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The phenology and clutch size of UK Blue Tits does not differ with woodland composition

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The deciduous tree-herbivorous caterpillar-insectivorous bird food chain is a well-studied system for investigating the impacts of climate change across trophic levels. To date, across Europe, most attention has focused on the impacts of increasing spring temperature on changes to phenology in Oak-dominated (*Quercus* spp.) woodlands. Paridae species and Pied Flycatcher *Ficedula hypoleuca* are the most studied secondary consumers, all of which demonstrate an advancement in reproductive phenology with increases in spring temperature. Shifts in climate and phenology may also impact on reproductive investment in clutch size, and the effects of climate on phenology and clutch size may vary depending on woodland composition. To date, the effects of among-habitat variation in phenology and reproductive investment have received little attention. Insectivorous birds inhabiting woodlands that differ in tree composition may differ in the timing of breeding, due to local tree leafing phenology acting as a cue for egg-laying date and/or clutch size. Moreover, for most insectivorous birds, woodland composition within a territory is likely to be the main determinant of food availability for both adults and chicks. Consequently, if warming springs affect the temporal patterns of food availability differently across different woodland compositions, this may affect the optimal average local phenology for nesting birds. Here, using data from 34 long-term (mean 15 years) nest monitoring sites across the UK, we investigate the effect of woodland tree composition and temperature on Blue Tit *Cyanistes caeruleus* first egg date (FED) and clutch size. We supplemented the nest monitoring data by quantifying woodland composition, at a site level, through modified point counts. We predict that birds breeding in woodlands with greater proportions of late-leafing species, such as Oak and Ash *Fraxinus excelsior*, will breed later than those breeding in woodlands with greater proportions of early-leafing species, such as Birch *Betula* spp. and Beech *Fagus sylvatica*. We found no evidence for differences in Blue Tit FED or clutch size in relation to the proportion of any of the tree species investigated, after controlling for temperature and latitude (FED: −3.4 and 2.2, clutch size: −0.4 and – 0.2 eggs for one-unit increase in temperature and latitude, respectively). In recent decades and across all sites, clutch size has decreased as spring temperatures have increased, a strategy which could allow birds flexibly to adjust their breeding phenology such that nestling demand coincides with peak food availability. The lack of an effect of woodland composition on Blue Tit phenology suggests Blue

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Tits do not fine-tune their reproductive phenology to the local tree composition. Whether this lack of evidence for phenological divergence is due to an absence of divergent selection on breeding phenology and clutch size or to gene flow is not clear.

Keywords: Blue Tit, climate, phenology, productivity, woodland composition..

INTRODUCTION

The timing of key events in an organism's life cycle, e.g. reproduction and moult in birds, is often precisely matched temporally with seasonal pulses in resources, or other favourable conditions. In recent decades, the timing of such events has been changing (Walther *et al.* 2002) and has been shown to be strongly temperature-dependent (Thackeray *et al.* 2016, Cohen *et al.* 2018), with the rate of phenological advance highest at higher latitudes due to accelerated warming in these areas (Cohen *et al.* 2018, Post *et al.* 2018). In many avian species, breeding phenology has advanced (Crick *et al.* 1997, McCleery & Perrins 1998) as spring temperatures have increased (McLean *et al.* 2016). When the phenology of key events in a species life cycle alters, there is a risk of asynchrony between the event and ephemeral resources that are relied upon, such as the availability of nesting sites, food or suitable habitat (Visser *et al.* 2004, Walther 2010).

In food chains specifically, if different trophic levels alter their phenology at different rates, this can result in an uncoupling of previously synchronous relationships (Durant *et al.* 2007). There is widespread evidence that species occupying higher trophic levels have advanced their phenology by less than those of lower trophic levels (Thackeray *et al.* 2010, 2016) and this asynchrony between predators and prey can lead to reduced fitness for individuals occupying higher trophic levels. The potentially detrimental fitness and demographic consequences of such asynchrony within ecosystems has generated substantial research interest (Visser & Gienapp 2019, Samplonius *et al.* 2021).

A temperate tri-trophic system, comprising deciduous tree-herbivorous caterpillar-insectivorous bird, is a well-studied system for investigating phenological change and mismatch (Visser *et al.* 2004). Secondary consumers that are commonly investigated as part of such tri-trophic systems include Blue Tits *Cyanistes caeruleus*, Great Tits *Parus major*, Pied Flycatchers *Ficedula hypoleuca* and Chickadees *Poecile* spp. Long-term phenological studies of these species across Europe and North America have demonstrated consistent advancements in first egg date (FED) and reproduction in relation to warming springs (Perrins 1991, Both & Visser 2001, Sanz 2002, Dolenec 2007, Potti 2009, Matthysen *et al.* 2011, Thorley & Lord 2015, McDermott & DeGroote 2016, Samplonius *et al.* 2018). With warming springs, if insectivorous secondary consumers do not advance their breeding phenology or advance at a different rate to their caterpillar prey, which typically develop faster at elevated temperatures (Buse *et al.* 1999, Charmantier *et al.* 2008), adult birds may no longer be able to exploit the best food resource for their chicks (Buse *et al.* 1999, Wilkin *et al.* 2009, Burger *et al.* 2012). This could result in prey-switching to suboptimal prey items with resultant reduced productivity (Buse *et al.* 1999, Wilkin *et al.* 2009, Pollock *et al.* 2017). To date, across Europe, insectivorous passerine bird populations have exhibited varying evidence for asynchrony with their caterpillar prey and tree leaf-out, with variation in the speed of phenological advances with warming springs (Visser *et al.* 2003, Both *et al.* 2009, Matthysen *et al.* 2011, Porlier *et al.* 2012, Burgess *et al.* 2018, Samplonius *et al.* 2018, Bailey *et al.* 2022).

In temperate environments, photoperiod is the main environmental cue that resident birds use to initiate the physiological processes of reproduction in spring (Visser & Lambrechts 1999, Dawson 2008). Additional environmental cues, such as temperature, local tree-leafing phenology and food availability at the time of laying (Dawson 2008, Martin *et al.* 2020), may also help to refine the exact timing of reproduction. Reproductive phenology can vary geographically, tending to be later at higher latitudes (Mainwaring *et al.* 2012) and in colder conditions, due to the negative relationship between phenology and local temperature (Post *et al.* 2018). However, the degree of asynchrony between peak nestling demand and caterpillar biomass does not covary with latitude (Burgess *et al.* 2018). Hetero- and conspecific density can impact laying date, but these impacts can differ between species; for example, higher breeding densities are correlated with later FED in Blue Tits but not in Great Tits (Møller *et al.* 2018). One challenge of identifying the precise combination of proximate cues that birds use to fine-tune breeding phenology is that all of these variables are highly correlated, such that warmer springs coincide with earlier leaf-out (Tansey *et al*. 2017) and greater resource availability (Shutt *et al*. 2019).

