, temporal and spatiotemporal components explained 78.30% (CIs: 73.24 – 83.83%) of the variance, with temporal and spatial components explaining similar proportions, 30.11% (CIs: 20.93 - 43.09%) and 29.09% (CIs: 18.33 - 36.31%) respectively (Fig. 3). Host tree taxon explained 6.04% (CIs: 1.36 – 13.40%) of the variance (Fig. 3).

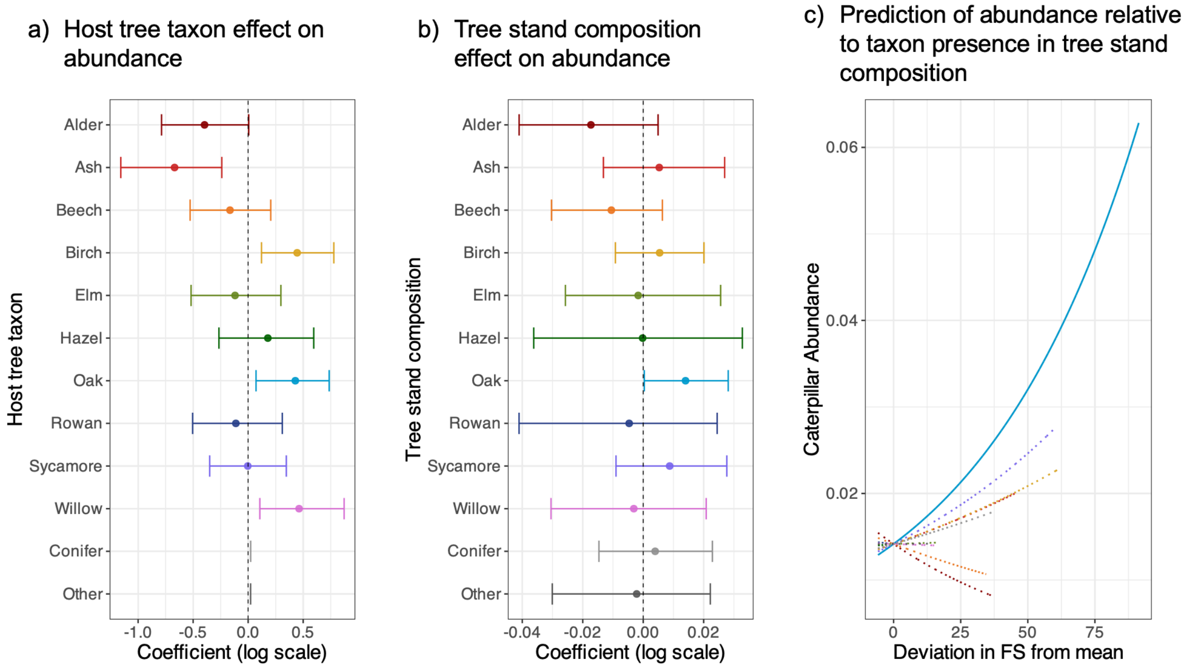

Figure 4: a-b) Posterior mean and 95% credible intervals for random effects in a Poisson GLMM (Table S3). Predicted coefficients for a) the log difference in abundance of caterpillars (number of caterpillars) sampled from each host tree taxon (conifers and other deciduous trees were not included) and 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 tree stand composition (globally mean centred foliage scores). c) Slope predictions from a Poisson GLMM (Table S3) analyzing the change in caterpillar abundance with change in the amount of foliage of each tree taxon present in the tree guild at each site (globally mean centered), colours consistent with taxa in a) and b). The intercept falls at the mean foliage score (FS) of any taxon at any site and

mean total FS across all sites. Dotted and solid lines indicate a non-significant and significant difference in slope from zero, respectively.

Tree taxon effects on caterpillar abundance

We found substantial variance in the abundance of caterpillars sampled among host tree taxa in the habitat abundance model (Table S3). Ash (0.53 CIs: 0.28 - 0.75) hosts roughly half as many caterpillars as an average tree taxon, whilst oak (1.56, CIs: 1.07 - 2.08), birch (1.58, CIs: 1.12 - 2.17) and willow (1.62, CIs: 1.03 - 2.26) all host roughly 1.5 times as many caterpillars as an average tree (Fig. 4a). The results are also suggestive of alder hosting proportionally fewer caterpillars than average, with the exponentiated coefficient posterior distribution CIs falling below one (0.69, CIs: 0.43 – 0.96), though the log-scale coefficient posterior distribution overlaps zero (-0.40, CIs: -0.79 – 0.01; Fig. 4a). In comparison with oak, six (alder, ash, beech, elm, rowan and sycamore) of the nine other tree taxa support significantly fewer caterpillars (Fig. S2).

We found that in general the stand-level foliage density was not associated with elevated caterpillar abundance and also found no evidence that stand-level tree taxon composition affects caterpillar abundance, with the variance posterior distribution not removed from zero (Table S3). However, within the stand-level taxon effects we found some evidence of oak exceptionalism, as the abundance of caterpillars increased with the stand-level amount of oak foliage (Fig 4b-c). Across the range of oak foliage that we observe among our sites, the increase in oak availability is associated with 5.52 (CIs: 1.14 – 11.20) times the caterpillar abundance on a branch of any taxon moving from a woodland with no oak trees to one dominated by mature oak trees (Fig. 4c).

Phenological distributions of Abundance, Mass and Biomass

Caterpillar abundance

A humped seasonal trend in the temporal distribution of caterpillar abundance is apparent in our data (Fig. S3) and supported by the significant negative quadratic date term from the abundance phenology model (-0.76, CIs: -1.02 - -0.52, Table S4). We found substantial among -host tree variance in intercepts and date slope effects, but not the date^2 effects (Table S4). For the average tree taxon, in an average site and year, the predicted peak date is ordinal day 154.68 (CIs: 149.59 – 159.84) or 2nd/3rd June, with a peak height of 0.04 (CIs: 0.02 - 0.07) caterpillars per branch, and peak width of 27.38 days (CIs: 23.03 – 31.95 days). The predicted duration of the phenological distribution is 38.21 days (CIs: 28.19 – 49.56 days). When we calculated peak 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 from calculations which will make the mean and CIs slight underestimates.

