Spatial variation in avian phenological response to climate change linked to tree health

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Article abstract

While there is overwhelming evidence for phenological responses of animal and plant populations to climate change, most studies have been conducted at the level of entire populations, thus neglecting the scale at which much selection operates and at which animals and plants respond to their environments. Here, using data from a 60-year study, we demonstrate marked small-scale spatial variation in the rate of change in timing of egg laying in great tits (*Parus major*). We show, further, that this variation is linked to changes in the health of a key primary producer, oak *Quercus robur*. The existence of small-scale spatial variability in responses to climate change has important implications for understanding the extent to which local adaptation and phenotypic plasticity govern responses to climate change, and for the role of behavioural responses such as habitat selection and dispersal to ameliorate challenges due to climate extremes.

Main

There is extensive evidence from a variety of biological systems for phenotypic responses to climate change, particularly with respect to phenological traits [1–5]. Studies that have explored the underlying mechanisms of these responses have often found that phenotypic plasticity, rather than evolutionary change, is the key process underpinning the tracking of environmental change [6–8]. However, while some species and populations successfully track shifting climates, rates of change may vary, leading to disruption of the synchrony between trophic levels [9]. This has led to concerns that trophic mismatch may become widespread in some systems, leading to population decline and potential extinctions (e.g., see [10–14]).

Longitudinal population studies have been instrumental in revealing the effects of climate change on the timing of seasonal activities and showing how unequal shifts in the phenology of interacting species can lead to a trophic mismatch. For example, they have provided evidence for climate driven changes in the timing of migration and breeding in birds [15,16], mammals [17,18], amphibians [19], and fish [20]. Similarly, they have provided examples of phenological mismatch for a variety of species, such as the mismatch between seasonal coat colour change and snow melt in snowshoe hares [21], between the breeding time of barnacle geese and peak food quality for their offspring [22], and between the timing of bay checkerspot butterfly egg hatch and the senescence of their host plants [23].

Population studies of the breeding phenology of birds have been a particularly important model both for characterising the effects of climate change, and for exploring the underlying mechanisms and constraints, chiefly because the behaviour of many individuals can be studied across time and space [24,25]. Of these, the tritrophic system of passerine songbirds (e.g., the great tit, *Parus major*), feeding on caterpillars (e.g., winter moth, *Opheroptera brumata*), that in turn feed on the newly emerged leaves of deciduous trees (e.g., Oak, *Quercus robur*), has been especially influential [14]. Within this system, the peak in food availability for birds during the breeding season is highly transient and, as secondary consumers, they rely on the timing of organisms belonging to several different trophic levels. Research within these long-term studies has shown that warmer spring temperatures are associated with advances in the phenology of all three trophic levels, but the degree of advancement is typically slowest for birds [26–28], often leading to greater mismatch between them and their prey [29,30], and strong selection for earlier breeding [15,29,31]. The replication of such studies across space has also facilitated comparisons of phenological change and mismatch between populations, thereby enabling conclusions about the generality of such patterns [15,29,32,33].

Though population-level studies have provided many critical insights on phenological responses to climate change, they have an important limitation, in that they typically analyse variation at scales that may differ from that at which selection operates, and at which individuals respond to their environment. Specifically, such studies implicitly assume that the environment is equivalent for all individuals within a population and thus that they experience the same biotic and abiotic conditions. For example, in characterising climate at the population level when investigating relationships between climate and phenology, in effect it is assumed that individuals experience identical climatic conditions at a given time point (e.g. [18,34,35]), or by assuming that they all experience the same peak in food availability, we expect that the degree of match or mismatch is equivalent for all individuals (e.g. [15,35–37]). Similarly, by neglecting other aspects of the environment that likely vary spatially, such as population density, we assume that all individuals are equally exposed to factors that may interact with climate in determining reproductive behaviour and success. Such assumptions are unlikely to hold in natural systems as individual organisms commonly use a restricted amount of space and key environmental and phenological factors often vary considerably at small spatial scales (e.g., [38–40]).