The number of eggs birds lay in each breeding attempt is influenced by several factors, including physiological and environmental constraints (Klomp 1970). Environmental factors that limit clutch size include the resources available to the female during egg-laying and incubation, the number of nestlings that the parents can support, the survival costs to the parents, the number of eggs the female can successfully incubate, and the density of hetero- and conspecifics (Godfray *et al*. 1991, Visser & Lessells 2001, Goodenough *et al*. 2009). Food availability has been hypothesized to be central in influencing clutch size, due to clutch size being limited in altricial birds by the number of offspring parents can feed (Lack 1947, 1954, Godfray *et al*. 1991). As the density of hetero- and conspecifics increases, reductions in clutch sizes have been observed, although the effects differ between species (Goodenough *et al*. 2009, Møller *et al*. 2018). Alterations to clutch size have also been suggested as a potential mechanism for maintaining synchrony with food resources, with smaller clutches typically hatching earlier than larger clutches laid on the same day, allowing birds to alter the timing of hatching after the first egg has been laid by modifications to clutch size or incubation initiation (Cresswell & Mccleery 2003, Lord *et al*. 2011, Simmonds *et al*. 2017).

Woodland tree composition may affect the reproduction of forest-nesting birds in several ways, from affecting phenology and plasticity in the timing of reproduction and clutch size, to altering reproductive success. The mean timing of reproduction may be influenced by both tree species composition and abundance, which will alter the mean timing of phenological cues birds receive, due to differing leafing phenology between tree species (Amininasab *et al*. 2016, Matthysen *et al*. 2021). During spring in UK woodlands, leafing phenology is typically earliest in species such as Sycamore *Acer pseudoplantanus* and Birch *Betula* spp. and latest in Oak *Quercus* spp. and Ash *Fraxinus excelsior*, though the order in leaf-out among species may also change with continued spring temperature rises (Roberts *et al*. 2015). Clutch size may also be affected by woodland composition through several pathways. For example, woodlands abundant in Oak, Birch and/or Willow *Salix* spp. will provide higher food availability to insectivorous birds, due to hosting a wide variety of Lepidoptera and other invertebrate orders, than Ash- or Beech-dominated woodlands (Kennedy & Southwood 1984) during both avian egg-laying and chick-rearing life stages. Clutch size can be impacted by the resources available to females at the time of egg-laying, as egg production is a nutritionally demanding process for small passerines and, in non-manipulative studies, larger clutch sizes are often correlated with higher food availability or more favourable habitats (Martin 1987, Perrins 1991, Amininasab *et al*. 2016). Certain woodland composition may be more favourable and productive for predator species of insectivorous woodland birds such as Sparrowhawks *Accipiter nisus* and Great Spotted Woodpeckers *Dendrocopos major* and mammalian predators such as Weasels *Mustela nivalis* and Pine Martens *Martes martes*, with higher predation risk often linked to reduced clutch sizes (Doligez & Clobert 2003, Dillon & Conway 2018).

Previously, Oak and, to a lesser extent, Birch have been the focal tree taxa in the majority of studies exploring changes in Paridae and Pied Flycatcher breeding phenology, despite species such as Blue and Great Tits being habitat generalists (Snow & Perrins 1998). Within UK woodland, the extent of Birch and Oak is similar, with much of the woodland being a mix of broad-leaved species (Forestry Commission 2013). The few studies that have considered the role that woodland composition plays in providing cues for the timing of reproduction in cavity-nesting insectivorous passerines have mainly focused upon differences between habitat categories, such as deciduous vs. coniferous woodlands, finding mixed evidence that birds are using local habitat cues (Blondel *et al*. 1993, Van Balen 2002, Atiénzar *et al*. 2010, Amininasab *et al*. 2016) and, with few exceptions (e.g. Shutt *et al*. 2019, Bailey *et al*. 2022), were at single sites, within single populations. Where woodland or territory composition has been considered in both Blue Tit and the closely related Great Tit, breeding phenology has been shown to be earlier in Oak-rich territories than in Oak-poor territories, although this was within a single site (Wilkin *et al*. 2007, Cole *et al*. 2015). At a multi-site scale, along a 220-km transect in Scotland, UK, comprising 40 deciduous woodland sites, both mean night-time temperatures in early spring and Birch budburst phenology were the most important predictors of FED in Blue Tits (Shutt *et al.* 2019).

The effect of habitat on clutch size has broadly focused upon comparisons between general habitat types, such as deciduous vs. evergreen woodland (Gibb & Betts 1963, Blondel *et al.* 1993, Lambrechts *et al.* 2004), or urban parkland or garden vs. woodland (Marciniak *et al.* 2007, Glądalski *et al.* 2017, Branston *et al.* 2021). Typically, birds nesting in deciduous woodland have higher productivity (clutch size and number of fledglings) than birds nesting in evergreen woodland or urban parkland or gardens (Gibb & Betts 1963, Blondel *et al.* 1993, Lambrechts *et al.* 2004, Glądalski *et al.* 2017, Branston *et al.* 2021), although it is worth noting that to date woodland categories have been biased towards Oak deciduous woodlands. It is widely accepted that Oak woodland is the optimal breeding habitat for nesting Blue Tits, Great Tits and Pied Flycatcher (Perrins 1979, Cody 1985) and rarely are the effects of other tree species considered (except Shutt *et al.* 2018, Matthysen *et al.* 2021). Matthysen *et al.* (2021) showed that for Blue Tits, but not Great Tits, clutch size was larger in territories with more Oak trees, but this did not translate into more fledglings. Shutt *et al.* (2018) demonstrated the availability of non-Oak tree species, such as Birch *and* Sycamore, were positively associated with fledging success, but reported no effect of tree species on clutch size. Climatic conditions can also influence productivity, with higher temperatures during May reducing the number of Blue Tit fledglings (Potti 2009); however, for clutch size, temperature during May has been reported either not to have had an effect or have led to a reduction in clutch size (Perrins 1979, Dolenec 2007, Potti 2009).

Here, we investigate the impact of spring temperature and woodland composition on Blue Tit FED and clutch size, using data spanning three decades from 34 Blue Tit populations nesting in deciduous woodlands across the UK.