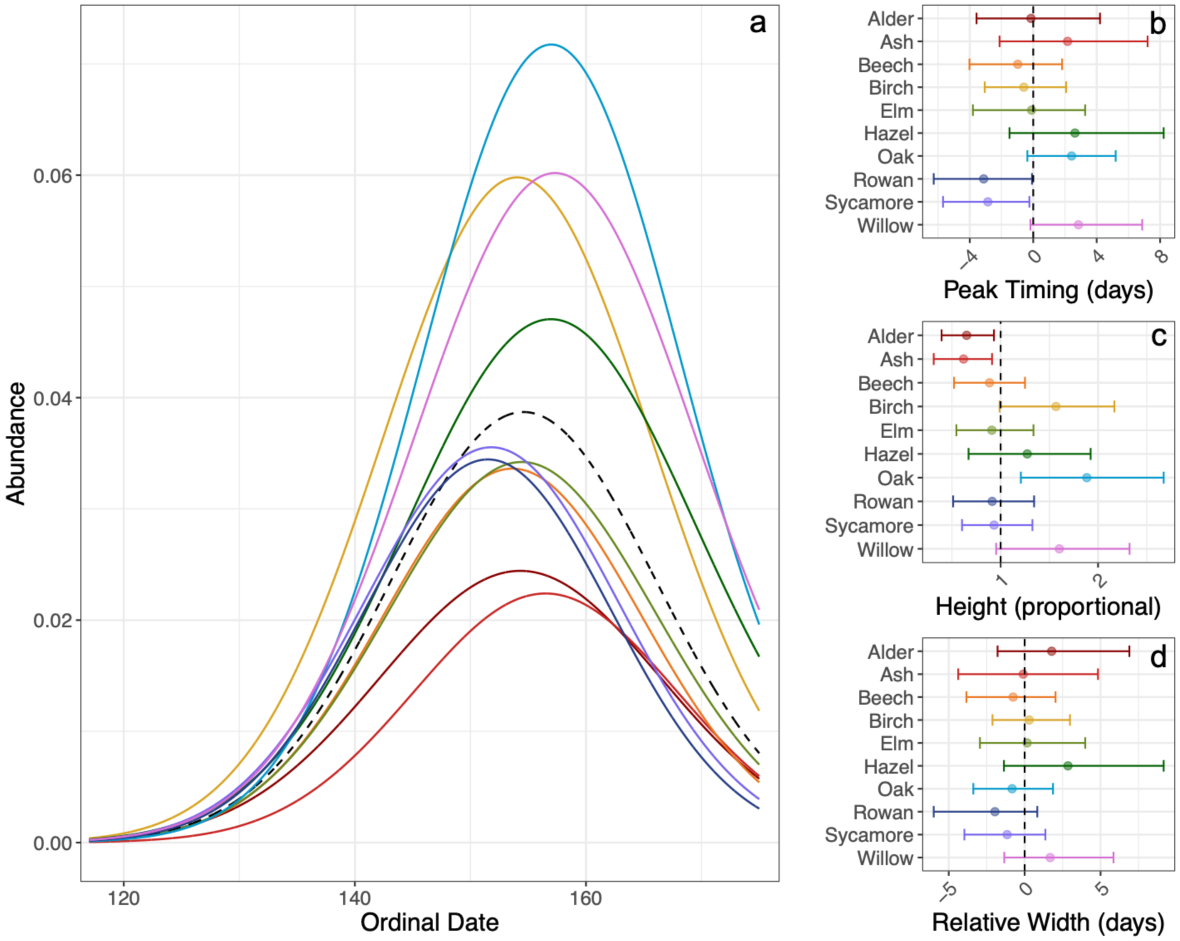

Figure 5: Model predictions for the phenological distribution of caterpillar abundance (number of caterpillars) on branches of different tree taxa (Table S4). a) shows the model predictions for the phenological distribution of caterpillar abundance (ordinal date) for each tree taxon, the black dashed line depicts the 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, c) proportional change in the height of the peak (maximum abundance) and d) width of the peak at half of the height. The mean and 95% credible interval were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

We found some evidence for among host tree taxon differences in the phenological distributions of caterpillar abundance (Fig. 5a). The peak timing of caterpillars on rowan (-3.12 days, CIs: -6.27 - -0.08) and sycamore (-2.86 days, CIs: -5.86 - 0.24) were significantly earlier than for the average taxon (Fig. 5b). The height of the peak in caterpillar abundance departed significantly from the average taxon for three taxa (Fig. 5c); alder (reaching 0.65, CIs:

0.39 - 0.93, times the average peak height), ash (0.62, CIs: 0.31 - 0.91) and oak (1.88, CIs: 1.21 - 2.67). The point estimates of peak height were relatively high for birch (1.57, CIs: 0.99 - 2.17) and willow (1.60, CIs: 0.95 - 2.32), though the CIs include zero.

The width of the abundance phenological distribution did not significantly differ between any host tree taxon (Fig. 5d). Due to the relatively consistent shape but variable peak height, duration showed more variation among host taxa, lasting for 6.60 days (CIs: 0.15 – 14.47) and 8.67 days (CIs: 1.20 – 18.31 days) longer than the average taxon on oak and willow respectively (Fig. S4); again the point estimate for birch (6.28 days, CIs: -0.11 - 13.44) was relatively high, though the CIs included zero. The caterpillar phenological distribution on oak was found to be significantly later than on beech, birch, rowan and sycamore, significantly higher than all tree taxa tested except birch and willow and lasting for a significantly longer duration than peaks on all tree taxa tested except birch, hazel and willow (Fig. S5).

When we tested for asymmetry in the caterpillar phenological abundance distribution (Table S6), we found that the cubic term was significant (Table S7), but the resulting asymmetry in the peak estimate was low (Fig. S9).

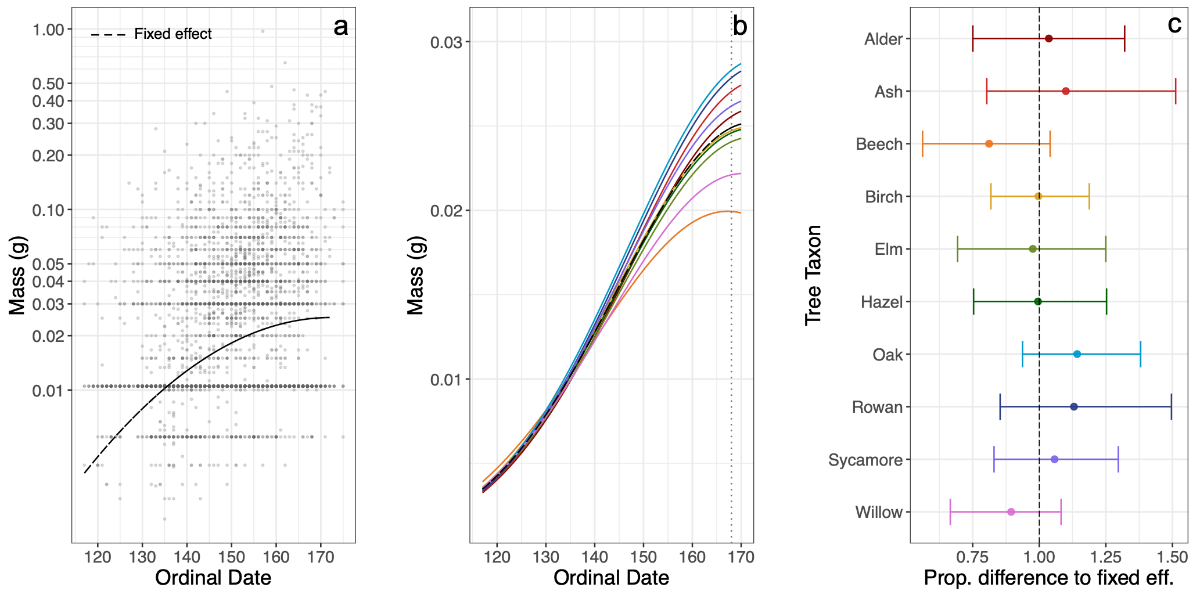

Figure 6: Model predictions for individual caterpillar mass over time (Table S5). a) Observed data (dots) and fixed effect prediction (line). b) Individual mass over time for caterpillars on each tree taxon, with the black dashed line showing the fixed effect trend from plot a). The grey dotted vertical line indicates the day 168 (16th June), the latest date with caterpillar mass data for all tree taxa. c) shows the posterior mean and 95% credible intervals for the proportional difference in day 168 mass between each tree taxon and the fixed effect prediction.

Caterpillar mass

Most caterpillars throughout spring weighed less than 0.1g, although caterpillars of up to 0.96g (n=1) were recorded (Fig. 6a). There was a pronounced trend for individual mass to increase over the course of the spring, with the rate of increase declining on the log scale (Fig. 6b, Table S5). The variances among tree taxa in the intercept and date slope were non-significant. The day 168 mass of individual caterpillars (in mid-June) predicted from the fixed effects was 0.025g (CIs: 0.017 - 0.034g) for an average tree taxon. Whilst the curves and day 168 masses do not differ significantly between any tree taxon and the fixed effect trend (Fig. 6b-c), we found the ultimate mass of individual caterpillars was significantly lower for those sampled from beech compared to oak (Fig. S6). Willow had similarly low point estimate for ultimate individual mass when compared to oak, though the CIs included zero (Fig. S6).

Caterpillar biomass

Based on the fixed effects from the abundance and individual mass phenology models (Tables S1, S4, S5), the predicted peak date for the total biomass phenological distribution on the average host tree taxon is day 157.32 (CIs: 152.67 – 162.26), 5/6th June, two days later than the peak in abundance. The total biomass peak height was predicted to be 0.9mg (CIs: 0.3 – 1.6mg) per branch, with a width of 25.23 days (CIs: 21.74 - 28.94), narrower than the distribution of abundance, but with overlapping CIs. The peak duration was 32.89 days (CIs: 21.73 – 44.20) at a threshold of 0.25mg of caterpillars per branch. Similarly to the abundance peaks, some iterations (≤3%) produced NAs in the calculations of peak duration so the mean and CIs are underestimates.