An enhanced appreciation of the importance of scale when considering responses to climate change is key given that we expect individuals to adjust their phenology depending on multiple cues that operate over various spatial scales. For example, research suggests that birds time the onset of reproduction using cues including photoperiod [41,42], temperature [43,44], and the local vegetation phenology [40,45,46]. These cues differ in the scales over which they act, from very large (photoperiod) to small spatial scales (local vegetation phenology), and therefore, we may expect scale to be an important consideration when exploring relationships between environmental cues and bird phenology.

Understanding how different cues may be used by organisms to time seasonal events is also critical given that human activity is disrupting cues by changing how the environment varies, altering correlations between environmental components, and inhibiting the detectability of cues [47]. For example, temperatures at different points during the year are changing at different rates, meaning that even where interacting species use temperature as a key cue for timing a phenological event they may still become mismatched [48]. Similarly, changes in habitat quality may alter the cues available to organisms when making behavioural decisions, resulting in the expression of inappropriate behaviours that may have fitness consequences [49].

By considering small-scale spatial variability in climate-phenology relationships, we will gain an improved understanding of the limits on the ability of individual organisms to adjust to changing environments and therefore of the scope for populations to cope with climate change. For example, by ignoring within-population variability in the impacts of and responses to climate change, we may draw inappropriate conclusions regarding the importance of phenotypic plasticity or local adaptation in facilitating population persistence under climate change. Similarly, if the effects of climate change vary spatially due to environmental heterogeneity, behaviours such as dispersal and habitat selection may enable individuals to reduce the effects of climate change [50]. Thus, examining within-population variability in climate change impacts may be critical for predicting population responses to climate change and uncovering novel methods to offset the expected impacts of climate change.

In this study, we use breeding data for more than 13 000 great tits spanning 1961 to 2020 to (i) quantify spatial structure in the rate at which the mean date of clutch initiation (hereafter laying date) has advanced over the study period, (ii) uncover the local environmental factors predicting between-nestbox variation in the rate of laying date change. In particular, we test whether the nestbox-level change in laying date is explained by the health of local oak trees given the key role that oaks play as a major host of caterpillars that form the main food resource for great tit chicks.

Fine-scale variability in phenological change

The great tit population in Wytham Woods, near Oxford, UK, has been intensively studied for more than six decades, enabling analysis of temporal and spatial changes in reproductive timing as the climate has changed. When we consider data for the population as a whole between 1961 and 2020, both female laying date and the annual timing of peak abundance of winter moth larvae have advanced by over two weeks (tits: $ß \pm SE = -0.27 \pm 0.04$, $P < 0.0001$; caterpillars: $ß \pm SE = -0.25 \pm 0.05$, $P < 0.0001$; Figure 1A & B). Both measures of phenology are strongly predicted by mean daily maximum temperature in early spring (Figure 1D & 1E), which has shown an increase of 2.6 ˚C over the last 60 years ($ß \pm SE = 0.04 \pm 0.009$, $P < 0.0001$; Figure 1C). Consequently, at the population level, mean laying date and half-fall date have remained closely matched within years ($r = 0.78$, $n = 46$ years, $P < 0.0001$).

However, these analyses sum observations over six decades from a 385-ha study site. Studies investigating ranging behaviour by territorial great tits show that when prospecting for a breeding site they use a relatively small area, inspecting boxes within 75 m of their preferred box [51]. Similarly, during breeding they spend 90% of their time within 45 m of their breeding site [52,53]. Given the study duration, and the short lifespan of individual great tits (mean generation time of 1.8 years [54]), we can use repeated observations in given spatial locations as a measure of how the population responds to changes in that location. Analysing rate of change in laying date at the level of individual nestboxes (964 boxes that were used at least three times between 1961 and 2020), revealed marked small-scale variation in rates of response that were masked by population scale analysis (Figure 2A). For example, laying dates for females breeding in boxes whose rates of change fall in the upper quartile advance at less than one third the rate of those breeding in boxes whose rates of change lie in the lower quartile (Figure 2B), corresponding to shifts of 7.5 and 25.6 days, respectively, over the 60-year study period, compared with the population mean response of 16.2 days. Nestbox-level variation was also spatially non-random, with spatial autocorrelation analysis revealing that boxes within c. 1 km of each other show more similar rates of change than those further apart (Figure 2C).