First, we test whether woodland composition influences the average timing of breeding. If birds adjust breeding timing based on tree-specific cues, such as later availability of resources, we hypothesize that birds breeding in areas with greater proportions of late-leafing species, such as Oak and Ash (Roberts *et al.* 2015), will breed later than those breeding in woodlands with greater proportions of early-leafing species, such as Birch and Beech (Roberts *et al.* 2015).

Secondly, we investigate whether spring temperature and/or woodland composition affects clutch size in Blue Tits. We predict that Blue Tit clutch size will decline with increasing spring temperatures, due to the potential for this to be a secondary mechanism for advancing reproductive phenology and the potential asynchrony with key nutrients and food resources females require to produce large clutches. We also predict that birds in woodlands with tree species compositions that tend to be rich in food resources during either the egg-laying or chick-rearing stage will have the largest clutch sizes, as greater resource availability (either actual or perceived) will lift the constraint on clutch size.

METHODS

Blue Tit nesting data

We used Blue Tit nest records, collected by volunteer recorders who monitor birds nesting attempts across the UK as part of the British Trust for Ornithology (BTO) Nest Record Scheme (NRS; Crick *et al.* 2003). Each record included the following data: year, grid reference, observer, the date the first egg was laid and the maximum number of eggs laid. If nests were found during egg-laying (e.g. after the first egg had been laid), FED was back-calculated assuming one egg was laid per day. FED is provided as a date range, of the minimum and maximum estimate of FED, with the minimum being the day after the last visit where no eggs were seen, and the maximum the date visited where eggs were observed minus the number of eggs found. Only records where the difference between the upper and lower estimates of FED was ≤ 10 days were retained (mean FED range $\pm$ sd $= 3.2 \pm 3.0$ days). Clutch size was taken as the maximum number of eggs recorded during a nesting attempt, and any records with a clutch size smaller than two or greater than 16 were removed, as these records may be incomplete records of clutch size, relay attempts or nests where two females have laid in the same nest, due to being outside the range recorded nationally (Robinson 2005).

Site and nest record selection

To identify long-running NRS sites, we identified 1 × 1-km cells where the same observer had submitted records for a minimum of 10 years, which were still active in 2015. That year was used as the cut-off point for inclusion of nest records, as complementary woodland composition data were collected at the suite of sites identified in 2016 and 2017. Sites were then ranked based on the number of records submitted, to target large, long-running schemes with the most observations. All such observers were then contacted to check whether the data did indeed refer to a single long-running study, and whether they gave their permission to use their data. The observers for 34 sites, with records from 1979 to 2015 (mean ± sd 15 ± 6 years), responded positively (for a map of the sites included, see Supporting Information Fig. S1). Sample sizes across these sites totalled 10 406 FED and 9319 clutch size records (mean number of records per site ± sd, FED: 306 ± 734, clutch size: 274 ± 715). These data were subsequently used in the analyses.

Woodland tree composition

Site-level tree density and taxa-specific densities were estimated using a modified point centred quarter method (PCQM; Khan *et al.* 2016), with sites sampled after the breeding season (July–August) in 2016 and 2017. PCQM is a modified distance sampling method which allows the total tree density of an area to be estimated quickly, along with taxa/species-specific density, if this information is also recorded at the time of sampling. Twenty-five stratified random sampling points were selected at each site, stratified using the location of nestboxes to ensure sampled areas were likely to be used by nesting birds. Twenty-five points per site were selected due to being robust in estimating tree density in natural forests, where 15, 20, 25, 30, 50 and 100 points were compared (Khan *et al.* 2016). Each sampling point was split into four equal quadrants and the distance to, and species of, the nearest tree recorded (using a digital laser rangefinder, Bosch PLR 25) to allow both total and species-specific tree density to be calculated. Due to all the nestboxes being situated in woodlands, and very few in edge habitats, there was never a case where the nearest tree could not be identified, or the distance measured. The maximum and minimum distances to the nearest trees were 200.83 and 0.2 m, respectively (mean distance 5.3 m).

Total tree density was estimated using the following equation (Khan *et al.* 2016):

$$\rho = 4\ (4N-1)/\pi\sum_{i=1}^{N}\sum_{j=1}^{4}R_{(1)\mathrm{ij}}^{2}$$

where ρ is overall tree density; R_{ij} is the distance from the ith random point to the closest tree in the jth quadrant; and N is the number of random points (25 for all of our study sites).

Individual tree species were grouped into species categories (referred to as tree species hereafter), following categorization used by Forestry Commission (2013). See Supporting Information Table S1 for a list of groupings used. Species categories were used due to how common hybridization is in many of the species, many of the species having similar ecological properties and similar hosting of invertebrates (Kennedy & Southwood 1984, Southwood *et al.* 2005).

The density of a single species category (ρ_k, trees per hectare) at each site was calculated as (Mitchell 2010):

$$\rho_k = \frac{\text{Number of quadrants with species } k}{4N} \times \rho$$

where k is a single species category recorded at the site; ρ is the calculated total tree density of the site; and N is the number of random points (always 25).

Species densities (Fig. 1) were also converted to proportions of the total tree density at each site (Fig. 2).

Shannon diversity index (H) was also calculated for each site from the density of each tree species category using the following equation:

$$H' = -\sum \frac{n_i}{N} \times \ln \frac{n_i}{N}$$

where n_i is the density of each of the i species and N is the total number of species at each site. Higher values of H represent a higher diversity and a value of 0 would represent just one species present.

Temperature

We used interpolated daily mean temperatures from across the UK, for the period spanning the bird data, at a resolution of 1 × 1 km (Hollis *et al.* 2019), to relate bird nesting traits to climate.