Whilst some slight differences in host taxon effects are visible depending on whether total biomass (Fig 7) or abundance (Fig 5) is the focal metric, timing, height and width are broadly consistent; though few effects are removed from zero for total biomass due to increased uncertainty in the estimates. No taxon differs significantly in total biomass mean timing when compared to the average tree taxa. For the peak height of total caterpillar biomass, oak is higher than average, reaching 2.20 (CIs: 1.35 – 3.22) times the abundance of an average tree, whereas alder is lower than average, reaching 0.66 (CIs: 0.37 – 0.98). No tree taxa differed in peak width to the average taxon, but oak and willow lasted for significantly longer durations than the average tree by 8.43 days (CIs: 1.67 – 16.48) and 7.28 days (CIs: 0.09 – 16.53) respectively. When compared to oak, the biomass peak height point estimates and CIs for birch and willow sit lower than the abundance peak height equivalents, though posteriors heavily overlap (Fig. S5, S8).

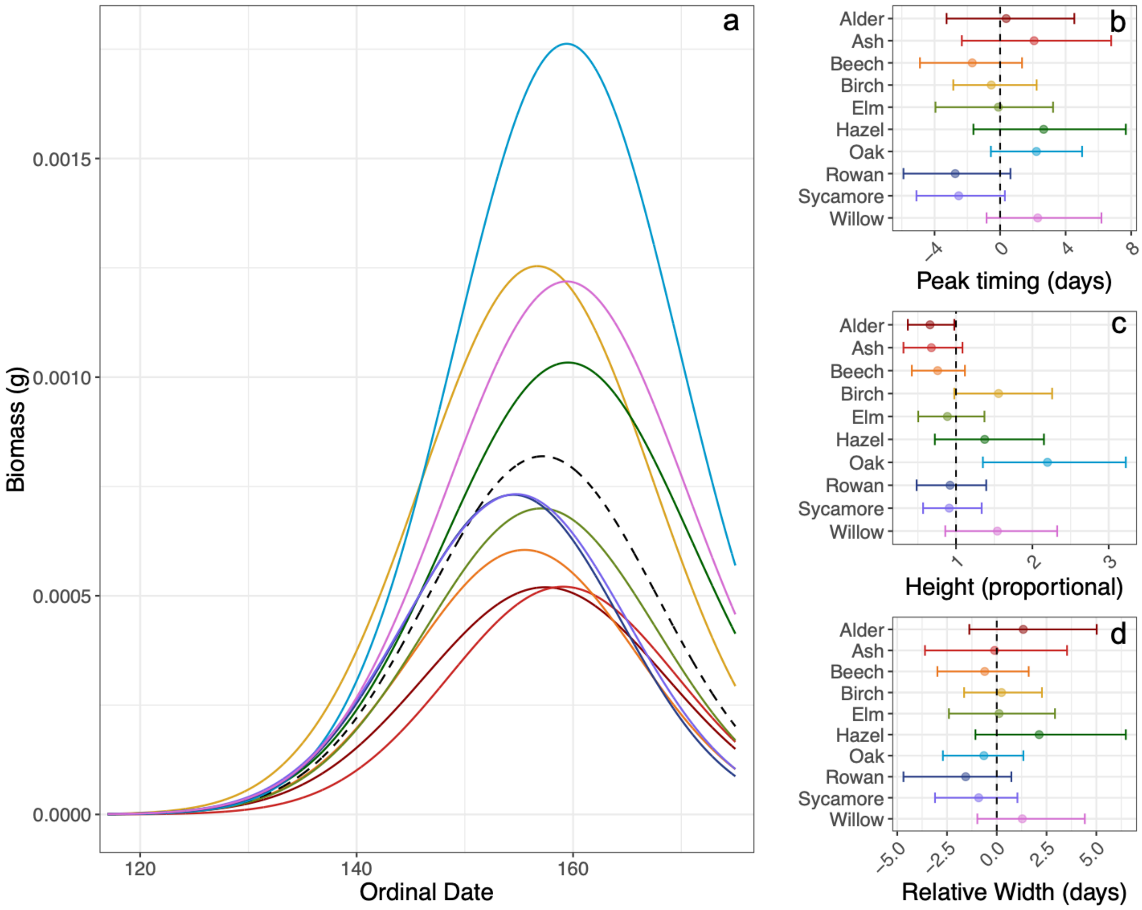

Figure 7: Model predictions for the phenological distribution of total caterpillar biomass on branches of different tree taxa (based on models in Table S4+5). a) shows the model predictions for the phenological distribution of caterpillar biomass (ordinal date) for each tree taxon, the black dashed line depicts the 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, c) proportional change in the height of the peak (maximum biomass) and d) width of the peak at half of the height. The mean and 95% credible were calculated using the posterior distributions for the fixed effects and tree taxa random effects and interactions.

Discussion

We show evidence of substantial variation in the height of the caterpillar peak among tree taxa, with some variation in mean timing and duration. Of the three scenarios presented in Figure 1 (e-g), we find most support for the exceptional host hypothesis (Fig 1g). The most exceptional host taxon identified was oak, with caterpillar abundance and total biomass being elevated on oak compared with most other species, and oak dominance in woodlands having a positive stand-level impact on caterpillar abundance. However, we find the caterpillar peak height on birch and willow to be broadly comparable to oak (Fig 1e), consistent with Shutt et al. (2019a), whilst the peaks on alder and ash reach lower heights than average. We also did not find any evidence for oak exceptionalism in terms of the average mass of individual caterpillars. At the host-level, we find effects of tree taxon on the timing of phenological distributions for abundance. Mean timing of the phenological distribution of caterpillar abundance falls earlier on rowan and sycamore trees than on an average taxon (Fig. 5b), however we note that the 3-day difference in timing estimated is a relatively small effect size and we suggest this is likely to contribute little to the buffering potential. Whilst the width of the peak varies rather little among tree taxa (Fig 5d, 7d), the height and width of each taxon taken together result in the duration of peaks on oak and willow lasting for roughly a week longer than for the average tree taxon (Fig. S4). We find minimal evidence for individual caterpillar mass gain differing among host tree taxa, and therefore, most of the among tree taxon differences in aspects of the phenological distribution of total biomass track the trends that we observe for abundance, albeit with broader credible intervals.

The positive stand-level impact of oak foliage density on caterpillar abundance (Fig. 4c), suggests that oak-dominated woodlands may be unique in the numbers of spring caterpillars that they support. This stand-level effect may be due to a combination of high caterpillar abundance on oaks and dispersal to other taxa, either via oak-raised females laying eggs or dispersal of caterpillars from oaks to other trees in spring. Another possibility is that oaks represent especially good hosts to generalist species, as was found earlier for the generalist winter moth (Shutt et al 2019), which could then mean that species dispersing from oak may be more likely to find a suitable host. Why stand-level impacts arise for oaks but not for other tree taxa that have a positive host-level impact on caterpillar abundance, such as willow, may be attributable to the greater size of oak. The crown areas and heights of oaks generally surpass most other tree taxa considered here, and may influence the likelihood of dispersal throughout an area for both the caterpillars and adults, particularly for species with wingless Lepidoptera females such as *Operophtera* spp., that made up 38% of previously identified samples in from these sites (Shutt *et al.* 2019a).

Our finding that caterpillar abundance on oak reaches a high peak but for a relatively short time period agrees with previous work (van Balen 1973; Varley *et al.* 1974; Visser *et al.* 2006; Veen *et al.* 2010), but we find this is similar to the abundance peaks observed on birch and willow. This positive host-level effect on caterpillar abundance must arise through either elevated survival through the life cycle, higher fecundity, greater species richness or a combination of these effects. A recent laboratory study has shown the developmental duration, mass at pupation and female fecundity of winter moth caterpillars to be lower when reared on oak foliage compared to a range of taxa, including lower fecundity and pupal mass than on birch *B. pendula* and willow *S. alba* and lower survival than on willow (Weir 2023). Winter moth make up approximately a third of individuals sampled from the caterpillar guild across our study sites (Shutt *et al.* 2019a), and these differing insights into the value of oak obtained in the field and laboratory are challenging to reconcile. One potential explanation is that winter moth caterpillar survival in-situ is distinct from that measured in the laboratory, possibly influenced by factors such as parasitism and predation or the density of leaves as a food source and their distribution across the tree. For birch and willow however, the high abundances reached *in-situ* may well be associated with the higher than average fecundity of caterpillars reared on them (Weir 2023). Conversely, those reared on alder had substantially lower survival and fecundity which suggests alder may serve as a sink habitat for some species (Weir 2023), in agreement with the low abundances we identified in-situ.