There are a number of lines of evidence to suggest that the small-scale spatial differences in rate of change of breeding phenology are unlikely to be driven by differential rates of change in spring temperature over time. First, although altitude does explain some spatial variability in temperature across the study site [55], it is unlikely that the change in average temperature over time has varied across the woodland. Second, we found no evidence that either altitude (measured at ground level) or slope aspect (the degree to which the slope faced north) explained significant variation in rate of laying date change (See Table 1) despite their known influence on temperature. Thus, systematic change in habitat over time is a more likely driver of the observed variation in rate of change in phenology. Such changes may influence the cues birds use to time their breeding or the resources they obtain prior to breeding.

Oak health predicts the rate of phenological change

Oak trees are an extremely important component of tit foraging habitat as caterpillars are at their highest densities on oak foliage [56,57]. Great tits breeding in oak rich territories tend to breed earlier and have higher reproductive success [58,59]. A survey conducted in Wytham in 2011 revealed considerable spatial variation in the crown health of the 5,748 mature oak trees (see ED 1 & Methods). Both of Britain's native oak species can suffer from a syndrome called Chronic Oak Decline. This condition develops over decades and leads to declines in crown condition [60]. Within Wytham, two lines of evidence suggest that the variation in crown health is indicative of a long-term decline in oak health, rather than short-term, dynamic change. First, long-term data collected for 163 plots across Wytham on oak contribution to the canopy reveal that local crown dieback scores correlate with declines in oak canopy over 44 years (ß = -0.32, SE = 0.14, P = 0.03). Second, local dieback scores were a strong predictor of oak survival between 1975 and 2014 (N=388 oaks, posterior mean = -92.75, 95% credible interval = -151.08 – -34.61; ED 2; see Methods for further details).

We tested whether spatial variation in local oak tree health explained variability in the rate of change in laying date while accounting for multiple environmental variables known to influence timing of breeding in our population. Of the environmental predictors considered (altitude, slope aspect, average territory size, number of oaks within a 75m radius of the nestbox, distance to the edge of the woodland and habitat type, average oak dieback score within a 75 m buffer around each box [see ED3 for results using different buffer sizes]), only oak health was a statistically significant predictor of rate of change in laying date at the nestbox level (posterior mean = 0.022, 95% credible interval = 0.004 – 0.041, Figure 3 & Table 1. See ED4 for posterior distributions). Birds breeding in boxes surrounded by healthy oaks (oaks within 75m scoring an average crown dieback of 1/5; see ED5) advanced their laying by 0.34 days/year (95% CI = 0.47 – 0.21), whilst those nesting in areas with oaks in poor health (oaks within 75m scoring an average crown dieback of 5/5; see ED5) only advanced by 0.25 days/year (95% CI = 0.38 – 0.09), corresponding to an advance of 20.4 and 15 days respectively over the 60-year study period. To understand whether this effect was driven by four boxes with oak dieback scores of five, we repeated the analysis with these data points removed. The estimated relationship between average oak dieback score and the rate of laying date change was similar (posterior mean = 0.018, 95% credible interval = -0.002 – 0.036) and although the credible interval did overlap zero in this case, there was still 97% posterior probability that higher oak dieback was associated with slower rates of laying date advancement.

Importantly, an oak's crown health did not predict the timing of its spring budburst (measured in 2013: ß = -0.10, SE = 0.09, P = 0.24, measured in 2014: ß = -0.22, SE = 0.20, P = 0.28, N = 193), suggesting that birds breeding in areas of poor oak health are not merely tracking changing phenology of lower trophic levels. Similarly, our results could not be explained by boxes with faster rates of change being occupied more frequently in recent years, due to yearling or old birds being more likely to breed in boxes with poorer oak health, or by areas with poorer oak health being occupied later in the breeding season (see Supplementary Analysis section in Supplementary Information). We also investigated whether oak dieback scores were predicted by other environmental factors (diameter at breast height, aspect, elevation, the number of other oaks within 50 m, and soil calcium) that might themselves generate a correlation between dieback and laying date change. We found little evidence for consistent effects of any of the environmental factors on oak dieback scores (ED6) suggesting it is unlikely that other sources of environmental variability are driving the observed relationship between oak health and the rate of laying date change. Instead, our findings suggest that birds nesting in areas with poorer oak health are less able to keep up with the advancement of spring. Whether this is due to birds being limited in their ability to gather the resources needed to start breeding or because declines in oak health affect the cues they use to time breeding is yet to be determined. Distinguishing between these two alternatives is challenging and will require fine-scale measurement of resources and responses to them, possibly coupled with experimental tests. Given the potential for interaction between climate change and tree disease (e.g. [61]), the possibility of cascading trophic effects in responses to climate change deserves more attention.