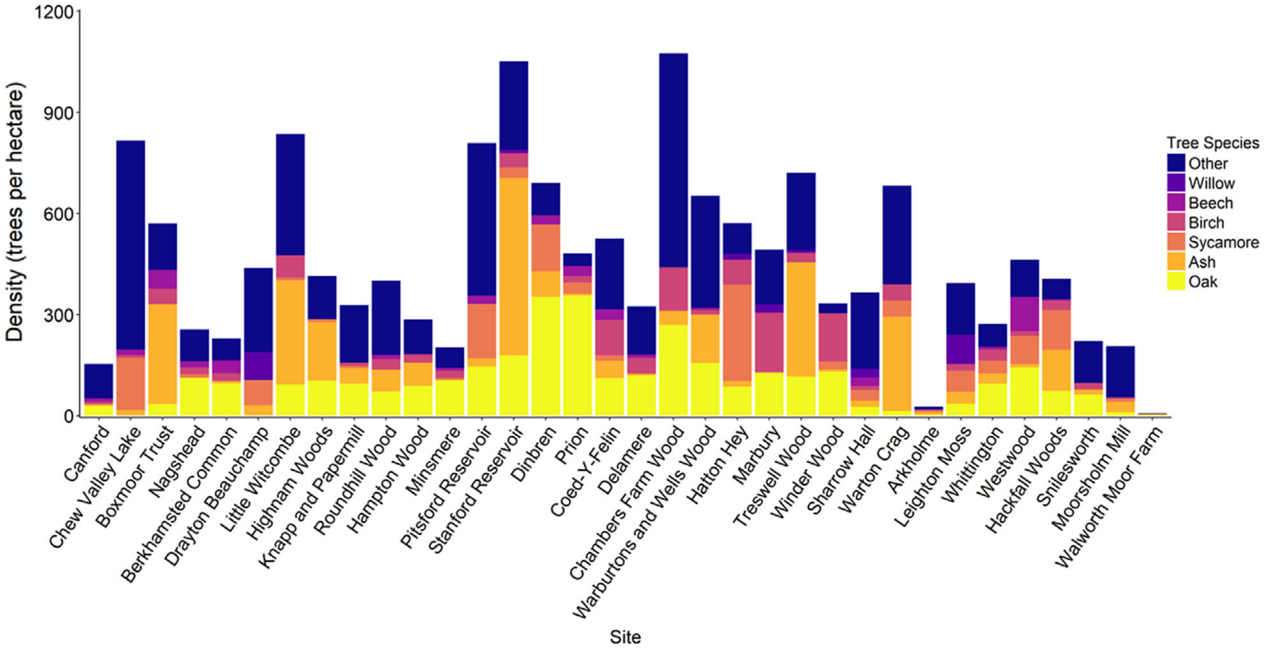

Figure 1. Densities of each tree species category used in the main analyses at each of the 34 sites included in this study (ordered from south to north, left to right). The total height of each bar represents the overall tree density at each site.

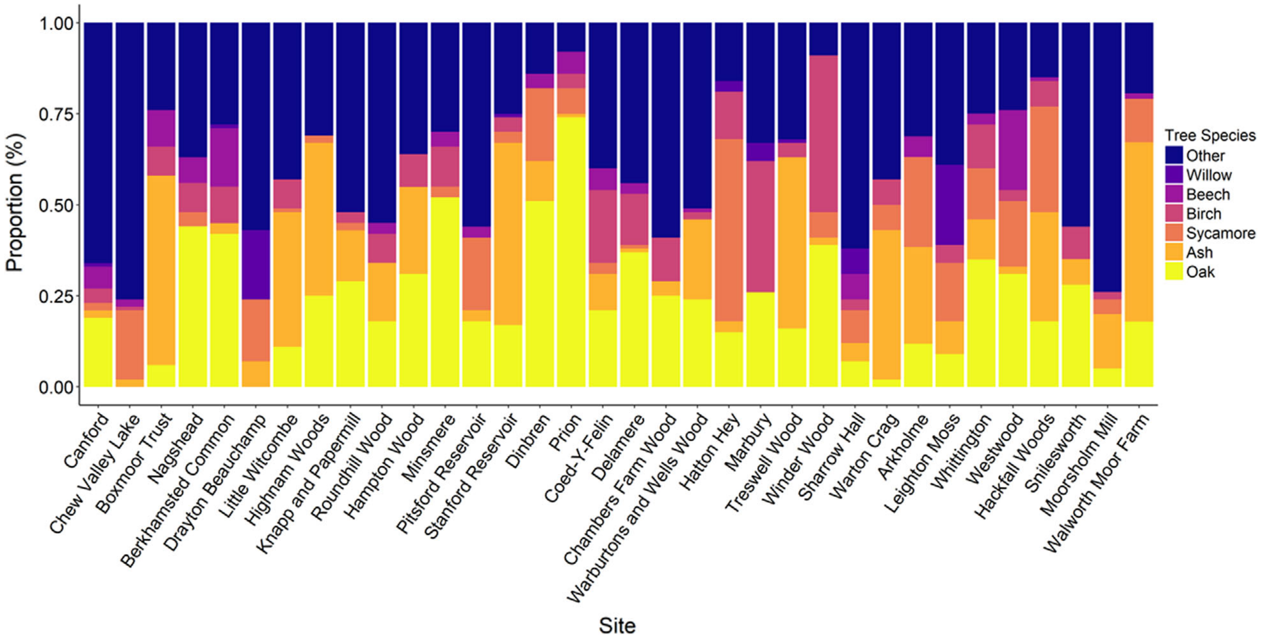

Figure 2. Proportion of each tree species category present at each of the 34 sites included in the study, ordered from south to north, left to right.

Each nest record was associated with temperature data of a single 1 × 1-km grid square, rather than averaging temperature across a site, as several sites spanned multiple grid cells (mean number of 1-km grid cells per site ± sd = 1.6 ± 1.3) and temperature may vary within sites. The mean daily temperature between day 75 and 128 (16 March to 8 May) was calculated for each nest record; this fixed period has been previously shown to best predict spatial and temporal variation in Blue Tit FED in the UK, in a dataset that overlaps substantially with this one (Phillimore *et al.* 2016). We used a within-subject mean-centring approach (van de Pol & Wright 2009) to capture temperature variables between sites and within a site across years.

Statistical analyses

We used FED, clutch size, or the annual coefficient of variation of either FED or clutch size at each site as the response variable in our models, with FED being an interval-censored Gaussian response between the minimum and maximum FED. Mean site temperature, yearly temperature deviations from site means, year, total tree density and latitude were all included as continuous, mean-centred, fixed effects in the FED and clutch size models. Latitude was included here to account for latitudinal variation in FED (Mainwaring *et al.* 2012, Burgess *et al.* 2018), and in the clutch size model, FED was also included to control for the decline in clutch size that is typically observed as spring progresses (Perrins 1979). In addition, the following cross-classified random effect structure was used: year (factor), site and site within year, all as random intercepts. We also included a random slope term to allow the within-site temperature slope to vary among sites. To explore the effect of the quantity of individual tree species present at a site on Blue Tit FED or clutch size we also included a multiple-membership random effect for woodland composition. Multiple-membership random effects are set up as a presence/absence matrix of each tree species at each site, which is then weighted by the proportion of total tree density each tree species density constitutes. Densities were converted to proportions to satisfy the assumption that all weights for multiple-membership random effects must add up to one. Including woodland composition in this way allowed us to test the effect that the proportion of total tree density comprised by a particular tree species category at a site had on FED or clutch size, by extracting best linear unbiased predictors (BLUPs) for each tree species, while accounting for covariance with other tree species present. BLUPs can be interpreted as you would interpret best linear unbiased estimates (BLUEs) of fixed effects.