An implication of particularly high abundance and total biomass hosted by oak is that the common practice of monitoring caterpillar prevalence purely on oak (Visser *et al.* 2006; Smith *et al.* 2011; Hinks *et al.* 2015; Burgess *et al.* 2018) is liable to overlook spatial-heterogeneity in caterpillar abundance both between locations and within larger sites. Nonetheless, the elevated caterpillar abundance on oak and in oak-dominated woodlands may make these habitats the most important to consumers, more so than birch and willow when considering the additional stand-level effect. Oak woodlands possibly act as a source that contributes to the repopulation of areas with lower consumer breeding success, as the prevalence of oak within a stand has been shown to increase blue tit fledging success (Shutt *et al.* 2018).

Whilst oak is often used as a baseline for comparison with other woodland compositions (Mägi *et al.* 2009), the high abundance and total biomass of caterpillars this taxon hosts appears to be unrepresentative of certain other woodland types across the UK (Stagg & Ward 2019). In fact, our results suggest the phenological distribution of caterpillars on beech, elm, hazel, rowan and sycamore are more representative of an average deciduous tree taxon. Analysis of this substantially expanded data set broadly agrees with previous findings that alongside oak, willow and birch host greater/longer caterpillar abundances than the average tree, whilst alder and ash host lower abundances (Shutt et al. 2019a). As this study considers abundance at the caterpillar guild level it is unclear whether host taxon impacts on abundance are across a range of caterpillar species or instead arise via turnover, with some tree taxa hosting greater diversity than others (Narango et al., 2020). Consistent with this latter explanation, Shutt et al. (2019a) found that oak, willow and birch hosted the greatest species richness of caterpillars within our study system, a finding supported by work on Lepidopteran diversity across the United States (Narango et al., 2020). Our results suggest that the seasonal peak in abundance contributes more than individual mass in dictating the timing of the total biomass peak and the among tree taxa differences in the phenological distribution. We find that the individual mass of the sampled caterpillar guild increases rapidly in early spring before asymptoting (Fig. 6), with minimal difference in caterpillar growth rate and individual mass at the end of spring. Caterpillars sampled from beech, however, weighed significantly less than those sampled from oak (Fig. S6), consistent with results from rearing experiments using winter moth (*O. brumata*) (Feeny 1970; Wint 1983). Our measure of individual mass will have captured various processes including individual growth, and the appearance and disappearance of species from the guild through both varied phenologies among caterpillar species and turnover between sites. The guild level individual mass pattern therefore does not necessarily represent the growth curve of any particular caterpillar species and is of most relevance when considering the guild's involvement in trophic interactions and estimations of the relative contributions of individual mass and abundance to total guild biomass.

Our work suggests that the potential for woodland stand tree composition to alter the consequences of trophic asynchrony may be stronger than previously appreciated (Bell *et al.* 2019; Shutt *et al.* 2019a), as we have identified further differences in the caterpillar peak among tree taxa, particularly in peak height but also some deviations in duration and timing. As the composition of tree taxa varies in space, within and between woodlands, the differences in peak height that we observe among tree taxa are expected to result in geographic variation in caterpillar abundance. The phenological distribution of caterpillar abundance and total biomass on oak and willow lasts for six-eight days longer than on the average tree taxon and the phenological distribution on oak lasts for longer than on alder, ash, beech, elm, rowan and sycamore by roughly 10-15 days (Fig. S5, S8). The extended duration of the peak on oak and willow prolongs the period of attack by herbivores and of resource availability for consumers from an average of 5.5 weeks to 6.5 weeks (at the level duration was measured at). Given many breeding passerines will feed young in the nest for up to three weeks, an additional week of resource availability may have substantial benefits for late or early birds. The lack of variation in peak width suggests that the shape of the peak does not differ substantially among taxa and thus the extended duration of the peak is predominantly associated with higher abundances of caterpillars and not a low but wide peak for some taxa. The distinction in duration between oak and willow and other taxa suggests the phenological distribution may vary substantially in duration between an oak- or willow-dominated woodland and one with a mixed composition, which may make the consequences of asynchrony more pronounced in woodlands that lack a substantial oak or willow component. Our results suggest that the within-site peak duration is unlikely to be greatly influenced by differences in mean timing among taxa as a three-day deviation from average is small relative to 5-6 week peak duration.

Whilst oak woodlands are thought of as the preferred habitat for many woodland passerines, many species breed and forage across a range of woodland compositions (Perrins 1979; Hagemeijer & Blair 1997; Simms 1971) and oak is not abundant across all woodland (Stagg & Ward 2019). In a mixed woodland, blue tits and great tits were found to spend more time foraging on oak than expected based on their prevelence, however they also spend longer than expected foraging on birch and sycamore trees (Peck 1989). A greater foraging effort by birds on oak and birch (Peck 1989), that we found host higher caterpillar abundances, may mean we have underestimated the extent of their true peak height, as would be estimated in the absence of natural predation (Böhm *et al*. 2011). The variation we have identified in the phenological distribution of caterpillars among tree taxa suggests that extending the study of the MMH into more varied woodland tree compositions will be key for understanding spatial variation in trophic interactions and how reforesting efforts might alter a key herbivorous guild.

Tree stand composition can be manipulated 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; Whittaker & Warrington 1985; Whitham *et al.* 1991; Marquis & Whelan 1994). Winter moth, the most common species in our study system (Shutt *et al.* 2019a), exhibits cyclic population dynamics with outbreaks causing severe defoliation (Tenow 1972; Hogstad 1997), also observed at one of our sites during spring 2019. Defoliation may be minimised if there is a lower density of oak, thereby preventing the additive effect it has on the abundance of caterpillars throughout the local tree stand. However, with the exception of oak, caterpillar abundance appeared to be insensitive to the amount of other tree taxa present at the stand-level. The second implication relates to the conservation of consumer populations for whom more caterpillars are expected to be beneficial, though the importance of resource abundance versus resource timing relative to breeding is relatively underexplored (but see Naef-Daenzer and Keller, 1999; Ramakers, Gienapp and 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). When considering consumer foraging effort, our results predict that on average a consumer foraging on an oak will encounter three times as many caterpillars per branch than when foraging on an alder or ash (Fig S5). For the benefit of consumers, the site-level peak height should be maximised through the addition of oak, willow and birch, though oak is likely to be of most benefit due to the additional stand-level effect on caterpillar abundance. The addition of oak and willow may also extend the duration of the caterpillar peak, potentially providing a valuable phenological buffer for early emerging caterpillars (Weir & Phillimore 2024). Our study also reveals substantial site and site-by-year effects in the phenological distribution of caterpillar abundance

(Table S4), and some site effects on individual mass (Table S5), which implies that factors in addition to woodland composition, as we have measured it, play an important role (Fig. 3). For example, elevational gradients may influence the phenological distribution of caterpillars via the effect of spatial temperature in space (Macphie *et al.* 2023).

In this study we have relied on repeated beating of a consistent length of marked branch as a standardised approach to caterpillar sampling. With this approach we cannot exclude the possibility that some of the differences in caterpillar abundance that we attribute to tree taxon actually arise from differences in structure and leaf area. However, such structural differences among tree taxa are unlikely to impact on our estimates of timing, duration or individual mass. Whether branch beating affects the defences produced by a branch and whether this imapct varies among tree taxa is unknown. It also remains to be tested whether the phenology estimated from repeated branch beating departs from the true phenlogical distribution of a tree due to removal of caterpillars or whether recolonisation is sufficiently rapid to mininise such effects. In this study we have identified certain trees to genus rather than species level, due to evidence of extensive hybridisation (Shutt et al. 2019a), and this precludes examination of intra-generic differences in phenology and abundance.

In summary, across 44 woodland sites we find partial support for oak providing an exceptional resource to the spring-feeding caterpillar guild. On a local scale this means that the contribution of tree species to phenological buffering may be quite limited. However, on a landscape scale our finding that additional tree taxa, particularly birch and willow, can provide an important resource and enhance the potential for woodlands that lack oak to contribute to buffering via spatial portfolio effects. Our findings have applications in woodland management and reforesting for the conservation of woodland lepidopteran and insectivore communities.