The existence of small-scale spatial variability in responses to climate change, as demonstrated in this study, has important implications for understanding the extent to which evolutionary change and phenotypic plasticity will facilitate responses to environmental change. Spatial heterogeneity in environmental conditions may alter spatial patterns of selection by having differential effects on individuals with different phenotypes [62]. For example, the fitness benefits of earlier laying may differ between sites where oaks are healthy and those where oaks are in poor health. Given that spatial variation in selection is a critical element underpinning many evolutionary processes, including the maintenance of heritable trait variation [63] and local adaptation [64], understanding the behavioural and fitness consequences of spatial environmental heterogeneity is likely to be important for predicting the potential for, and likely trajectory of, evolutionary change in response to climate change. Nevertheless, we currently have very little empirical understanding of how environmental variation over variable spatial scales may influence selection within populations [65].

The spatial variability in laying date change uncovered here also sheds light on how small-scale environmental heterogeneity may impose constraints on phenotypic plasticity. Phenotypic plasticity is thought to be the key process enabling effective responses to climate change over short timescales [6,24], but it has become clear that the role that phenotypic plasticity plays in facilitating responses to environmental change varies considerably between populations [36,66]. One potential reason for this is that plastic responses may be influenced or constrained by combinations of multiple environmental components [6]. For example, birds use a variety of cues when determining when to breed, including temperature [44], rainfall [67], and the social environment [68]. Therefore, plasticity in breeding timing is likely to be affected by the specific combination of these factors. Nevertheless, we still have a limited understanding of how the ecological context itself can alter the degree of plasticity displayed by individuals (but see [69]). Here, we have shown that the health of oak trees is linked to the ability of birds to track warming spring temperatures. Thus, our work suggests that plastic responses to climate in one species are likely to depend on fine-scale variation in characteristics of connected species. When we consider that small-scale patterns of plasticity will influence the population-level response to the environment [70], it follows that an understanding of how suites of environmental components interact to determine plastic responses will be important for understanding why some populations are coping better than others, and for accurately predicting whether phenotypic plasticity will enable effective tracking of environmental change in the future.

The presence of fine-scale spatial structure in responses to climate change also has implications for the extent to which behavioural responses, such as habitat selection, may ameliorate challenges due to changing climate. Habitat selection, whereby individuals use or occupy certain habitats over others [71], is a major way in which individuals adjust their exposure to environmental factors that influence fitness [72]. Given that habitat characteristics are expected to modify the impacts of climate change, for example by altering microclimate, habitat heterogeneity is likely to alter the ability of organisms to respond to environmental change. Therefore, habitat selection may be an important mechanism by which individuals can maximise their fitness under environmental change. The success of habitat selection strategies will depend on multiple factors, including the degree of spatial heterogeneity and its spatial scale, the availability and reliability of information regarding habitat quality, and the relative costs and benefits to individuals of altering their habitat selection behaviour [73,74]. Nevertheless, where they occur, adaptive habitat choice decisions may have profound population-level consequences, buffering populations against the effects of climate change and potentially preventing population extinction, as well as providing additional time for the evolutionary change that is likely to be key in enabling effective long-term responses to climate change [50,75]. Despite this, little work has explored fine-scale spatial heterogeneity in climate change responses (but see [76,77]), and thus studies examining changes in habitat selection behaviour in response to climate change, and its fitness consequences, are extremely rare (but see [78,79]).

Our findings suggest that studying phenological change and resource utilisation at a scale relevant to individuals can provide new insights into the processes and constraints governing the extent to which animals can adjust to environmental change. For example, there may be cascading effects across trophic levels linked to systematic changes in producer health. Further work should test how phenological change varies at different spatial scales in a range of systems and explore both the underlying mechanisms and the ecological and evolutionary consequences of these processes.