In the models exploring variation in FED and clutch size, mean site temperature, yearly temperature deviations from site means, year, latitude, Shannon diversity index and the number of records submitted at that site in that year were all included as continuous, mean-centred, fixed effects. In the variation in clutch size model, FED was also included as a continuous, mean-centred, fixed effect. In addition, the following cross-classified random effect structure was used, as described above: year (factor), site and site within year (random intercept), a random slope term allowing the within-site temperature slope to vary among sites.

All analyses were conducted in R version 4.20 (R Core Team 2018) and implemented as maximal Bayesian mixed effects models using *MCMCglmm* (Hadfield 2010), with no model selection or simplification undertaken due to the risk of bias in parameter estimation when removing non-significant variables (Whittingham *et al.* 2006).

Priors in the Markov chain Monte Carlo (MCMC) models were defined as default inverse-Wishart distributions for the residual terms and flat, parameter-expanded priors for the variance terms in all models. For the FED and clutch size model, the burn-in period was set to 20 000, with 650 000 iterations carried out, and every 500th iteration stored. For the variation in FED model, the burn-in period was set to 75 000 with 1 000 000 iterations carried out, and every 750th iteration stored. For the variation in clutch size model, the burn-in period was set to 300 000, with 4 000 000 iterations carried out, and every 3000th iteration stored. The number of iterations and the thinning interval used were set to maintain an effective sample size above 1000, while ensuring autocorrelation between successively stored iterations did not exceed 0.1 (Hadfield 2010). Model convergence was assessed visually from trace and posterior density plots.

RESULTS

Woodland composition, latitude and temperature

The spatial temperature variable correlated negatively with latitude, but the yearly deviation in temperature from this spatial temperature variable did not correlate with latitude (see Supporting Information Fig. S2). Neither of the temperature variables correlated strongly with the proportion of any of the tree species present at a site or Shannon tree diversity (Fig. S2).

The proportion of each tree species in a woodland varied with latitude, with the highest correlation coefficient for Ash; more Ash was typically found in woodlands at higher latitudes (Fig. 2 and Fig. S2). In comparison, Beech was associated more with woodlands at lower latitudes (Fig. 2 and Fig. S2).

First egg date

Blue Tit FED was negatively related to yearly temperature deviations from the long-term site mean, and positively related to latitude (Table 1), with birds nesting in more northerly latitudes laying their first eggs later than their southerly counterparts. For every degree Celsius increase in the yearly temperature deviation from the site mean, FED was, on average, 3.4 days earlier (Table 1), and for every degree increase in latitude (heading north in UK) FED was on average 2.2 days later. Across the sites investigated here, no tree species induced a significant deviation in FED from the average site (Fig. 3), nor did overall tree density within a site (Table 1).

Table 1. Censored Gaussian generalized linear mixed model (GLMM) to investigate the effect of woodland composition on Blue Tit first egg date, with significant predictors highlighted in bold.

	Coefficient/variance (mean and 95% credible interval)	Effective sample size
Fixed effects		
Intercept	**113.70 (109.75–116.53)**	**1260**
Spatial mean temperature (8.25)	−1.73 (−3.65 to 0.26)	1372
Yearly deviation in mean temperature (0.39)	**−3.44 (−4.34 to −2.57)**	**1529**
Latitude (52.4)	**2.18 (0.97–3.38)**	**1111**
Year (2004)	−0.09 (−0.20 to 0.03)	1260
Tree density (428)	0.00 (−0.004 to 0.003)	1260
Random effects		
Year	9.5 (4.4–15.5)	1260
Site	6.5 (3.2–10.8)	1086
Year : Site	5.4 (4.0–6.6)	1260
Yearly deviation in temperature : Site	0.2 (5.4×10^{-7} to 0.6)	1260
Woodland composition	12.93 (1.5×10^{-4} to 52.82)	1260
Residual	36.6 (35.5–37.6)	1260

Note: all variables were mean-centred, with mean values in parentheses after predictor name. Significance was assessed by credible intervals which did not overlap zero.

Variation in Blue Tit FED was not significantly related to any of the temperature variables, tree diversity, latitude, year or the number of records submitted in that year at that site (Table 2).

Clutch size

Blue Tit clutch size was negatively related to the long-term site mean temperature and the yearly deviation in mean temperature (Table 3, Fig. 4a, b). For each degree Celsius increase in the mean site temperature (1979–2015) Blue Tit clutch size reduced by 0.75 eggs (Fig. 4a). For each degree Celsius increase in the yearly deviation in mean temperature, clutch size reduced by 0.4 eggs (Fig. 4b). Clutch size was also negatively related to year and FED, but there was no effect of latitude or total tree density within a site (Table 3). No single tree species had a significant effect on Blue Tit clutch size (Fig. 4c).

Variation in clutch size was positively related to FED but not significantly related to either of the temperature variables, tree diversity, latitude, year or the number of records submitted in that year at that site (Table 4).

DISCUSSION

The aim of this study was to investigate the impact of both spring temperature and woodland composition on Blue Tit breeding phenology and clutch size across the UK, in a long-term and multi-site study.