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Tree taxon effects on the phenology of caterpillar abundance and biomass: Supplementary Information

Supplementary Methods

Table S1: Terms included in abundance and mass models. Date refers to ordinal date, which was z-transformed (mean = 147.47, SD = 14.19), 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 S2)	Habitat abundance (Table S3)	Abundance phenology model (Table S4)	Mass phenology model (Table S5)*
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 variable	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 by year Day by site by year Year Year-day Recorder	Tree taxa Woodland-composition Site Year Site by year Day by site by 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 by year Day by site by year Tree ID Recorder	Int and Date VCV across Tree taxa Int and Date VCV across Site Year Site by year Sqrt(1/abund) VCV across observations Day by site by year Tree ID Recorder
Family	Poisson	Poisson	Poisson	Censored-Gaussian
MCMC Iterations (thinning intervals)	4000000 (1500)	9000000 (2500)	3300000 (1000)	2500000 (2000) 2500000 (2000) 2500000 (2000)
Burnin	100000	500000	300000	500000 for each
Posterior Sample Size	2600	3400	3000	3000 (1000 x3)

*Mass phenology model was run as three chains that were then combined

Sampled trees vs local stand tree composition

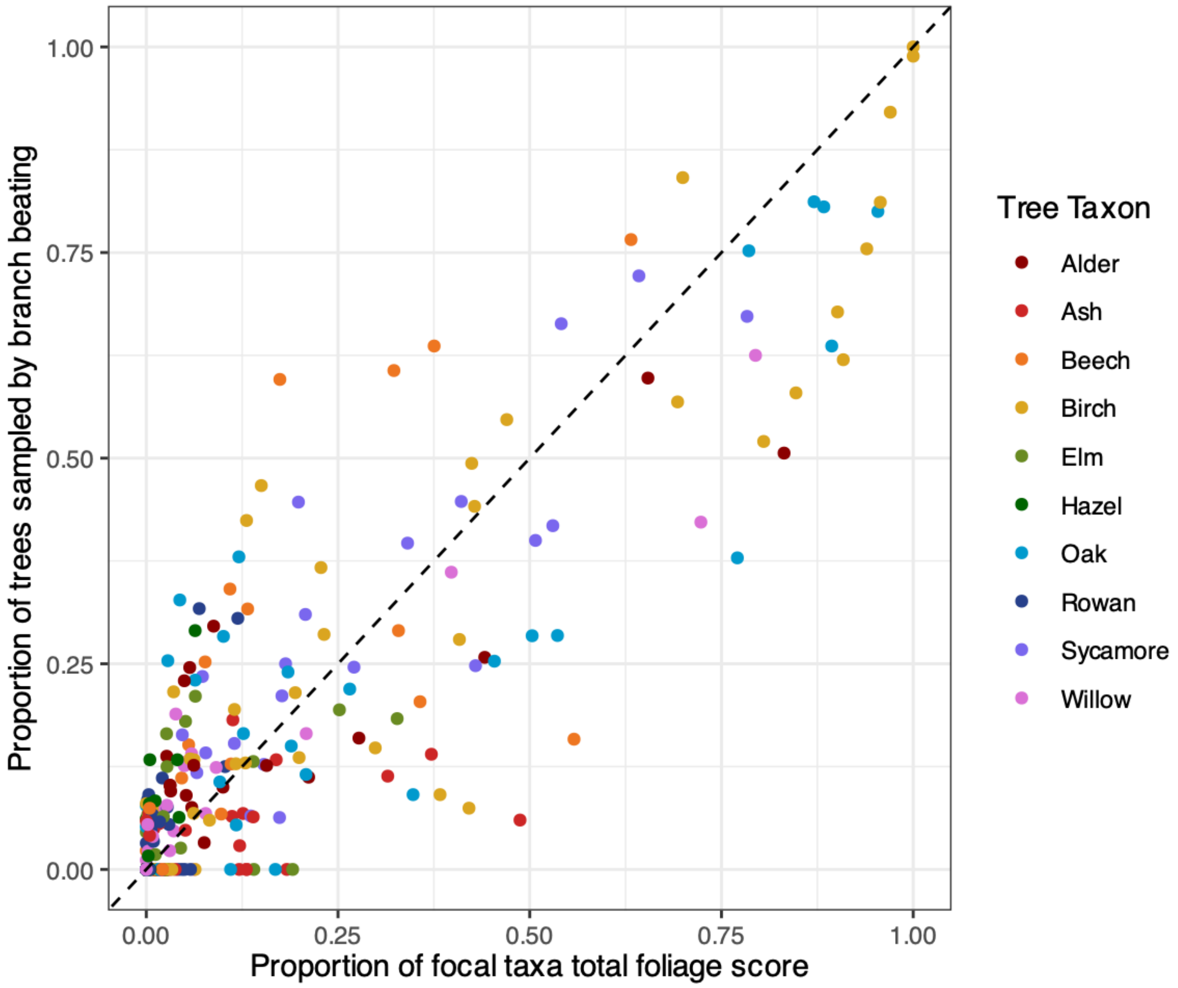


Figure S1: Taxon-specific proportion of trees sampled via branch beating at each site across years plotted against the taxon-specific proportion of the total foliage score among focal tree taxa (those sampled in branch beating), coloured by tree taxon. Dashed black line shows 1:1 relationship. Data points where the proportion of the total foliage score = 0 but the proportion of sampled trees > 0 can occur because habitat surveys are conducted at a 15m radius around installed nestboxes, whilst some beaten trees fall between nest boxes.

Supplementary results

We found that alder, ash, beech, elm, rowan and sycamore all support significantly fewer caterpillars than oak (Fig. S2), hosting 0.44 (CIs: 0.30 - 0.58), 0.34 (CIs: 0.21 - 0.49), 0.56 (CIs: 0.42 - 0.72), 0.59 (CIs: 0.40 - 0.78), 0.59 (CIs: 0.39 - 0.79) and 0.66 (CIs: 0.51 - 0.80) times as many caterpillars respectively.

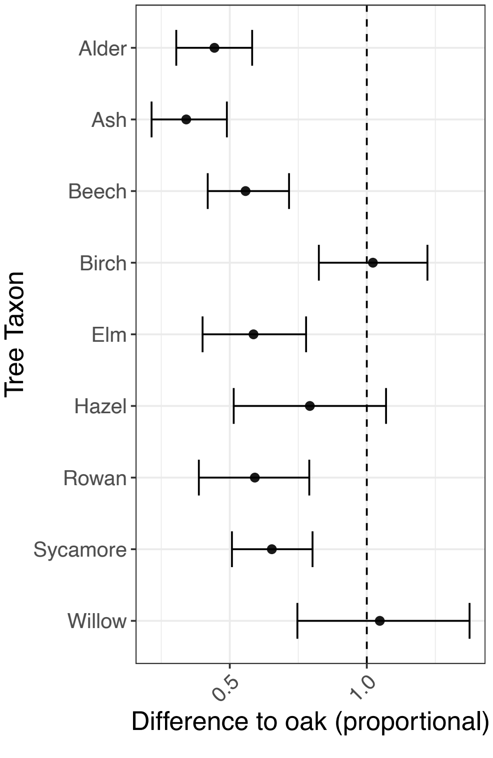


Figure S2: Posterior mean and 95% credible intervals of the model prediction for the proportional difference in caterpillar abundance between each tree taxon and oak. Calculated from tree taxa random effects in a Poisson GLMM (Table S3). Black dashed line at 1.0 indicates no difference to oak/significance threshold.