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Methods

Study site

Wytham Woods (National Grid Reference SP4608; 51° 46′ N, 1° 19′ W) is a mixed-deciduous 385-ha woodland located on a hill (altitude range 60–170 m) in Oxfordshire, UK.

Wytham Woods is a mosaic of ancient and recent woodland, semi-natural and planted stands of different ages. The dominant tree species are: European ash (*Fraxinus excelsior*), Sycamore maple (*Acer pseudoplatanus*), pedunculate oak (*Quercus robur*), birch (*Betula spp.*) and European beech (*Fagus sylvatica)* [80].

Data collection

Bird phenology data

The great tit population at Wytham Woods has been studied using standardised methods since 1947 [81]. Since 1961, 996 fixed location nestboxes, attached to trees of various species, have been available to breeding great tits, the locations of which have been digitally mapped [82]. On average, 302 of these boxes are used by breeding great tits each year (1961-2020: mean = 302.4, SD = 105.5). During April and May, all nestboxes are visited weekly to obtain records of the date when the first egg is laid in a nest (hereafter laying date). Tits generally lay one egg a day [83], and therefore laying date can be inferred from the number of eggs observed on a weekly visit.

Caterpillar phenology data

The timing of peak availability of winter moth caterpillars has been recorded in Wytham since 1961. This peak is defined as the half fall date, which is the date by which 50% of the seasonal total of final instar winter moth caterpillars are collected in water traps as they descend from trees to pupate. These data were not collected between 1972-1974, 1976-1982 and 1989-1992 (14 of the 60 years), but the data that are available span the whole period of analysis. For further details see [15].

Oak data

In 2011 the location of every oak tree in Wytham Woods with a diameter at breast height (DBH) greater than 30cm (n = 5 748) was mapped using GPS. When this mapping was done, the DBH and crown health of each was also recorded. Health was scored on a scale from 1 to 5, where a score of 1 denotes a tree whose canopy has 0 to 25 % die-back and a value of 5 denotes a tree that is dead. In order to establish whether these health scores were indicative of long-term decline rather than more short-term, dynamic change, we compared them with two additional datasets. The first is one collected as part of a long-term study of vegetation change in Wytham Woods [80]. Oak tree presence/absence and an estimate of oak canopy cover were collected at 163 10 × 10 m quadrats located on alternate intersections of the 100 m Ordnance Survey grid across Wytham Woods in 1974, 1991, 1999, 2012 and 2018 (see [80] for further details). The second dataset estimates oak tree survival over a 39-year period using a sample of 388 oaks that were known to have fixed-location nestboxes on them in 1975. These 388 nestboxes were revisited in 2014 to establish whether the focal oak was still alive. If the oak was dead but still standing, or the nestbox had been moved to another tree due to the focal tree falling, the focal oak was recorded as dead.

To test whether an oaks crown health was related to its spring phenology we used spring leaf development data for 193 oak trees across the woodland between March and May in 2013 and 2014 (for details on oak tree selection see [55]). Observations began when leaf buds started to swell and continued at 3-day intervals until all shoots on the tree had developed small, unfolded leaves (see [55,84]). Developing buds were scored using a key of phenological stages ranging from “dormant buds” to “visible unfurled leaves” over the seven-stage key for oaks described by [40]. For each visit to a tree, a leaf development score was calculated by averaging visual scores for 12 sections of the canopy (three equal-sized vertical sections, each split into four quarters). Any dead parts of the canopy were omitted from this calculation. Crown health was measured here as the number of twelfths of the canopy alive.

Additional habitat data

Across Wytham Woods, there is considerable spatial heterogeneity in a range of environmental and habitat characters known to be associated with variation in great tit phenology and reproductive success [58,59]. For each nestbox, we calculated six environmental measures previously shown to be important to breeding great tits: altitude, slope aspect, average territory size, number of oaks within a 75m radius of the nestbox, distance to the edge of the woodland and habitat type. The altitude and slope aspect of each nestbox were extracted from a digital terrain model (see [82] for details), with aspect angles transformed into a linear measure of northness (cosine of the aspect angle), where a value of 1 represents due north, whilst a value of -1 corresponds to due south. A measure of territory size was estimated for each nestbox in each breeding season by creating Thiessen polygons around all boxes occupied by great tits. This approach places a boundary mid-way between a focal nestbox and all adjacent occupied nestboxes, with a boundary also imposed by the edge of the woodland. The area of Thiessen polygons was capped at a maximum of 1 ha to prevent biologically unreasonably territory sizes (see [58]). Average territory estimates were then calculated as the mean Thiessen polygon size for each box across the full dataset. Finally, to define habitat type, we used four habitat categories that correspond to successional stages ranging from recent 20th-century plantations to areas of ancient seminatural woodland [85].