Overall, we found little evidence for differences in Blue Tit breeding phenology in relation to the presence of any single tree species present in woodlands, after controlling for temperature and latitude. Therefore, we found no support for our prediction that breeding phenology would be earlier when large proportions of early leafing species, such as Sycamore or Birch, were present, and later when large proportions of later-leafing species were present, such as Ash and/or Oak (Roberts *et al.* 2015). There are several possible explanations for our finding of a lack of a relationship between habitat and Blue Tit egg-laying phenology. First,

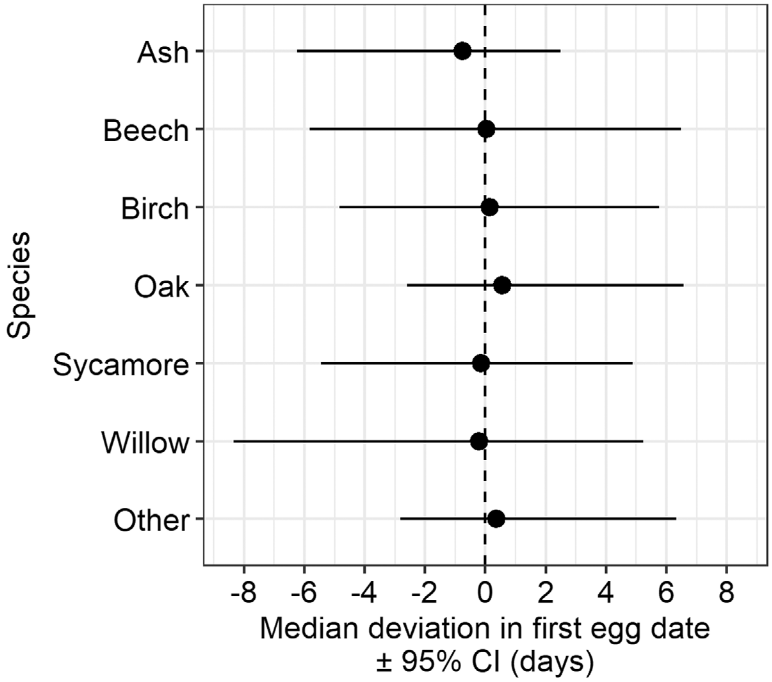

Figure 3. Deviations in first egg dates, calculated from the random effect coefficients from a GLMM multiple membership model, which shows how much earlier or later, on average, first egg dates are based upon the presence of each tree genus within a site. CI, credible interval.

Table 2. Gaussian GLMM used to investigate the effect of woodland composition on the coefficient of variation in Blue Tit first egg date, with significant predictors highlighted in bold.

	Coefficient/variance (mean and 95% credible interval)	Effective sample size
Fixed effects		
Intercept	**0.05 (0.04–0.05)**	**918**
Spatial mean temperature (8.14)	0.002 (−0.003 to 0.007)	1358
Yearly deviation in mean temperature (0.45)	0.002 (−0.001 to 0.005)	1234
Tree diversity (1.27)	−0.001 (−0.005 to 0.002)	1234
Latitude (52.9)	-8.3×10^{-5} (−0.005 to 0.005)	1234
Year (2005)	0.002 (−0.002 to 0.005)	1234
Number of records (20.3)	0.002 (−0.002 to 0.005)	1234
Random effects		
Year	2.7×10^{-5} (4.9×10^{-9} to 6.2×10^{-5})	1234
Site	7.3×10^{-5} (2.6×10^{-5} to 1.3×10^{-4})	1234
Year : Site	5.5×10^{-5} (1.6×10^{-11} to 1.8×10^{-4})	1234
Yearly deviation in temperature : Site	3.9×10^{-6} (6.3×10^{-13} to 1.4×10^{-5})	1234
Residual	3.7×10^{-4} (2.3×10^{-4} to 4.7×10^{-4})	1234

Note: all variables were mean-centred, with mean values in parentheses after predictor name. Significance was assessed by credible intervals which did not overlap zero.

Blue Tits may not use local habitat as a cue to fine-tune initiation of their breeding. The lack of difference in FED could be due to birds being constrained by their physiology and/or being unable to process or interpret habitat cues. Our findings substantiate the experimental work that suggested habitat plays an insignificant role in breeding phenology of Blue Tits (Schaper *et al.* 2011). However, Shutt *et al.* (2019) found that Blue Tits FED in Scotland was predicted by Birch leafing

Table 3. Gaussian GLMM used to investigate the effect of woodland composition on Blue Tit clutch size, with significant predictors highlighted in bold.

	Coefficient/variance (mean and 95% credible interval)	Effective sample size
Fixed effects		
Intercept	**8.93 (8.16–9.82)**	**1444**
Spatial mean temperature (8.24)	**−0.75 (−1.12 to − 0.35)**	**1136**
Yearly deviation in mean temperature (0.41)	**−0.40 (−0.53 to − 0.24)**	**1260**
Latitude (52.4)	−0.17 (−0.41 to 0.03)	1260
Year (2003)	**−0.045 (−0.062 to − 0.027)**	**1260**
Tree density (427)	7.1×10^{-5} (-5.8×10^{-4} to $6.90 \text{ x } 10^{-4}$)	1508
First egg date (117)	**−0.115 (−0.12 to − 0.10)**	**1092**
Random effects		
Year	0.13 (0.05–0.24)	1415
Site	0.20 (0.09–0.37)	1120
Year : Site	0.26 (0.17–0.35)	1260
Yearly deviation in temperature : Site	0.005 (3.7×10^{-9} to 0.02)	1193
Woodland composition	0.87 (3.4×10^{-5} to 2.88)	1260
Residual	3.85 (3.74–3.97)	1071

Note: all coefficients were scaled and mean-centred, with mean values in parentheses after predictor name. Significance was assessed by credible intervals which did not overlap zero.

phenology, suggesting some physiological response to tree phenology or a resource that coincides with this (Visser & Lambrechts 1999).

A second potential explanation for the lack of difference in breeding phenology with woodland composition may be because many of the sites included in this study had diverse tree species compositions, which could result in low power to detect small effect sizes of individual tree species. We found no evidence that variation in FED differed with tree diversity, suggesting that variability in FED is not driven by the environmental variables investigated at these sites. The spatial scale at which habitat was recorded (at a site level) may have been too broad to detect fine-scale effects, with fine-scale studies reporting that environmental variables sampled at between 25 and 75 m of the nest showed the strongest associations with FED (Wilkin *et al.* 2007, Hinks *et al.* 2015, Matthysen *et al.* 2021), although not all of these investigated associations at larger spatial scales, and it is still unclear at what scale birds do interpret cues. In previous studies, where woodland composition was broadly homogeneous within a site, and was compared with another distinct woodland type, differences in FED have been documented. For example, FED differed between deciduous Oak woodlands and evergreen Oak woodlands in France and Corsica, although these sites also differed in mean temperature and rainfall (Blondel *et al.* 1993), and in Oak and Pine woodland areas in Sicily, Italy (Massa *et al.* 2004). Future work could extend the current study, by including tree phenology, such as budburst or leaf-up, as well as or instead of tree species density, which we used as a proxy for tree phenology, to see whether the lack of effect remains across such a large geographical scale. Previously, across both a 220-km transect in Scotland and at a national scale, Birch budburst has been shown accurately to predict Blue Tit FED (Shutt *et al.* 2019). However, at a single site in northern Belgium, Blue Tits, but not Great Tits, had earlier FED in nestboxes with more Oak but less Beech present; however, there was no relationship between FED and budburst (Matthysen *et al.* 2021) Notwithstanding the examples provided above, differences in reproductive phenology of birds nesting in non-Oak-dominated habitats to changes in spring climate, as well as the effect of phenological mismatch in non- (or low-density) Oak habitats, are poorly understood in comparison with Oak woodlands (e.g. Burgess *et al.* 2018). This should be a focus for future research given the continued increase in spring temperature, the impacts of warming springs in Oak woodlands and the abundance of non-Oak woodland, and species reliant on them, across the UK.