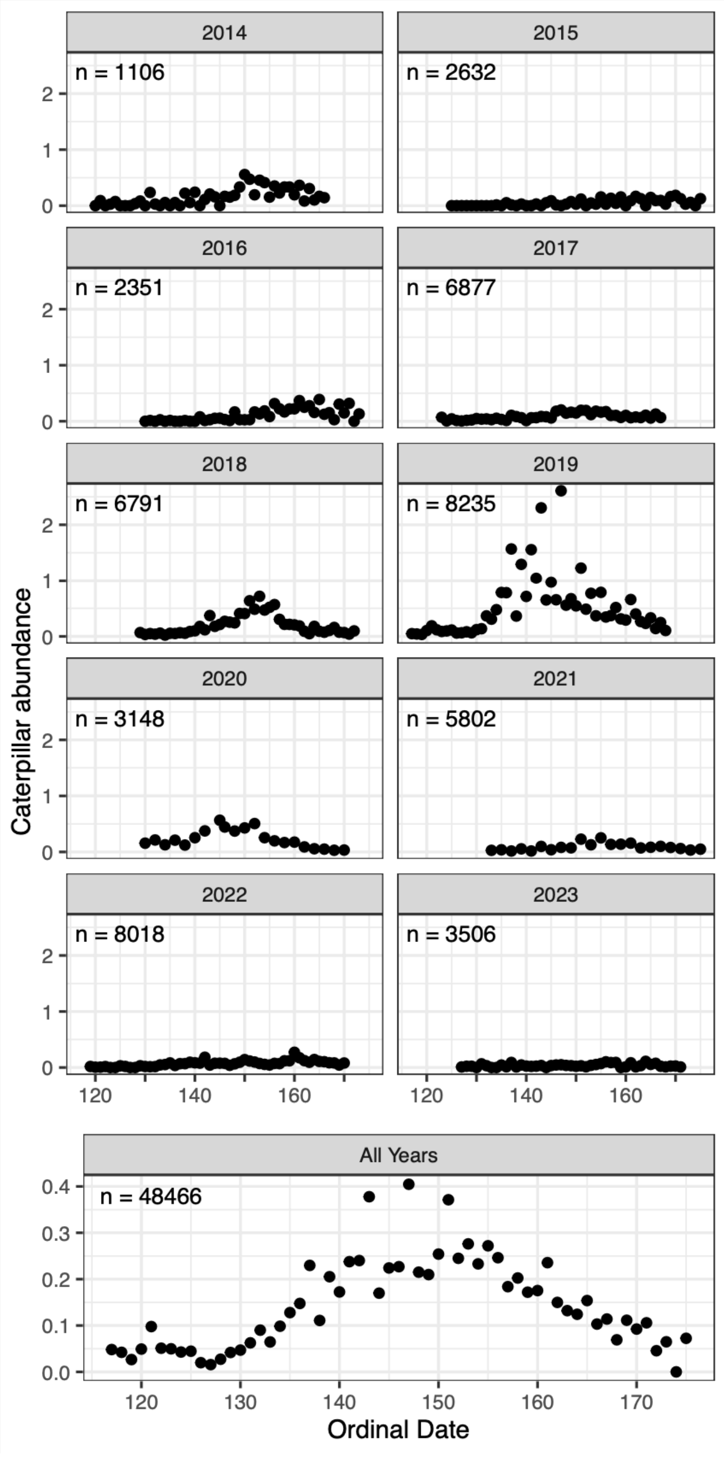


Figure S3: Plots shows the mean abundance of caterpillars sampled on each day among sites for each year and as the mean across all years; n shows the number of branch beatings carried out in each year or across all years.

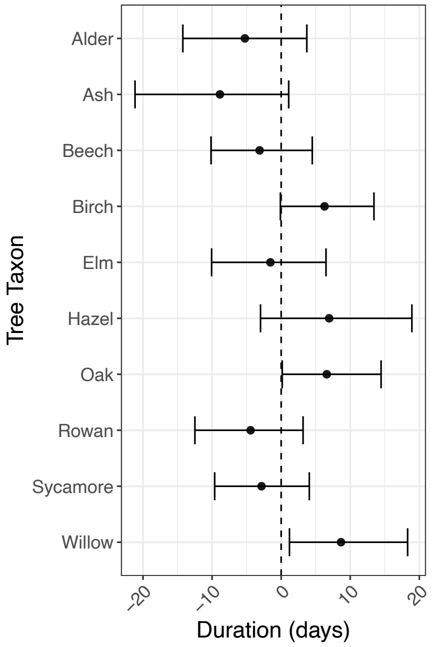


Figure S4: Posterior mean and 95% credible intervals for model prediction of the difference in peak duration (at an abundance of 0.01 caterpillars) for each taxon compared to the fixed effect trend. Calculated from the posterior distributions for the fixed effects and tree taxa random effects and interactions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

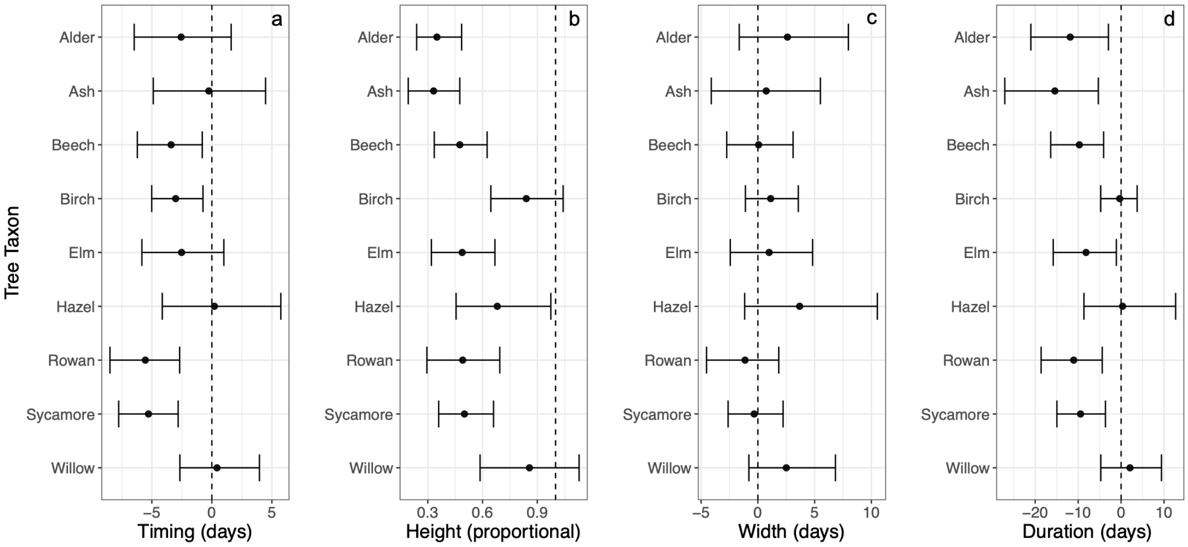


Figure S5: Posterior mean and 95% credible intervals for (Table S4) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar abundance in spring, calculated from the posterior distributions for the fixed effects and tree taxa 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 found a greater number of significant differences than compared to the average trend. The peak was significantly later than on oak than on beech (3.40 days, CIs: 0.80 - 6.21), birch (3.01 days, CIs: 0.74 – 5.01), rowan (5.54 days, CIs: 2.81 – 7.76) and sycamore (5.28, CIs: 2.81 – 7.76) trees (Fig. S5a). The peak on alder, ash, beech, elm, hazel, rowan and sycamore were all found to have a significantly lower height, reaching 0.35 (CIs: 0.24 - 0.49), 0.33 (CIs: 0.19 - 0.48), 0.48 (CIs: 0.34 - 0.63), 0.49 (CIs: 0.32 - 0.67), 0.68 (CIs: 0.46 – 0.97), 0.49 (CIs: 0.30 - 0.69) and 0.50 (CIs: 0.36 - 0.66) times the height of the peak on oak trees, respectively (Fig. S5b). The width of the peak at half the height did not differ significantly between any taxon and oak (Fig. S5c). The peaks on alder, ash, beech, elm, rowan and sycamore last for a significantly shorter duration by -11.84 (CIs: -21.01 - -2.95), -15.42 (CIs: -27.08 - -5.31), -9.72 (CIs: -16.39 - -4.07), -8.17 (CIs: -15.80 - -1.11), -11.03 (CIs: -18.62 - -4.40) and -9.45 (CIs: -14.95 - -3.65) days respectively (Fig. S5d).

When comparing the day 168 mass of caterpillars on each tree taxa to those from oak, I found caterpillars sampled from beech weighed significantly less at 0.72 (0.49 - 0.99) times the mass of those sampled from oak (Fig. S6).