To explore potential predictors of oak health, we calculated five local environmental measures for each oak tree: altitude, slope aspect and habitat type (all as per above), local oak density and local soil calcium levels. Local oak density, defined here as the number of oak trees within a 50 m radius of the focal oak, was included in case disease transmission plays a role in driving the observed variation in oak health. Soil calcium levels have been measured for each of 163 alternate intersections of the 100 m Ordnance Survey grid across Wytham Woods and have been shown to vary considerably across the woodland, from 63 to 21,000 mg100g^{-1} (for full survey details, see [86,87]). Following [88], we interpolated between these sample points to produce a map of soil calcium distribution and extracted an estimated measure for each individual oak tree.

Data analysis

Population level trends in laying date, half fall date, and spring temperature

We quantified the population level changes in laying date, caterpillar half fall date, and spring temperature between 1961 and 2020. For the laying date analysis, we focused on first clutches only, defined as those laid within 30 days of the first clutch in each year (as in [89]). In each case laying date was expressed relative to the first of April (i.e., April = 1). For the spring temperature analysis, we used the Hadley Centre Central England Temperature dataset (https://www.metoffice.gov.uk/hadobs/hadcet) to calculate the mean maximum daily temperature for the period of 14th March to 1st May in each year. This was the time period in which mean maximum daily temperature best predicted mean great tit laying date between 1961 and 2020 as calculated using an absolute sliding window analysis performed using the package ‘climwin’ [90,91]. In this analysis we considered all possible windows spanning the day before the laying date record to 365 days prior to the laying date record. We used AIC_c to select the best fit model by comparing all models with different sliding windows to an intercept-only model of annual mean laying dates. For all three analyses, each measure was used as the single response variable in a linear regression with year as the single fixed effect. We compared models with both linear and quadratic fits, with the best fit model selected based on AIC_c. It is important to note that sliding window analysis have recently received some criticism [77], and comparative work has shown that different sliding window analysis methods may select markedly different time windows, with some methods producing biologically implausible results [92]. Nevertheless, a wide range of studies indicate that early spring temperatures are predictive of timing of breeding in this species, and a causal effect of temperature has been demonstrated in captive studies.

Spatial structure in laying date change

We estimated the rate of change in laying date for all nestboxes installed in or prior to 1961 that were occupied at least three times (n = 953) between 1961 and 2020. As before, we used data for first clutches only, and we also excluded all clutches that had been subject to an experimental manipulation in a given year (1824 of 18200). To estimate slopes and their associated standard errors, we carried out a linear regression for each box with laying date as the response variable and year as the only covariate. We then tested for non-random spatial structure in laying date slopes using a Mantel correlogram analysis using the 'mantel.correlog' function in the package 'vegan' [93]. In this analysis, we restricted our data to the 703 boxes with 10 or more occupancies due to the greater uncertainty around the slope estimates for boxes occupied fewer than 10 times and the inability to account for this in this particular analysis. We used a matrix of laying date change similarity (Euclidean distance between pairs of boxes) and a geographical distance matrix as input to the Mantel correlogram analysis to quantify the degree to which the laying date slope of boxes resembled the slopes of neighbouring boxes at increasing spatial distances. We used 999 permutations, and the distance classes were automatically calculated using the Sturges' equation [94].