We show that clutch size has decreased as spring temperatures have increased both over

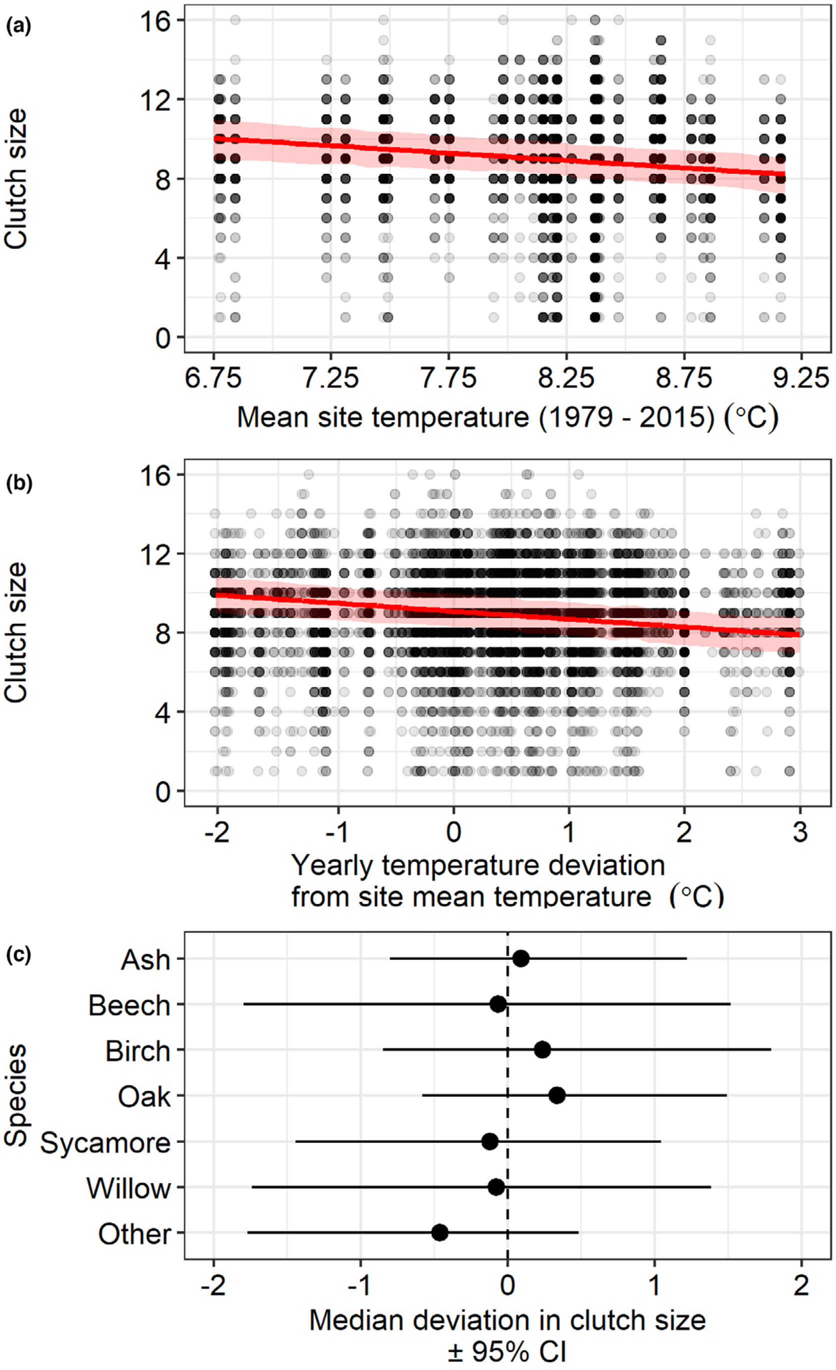

Figure 4. (a) The relationship between mean site temperature (1979–2015) and Blue Tit clutch size across the UK. The red line is the fitted line from a Bayesian GLMM, controlling for the effects of latitude, first egg date and year, with the lighter shaded areas showing the 95% credible intervals. The points show the raw underlying data from which the model was fitted, with darker points representing points where there are more data points at this position. (b) The relationship between deviations in yearly mean temperature from the site-level mean (1979–2015) and Blue Tit clutch size across the UK. The red line is the fitted line from a Bayesian mixed effects model, controlling for the effects of latitude, first egg date and year, with the lighter shaded areas showing the 95% credible intervals. The points show the raw underlying data from which the model was fitted, with darker points representing points where there are more data points at this position. (c) Deviations in clutch size, calculated from the random effect coefficients from a GLMM multiple membership model with woodland composition, showing how much bigger or smaller, on average, clutch sizes are due to the presence of each different tree genus within a site. CI, credible interval.

Table 4. Gaussian GLMM used to investigate the effect of woodland composition on the variance in Blue Tit clutch size, with significant predictors highlighted in bold.

	Coefficient/variance (mean and 95% credible interval)	Effective sample size
Fixed effects		
Intercept	**0.21 (0.20–0.23)**	**1234**
Spatial mean temperature (7.56)	−0.0004 (−0.01 to 0.01)	1234
Yearly deviation in mean temperature (−0.03)	0.009 (−0.002 to 0.02)	1234
Tree diversity (1.27)	0.006 (−0.005 to 0.02)	1457
Latitude (52.9)	−0.008 (−0.02 to 0.006)	1234
Year (2006)	−0.0009 (−0.01 to 0.01)	1234
Number of records (16.5)	0.001 (−0.01 to 0.02)	1234
First egg date (115)	**0.02 (0.003–0.04)**	**1113**
Random effects		
Year	2.1×10^{-4} (3.6×10^{-11} to 6.8×10^{-4})	1234
Site	1.7×10^{-4} (1.4×10^{-12} to 6.2×10^{-4})	1234
Year : Site	0.01 (0.009–0.01)	1085
Yearly deviation in temperature : Site	2.2×10^{-4} (5.5×10^{-11} to 8.3×10^{-4})	1281
Residual	8.4×10^{-5} (4.5×10^{-5} to 1.4×10^{-4})	1234