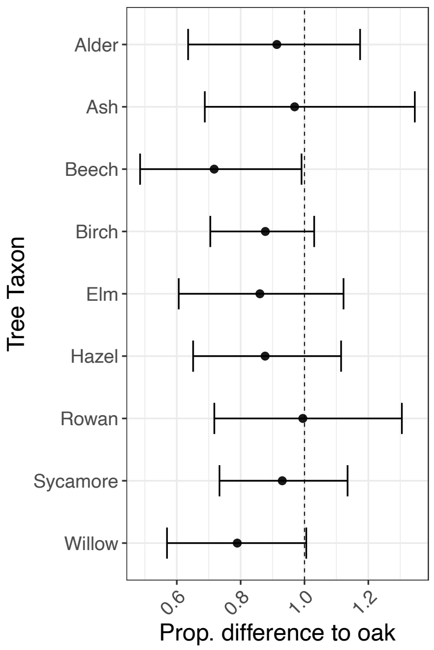
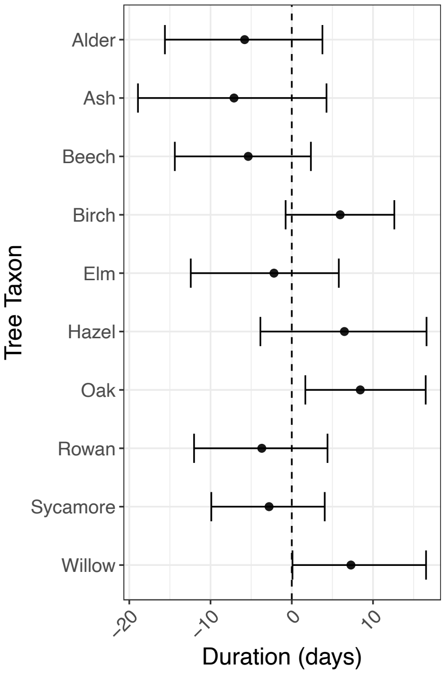


Figure S6: Posterior mean and 95% credible intervals for model predictions of the proportional difference in caterpillar mass between each tree taxon and caterpillars sampled from oak (Table S5). Calculated for day 168 (16th June) for the average year and site, the latest date with caterpillar mass data 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 S7: Posterior mean and 95% credible intervals for model prediction of the difference in peak duration (at a biomass of 0.25mg 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. S8). The peak on beech, birch, rowan and sycamore trees was significantly earlier than on oak by -3.92 (CIs: -7.11 - -0.98), -2.75 (CIs: -5.03 - -0.71), -4.96 (CIs: -7.95 – 2.01) and -4.74 (CIs: -7.44 - -2.41) days respectively (Fig. S8). The biomass peaks on all tree taxa except willow were found to have a significantly lower height than oak; with alder reaching 0.31 (CIs: 0.19 - 0.44) times the height of the peak on oak trees), ash 0.31 (CIs: 0.15 - 0.49), beech 0.35 (CIs: 0.21 - 0.50), birch 0.72 (CIs: 0.52 - 0.91), elm 0.41 (CIs: 0.24 - 0.60), hazel 0.63 (CIs: 0.35 - 0.90), rowan 0.43 (CIs: 0.24 – 0.62) and sycamore 0.42 (CIs: 0.29 – 0.56). The width of the peak at half the height did not differ to oak on any taxa. The peak duration on lasted for a significantly shorter duration on the following taxa than on oak by: alder -14.15 days (CIs: -24.88 - -4.97), ash -15.41 days (CIs: -28.64 - -5.14), beech -13.74 days (CIs: -22.22 - -6.27), elm -10.06 days (CIs: -19.11 - -2.63), rowan -12.11 days (CIs: -20.05 - -4.45) and sycamore -11.22 days (CIs: -17.46 - -5.47) (Fig. S8).

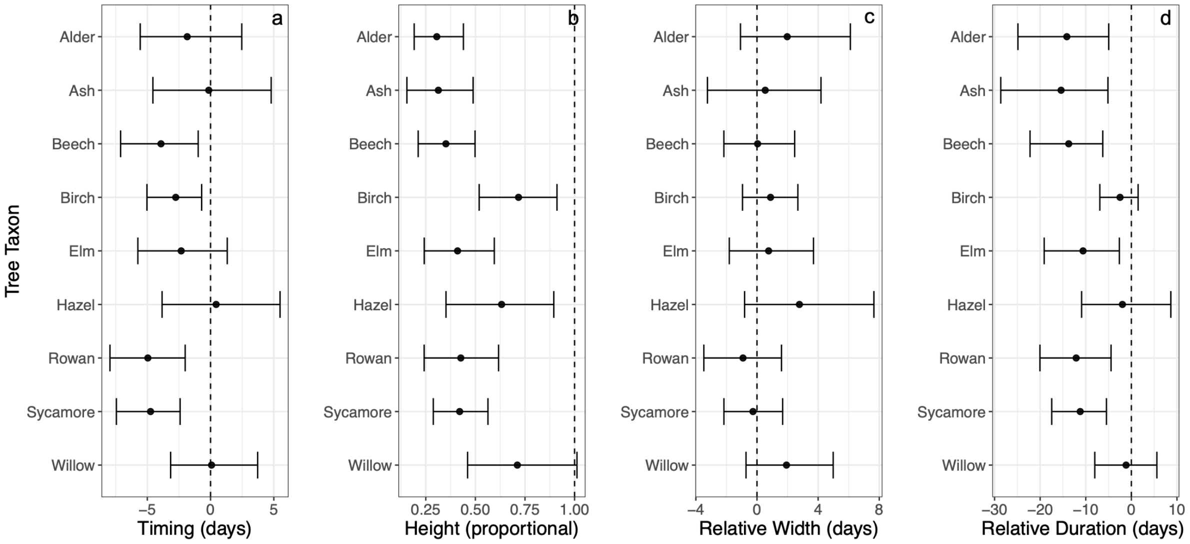


Figure S8: Posterior mean and 95% credible intervals for combined censored-gaussian (mass) and Poisson (abundance) GLMM (Table S4+5) predictions of the difference between each tree taxon and oak for different properties of the phenological distribution of caterpillar biomass in spring, calculated from 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 0.25mg of caterpillars).

Model output tables

Table S2: Poisson GLMM for variance composition of caterpillar abundance. Date refers to ordinal date (scaled: mean = 147.4742, SD =14.19027).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.527 (-4.128 - -2.904)	2600
Date (scaled)	0.453 (0.381 - 0.527)	2456
Date^2 (scaled)	-0.441 (-0.513 - -0.371)	2600
Random Terms		
Site	0.464 (0.273 - 0.82)	2041
Tree ID	0.288 (0.24 - 0.354)	2600
Tree Taxa	0.15 (0.051 - 0.55)	1963
Site Day	0.482 (0.42 - 0.577)	2288
Day	0.21 (0.165 - 0.284)	2418
Site Year	0.333 (0.247 - 0.412)	2470
Year	0.301 (0.119 - 1.252)	1024
Recorder	0.129 (0.066 - 0.291)	2183
Residual	0.684 (0.589 - 0.755)	2600

Table S3: 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	-4.257 (-4.947 - -3.554)	3400
Total Foliage Score	0.002 (-0.014 - 0.018)	3106
Random Terms		
Sampled Tree Taxa	0.165 (0.043 - 0.539)	2693
Habitat Composition	0 (0 - 0.001)	1330
Site	0.246 (0.131 - 0.506)	2937
Year	0.35 (0.107 - 1.135)	1900
Site Year	0.296 (0.223 - 0.39)	3400
Tree ID	0.295 (0.232 - 0.346)	3400
Site Day	0.965 (0.87 - 1.078)	3400
Recorder	0.202 (0.094 - 0.385)	3400
Residual	0.68 (0.593 - 0.757)	3400