Note: all variables were mean-centred, with mean values in parentheses after predictor name. Significance was assessed by credible intervals which did not overlap zero.

space (with mean site temperature) and over time (with yearly temperature deviations), which increases our confidence that the effect of temperature is causal. This relationship has not previously been demonstrated in this species, or at a large scale. Our findings are opposite to those from a single site in southern England which found that Blue Tits nesting in warmer territories had larger clutch sizes in warm years, but are in line with their findings for birds nesting in cooler territories, which had a reduction in clutch size with increasing temperature (Shutt *et al.* 2022). In contrast, in Croatia, no relationship between temperature and clutch size was found (Dolenec 2007), and in Collard Flycatchers *Ficedula albicollis* breeding in Sweden there was no association between North Atlantic Oscillation Index (a proxy for temperature) and clutch size (Przybylo *et al.* 2000). Ambient temperature is likely to exert effects upon the female during egg-laying through influencing resource availability, as invertebrate prey phenology has been shown to be closely related to temperature (e.g. Buse & Good 1996). Temperature could also act as a cue for when peak invertebrate availability may occur, and therefore influence bird breeding parameters to allow synchrony between nestling demand and resource availability, which Blue and Great Tits must accurately predict up to approximately 30 days in advance. An example of such alterations could be to the onset of incubation, either through laying fewer eggs or commencing incubation prior to laying the final, or penultimate, egg, which is most common in Blue Tits (Perrins 1979, Cresswell & Mccleery 2003, Lord *et al.* 2011). Alterations to the onset of incubation have been shown to help synchronize nestling demand and food resources (Simmonds *et al.* 2017). Female age has also been shown to influence clutch size, with older females typically laying smaller clutches later in the breeding season (Amininasab *et al.* 2017). The impact of female age could not be explored with this dataset and could be contributing to the negative effect of temperature on clutch size, which should be noted when interpreting these results. However, the negative relationship between clutch size and temperature remains, even when controlling for FED, so this analysis should adequately account for differences in clutch size due to differences in breeding phenology due to female age (Bonamour *et al.* 2020).

No individual tree species exerted a significant effect on clutch size, contrary to our prediction that in woodlands with greater amounts of tree species that provide rich food resources for insectivorous breeding birds, such as Oak and Birch (Kennedy & Southwood 1984), clutch sizes would be larger. Previous work has shown that woodland composition had mixed effects on the clutch size of Blue Tits (Shutt *et al.* 2018, Matthysen *et al.* 2021). We suggest that the lack of a strong habitat effect may be due to birds being unable to predict nesting site quality during the initial nesting period, which supports findings from Shutt *et al.* (2018). Variation in clutch size did not differ with any of the environmental variables investigated across these sites, but variation in clutch size was higher later in the breeding season, which may be linked to the age of the breeding female. Typically, laying date decreases and then increases with age, and older females lay smaller clutches (Auld *et al.* 2011, Amininasab *et al.* 2017, Bonamour *et al.* 2020). If the populations have a mixed age-structure this may explain why variation in clutch size increases as the season progresses, as young females may produce larger clutch sizes than older females, and both may breed later in a breeding season, increasing the variability observed as the season progresses.

The implications of reduced clutch sizes with increasing spring temperature could be great, given future climate projections for further warming (IPCC 2021). However, how this translates into effects on population size will depend on whether recruitment remains stable (Reed *et al.* 2001). Moreover, the relationship with temperature is stronger than that of woodland composition, so woodland composition is unlikely to be able to counteract any negative effects of temperature.

We are aware of some limitations in our study, and we offer some suggestions for development in future work. First, we measured woodland composition at a site level, as opposed to at a territory level. This may have been too broad to detect subtle effects, as discussed previously, but was the only way possible to match woodland composition and breeding records using the BTO nest record dataset. For future studies, it would be interesting to compare site- and territory-level measures of woodland composition to tease apart the spatial scale most relevant to breeding insectivorous birds across a wide geographical scale. The results from this would be useful for informing woodland regeneration and planting schemes of species composition most beneficial for breeding insectivorous woodland birds. Secondly, we have no measure of hetero- or conspecific density, both of which have been shown to influence Blue Tit FED and clutch sizes (Goodenough *et al.* 2009, Møller *et al.* 2018), and this should be noted when interpreting our results. A possible proxy for this in future would be asking BTO nest recorders to submit annually how many nestboxes were present at their site, and how many were occupied (regardless of how many were monitored, species occupying and whether subsequent nest records were submitted) to be used as a proxy for breeding density.

In summary, considering the effects of habitat composition in assessments of the impacts of climate change on the phenology and clutch size of generalist consumers is important if we are to understand the full implications of increasing spring temperatures on species and how they may fare with continued spring warming. We found that there was no difference in the absolute timing of breeding in woodlands with different tree compositions. We also showed that Blue Tit clutch size decreased as spring temperatures increased but did not differ with different woodland compositions. The lack of effect of woodland composition suggests that Blue Tits do not fine-tune their reproductive phenology and investment to the local tree composition. However, whether this lack of evidence for phenological divergence is due to an absence of divergent selection, inability to interpret cues or gene flow is unclear. A crucial next step is to investigate whether phenological asynchrony between trophic levels is uniform across different woodland compositions, which should be coupled with exploring whether recruitment of Blue Tits differs, and would extend our findings to the impact at the population level and allow an understanding of whether woodland composition may be able to buffer any negative effects of warming springs.

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AUTHOR CONTRIBUTIONS

Claire J. Branston: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; writing – original draft; writing – review and editing. **Mark J. Whittingham:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Albert B. Phillimore:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Dave Leech:** Conceptualization; data curation; methodology; supervision; writing – review and editing. **Stephen G. Willis:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest to declare.

Data Availability Statement

All bird breeding data used in this paper are housed with the British Trust for Ornithology as part of the maintained National Database on Bird Ringing and Nest Recording. Data can be requested via https://www.bto.org/our-science/data/data-request-system. All temperature data are available on request from the MET Office and habitat data are archived in Figshare (https://doi.org/10.6084/m9.figshare.14912637).

ETHICAL STATEMENT

None.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Description of the species which comprise each tree category.

Figure S1. Map of the 34 study sites.

Figure S2. Correlation coefficients between predictor variables: temperature, woodland composition and tree diversity.