Table S4: Poisson GLMM for analysing variations among tree taxa in the phenological distribution of caterpillar abundance throughout spring. Date refers to ordinal date (scaled: mean = 147.4742, SD =14.19027).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.443 (-4.196 - -2.72)	3000
Date (scaled)	0.763 (0.249 - 1.34)	3000
Date^2 (scaled)	-0.761 (-1.018 - -0.524)	3000
Random Terms		
TreeTaxa- Intercept var	0.146 (0.038 - 0.629)	1477
TreeTaxa- Intercept:Date slope covar	0.004 (-0.117 - 0.131)	3000
TreeTaxa- Intercept:Date^2 slope covar	-0.001 (-0.075 - 0.06)	2817
TreeTaxa- Date slope var	0.037 (0.011 - 0.21)	2347
TreeTaxa- Date slope:Date^2 slope covar	0 (-0.029 - 0.047)	2975
TreeTaxa- Date^2 slope var	0 (0 - 0.068)	2793
Site- Intercept var	0.717 (0.445 - 1.222)	3000
Site- Intercept:Date slope covar	-0.138 (-0.32 - 0.017)	3000
Site- Intercept:Date^2 slope covar	-0.184 (-0.341 - -0.102)	3000
Site- Date slope var	0.222 (0.149 - 0.422)	2721
Site- Date slope:Date^2 slope covar	0.033 (-0.026 - 0.086)	2742
Site- Date^2 slope var	0.067 (0.035 - 0.126)	2805
Year- Intercept var	0.439 (0.214 - 1.889)	1431
Year- Intercept:Date slope covar	-0.197 (-1.049 - 0.186)	3000
Year- Intercept:Date^2 slope covar	-0.006 (-0.267 - 0.189)	2504
Year- Date slope var	0.401 (0.129 - 1.418)	1545
Year- Date slope:Date^2 slope covar	-0.066 (-0.325 - 0.083)	2824
Year- Date^2 slope var	0.062 (0.015 - 0.222)	1870
Site-Year	0.352 (0.274 - 0.444)	3000
Recorder	0.152 (0.079 - 0.321)	2696
Site-Day	0.295 (0.236 - 0.361)	2845
Tree ID	0.283 (0.237 - 0.347)	3000
Residual	0.653 (0.578 - 0.737)	3000

Table S5: 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 = 147.4742, SD =14.19027).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-4.082 (-4.403 - -3.785)	3000
Date scaled	0.458 (0.334 - 0.574)	2236
Date^2 scaled	-0.13 (-0.184 - -0.081)	1961
Random Terms		
TreeTaxa- Intercept var	0 (-0.005 - 0.015)	2845
TreeTaxa- Intercept:Date slope covar	0 (-0.005 - 0.015)	2845
TreeTaxa- Date slope var	0 (0 - 0.035)	1387
Site- Intercept var	0.039 (0.015 - 0.087)	1220
Site- Intercept:Date slope covar	-0.009 (-0.036 - 0.019)	1852
Site- Date slope var	0.063 (0.021 - 0.104)	1157
Year	0.048 (0.013 - 0.401)	473
Site-Year	0.018 (0 - 0.044)	1134
Recorder	0.008 (0 - 0.046)	1447
Site-Day	0.146 (0.093 - 0.186)	1845
Tree ID	0.04 (0.023 - 0.068)	2430
Weighting	0.968 (0.883 - 1.074)	1090
Residual	0.029 (0.008 - 0.066)	617

Asymmetry in the abundance peak

Methods

It is already established that there is a humped phenological distribution of caterpillar abundance throughout spring in temperate deciduous woodlands (Gibb 1950; van Balen 1973; Southwood *et al.* 2004; Shutt *et al.* 2019a), though the shape of the 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 S6). Date refers to ordinal date and was scaled (prior to scaling: mean = 147.47, SD = 14.19). The random terms allowed for each site*year to have a separate intercept, date, date^2 and date^3 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 primary interest was 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 S6: Model composition for the peak asymmetry model. Date refers to ordinal date which was scaled (scaled: mean = 147.4742, SD = 14.19027). Int = intercept and VCV = variances and covariances.

Model	Peak asymmetry (Table S7)
Motivation	Evidence of asymmetry in peak shape
Response	Caterpillar abundance
Fixed effects	Date Date^2 Date^3
Random terms	Int, Date, Date^2 and Date^3 VCV across Site by year Day by Site by Year Tree ID Recorder
Family	Poisson
Iterations (thin)	3500000 (2000)
Burnin	100000
Sample Size	1700

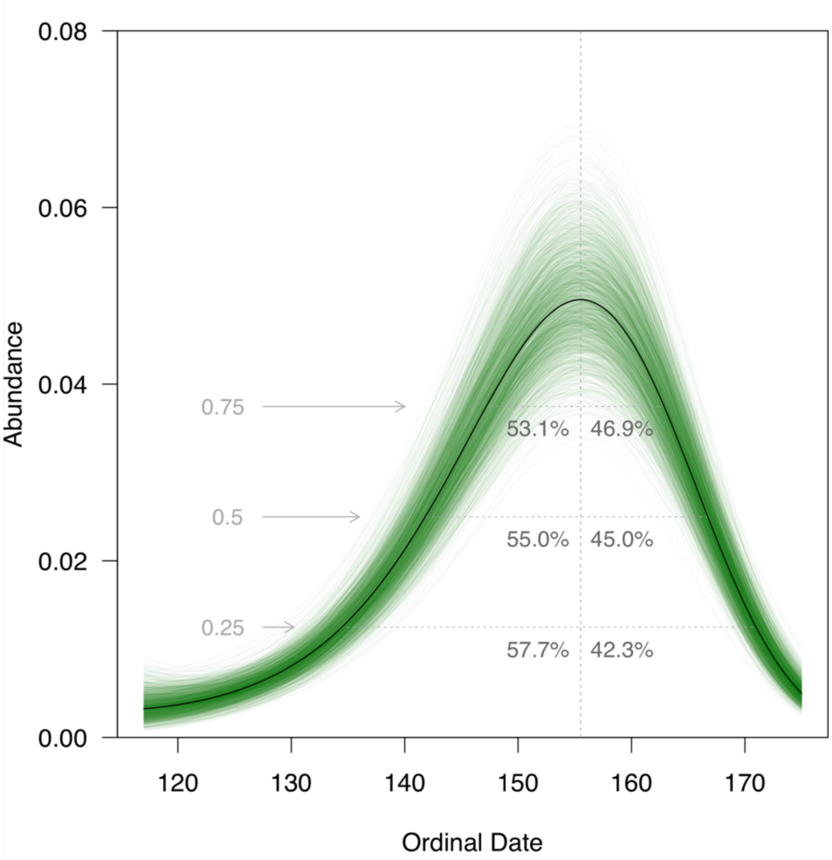


Figure S9: Posterior distribution for Poisson GLMM allowing a cubic (asymmetrical) relationship between caterpillar abundance and ordinal date (Table S7). Percentage of peak width falling before and after the peak date at 0.25, 0.5 and 0.75 of the peak height are shown in grey.

Table S7: Poisson GLMM using a cubic function to analyse possible skew in the distribution of caterpillar abundance across ordinal date (scaled: mean = 147.4742, SD = 14.19027).

	Coefficient/Variance (Mean/mode and CI)	Effective sample size
Fixed Terms		
Intercept	-3.267 (-3.485 - -3.034)	1700
Date (scaled)	0.859 (0.701 - 1.005)	1700
Date^2 (scaled)	-0.58 (-0.673 - -0.488)	1393
Date^3 (scaled)	-0.208 (-0.277 - -0.137)	1511
Random Terms		
SiteYear- Intercept var	1.644 (1.327 - 1.985)	1345
SiteYear- Intercept:Date slope covar	-0.339 (-0.584 - -0.158)	1822
SiteYear- Intercept:Date^2 slope covar	-0.432 (-0.574 - -0.331)	1700
SiteYear- Intercept:Date^3 slope covar	0.021 (-0.042 - 0.082)	1700
SiteYear- Date slope var	0.75 (0.572 - 1.057)	1700
SiteYear- Date slope:Date^2 slope covar	0.075 (-0.021 - 0.154)	1700
SiteYear- Date slope:Date^3 slope covar	-0.093 (-0.169 - -0.026)	1535
SiteYear- Date^2 slope var	0.192 (0.138 - 0.263)	1700
SiteYear- Date^2 slope:Date^3 slope covar	0.007 (-0.018 - 0.032)	1700
SiteYear- Date^3 slope var	0.016 (0.001 - 0.042)	1635
Recorder	0.156 (0.079 - 0.322)	1700
Site Day	0.21 (0.165 - 0.277)	1700
Tree ID	0.356 (0.297 - 0.43)	1700
Residual	0.683 (0.586 - 0.749)	1586

Results

Annual peaks in the temporal distribution of caterpillar abundance in our data are clear (Fig. S3), and supported by the significant date^2 term (-0.58, CIs: -0.673 - -0.488, Table S7) in the peak asymmetry model. The cubic parameter was significant and negative (-0.208, CIs: -0.277 - -0.137) indicating a negatively skewed peak (Table S7), however the resulting asymmetry in the curve is quite small (Fig. S9). Each quartile shows 53-58% of the peak duration to the left and 42-47% to the right. On the basis of the quite minor asymmetry we conclude that inclusion of the quadratic date term, without cubic, is sufficient.