Predictors of spatial heterogeneity in laying date change

To explore the environmental determinants of spatial variation in the rate of laying date change, we analysed the nestbox level laying date slopes (as estimated above) using a mixed-effects meta-analytic approach in MCMCglmm [95]. We considered multiple fixed effects; the average oak dieback score within a 75 m buffer around each box (see ED3 for results using different buffer sizes), the distance of each nestbox from the woodland edge, nestbox altitude, nestbox slope aspect, average territory size, the number of oak trees within 75 m of each nestbox, and habitat type. We used 75 m because previous work has shown that oak availability at this scale is a key predictor of laying date in this system [82]. Because our response variable is itself an estimate with associated error, we incorporated the squared standard error of each slope as a sampling error random effect, meaning that boxes whose slopes were estimated with greater certainty were given more weight in the analysis. In addition, because spatial autocorrelation in unmeasured environmental factors may lead to nearby boxes having more similar slopes, we also accounted for the spatial arrangement of boxes. To do this, we constructed a spatial similarity matrix by calculating the straight-line distance between each pair of nestboxes and then scaling this value so that each box had a similarity of 1 with itself and a similarity of 0 denoted the greatest distance observed between any pair of boxes (3972 m). We then included nestbox identity as a random effect associated with this matrix to estimate the variance explained by spatial similarity (models without the spatial similarity effect showed a similar effect of oak health on laying date change – see Supplementary Table 1).

Random effects were assumed to follow normal distributions with variances to be estimated, except in the case of the sampling error effects, where the variance was fixed at 1. We used the default priors for the fixed effects, an inverse-Wishart prior for the residual random effect term, and a parameter expanded prior for the spatial similarity random effect. We re-ran models with an inverse-Wishart prior for the spatial similarity effect and this did not alter the conclusions drawn from the analysis. Models were run for 250,000 iterations, with the first 25,000 discarded as the burn-in and a sample taken every 150 iterations as this resulted in low autocorrelation between retained samples (< 0.10). We determined a fixed effect to be statistically significant when its 95% credible intervals did not include zero.

Context specificity of oak health effect

To understand whether the effects of oak health on laying date change varied depending on other characteristics of the local environment, we performed a post-hoc analysis where we tested first order interactions between oak dieback around a nestbox and factors known to affect territory quality. These were (i) the number of oaks within 75 m of a nestbox, (ii) altitude, (iii) distance from the woodland edge, and (iv) average territory size. These models were also carried out in MCMCglmm using the same model structure as above but containing each interaction separately.

Predictors of oak survival

To determine whether high oak dieback scores predicted a tree's probability of surviving, we used a mixed model to estimate the relationship between survival probability and oak dieback score after accounting for the number of other oak trees within 75 m, elevation, and distance from the woodland edge. To account for potential spatial autocorrelation in survival probability, we associated a tree identity random effect with a spatial similarity matrix (obtained as above). We used an inverse-Wishart prior for the residual random effect and a parameter expanded prior for the spatial similarity term. We ran the model for 1,200,000 iterations, with a burn-in of 200,000 iterations, and a thinning interval of 1000 iterations.

These values were chosen to ensure low autocorrelation between successive samples and thus a good effective sample size. As above, the significance of fixed effects was determined based on whether the 95% credible intervals crossed zero.

Relationship between oak health and oak phenology

To understand whether an oak's dieback score may predict the rate of change in bird laying date due to effects on budburst timing, we performed a post-hoc analysis where we tested the relationship between oak dieback score and budburst timing for trees in 2013 (n = 193) and 2014 (n = 181). We ran analyses separately for each year, with budburst date as the response and the number of twelfths of the canopy alive as the single fixed effect.

Predictors of oak dieback scores

To establish whether oak dieback scores were predicted by other environmental factors that might themselves generate a correlation between dieback and laying date change, we used a mixed model to test whether a tree's dieback score was predicted by a tree's diameter at breast height, aspect, elevation, the number of other oaks within 50 m, and soil calcium. To account for potential spatial autocorrelation in oak dieback scores we incorporated a spatial similarity matrix (as described above) that was associated with an oak identity random effect. Because we were unable to obtain spatial similarity matrices for the full dataset of 4483 trees due to the matrix being singular, we ran the model 100 times with a random sample of 200 trees to determine the support for effects of each term on oak dieback score. We use the 'threshold' family for each model, an inverse-Wishart prior for the residual random effect and a parameter expanded prior for the oak identity effect. We ran each model for 250 000 iterations, with a burn-in of 50 000 iterations, and a thin of 200.

Data availability

The data needed to replicate the analyses presented in this paper are available at https://doi.org/10.6084/m9.figshare.14345960.v1

Code availability

The code needed to replicate the analyses presented in this paper are available at https://doi.org/10.6084/m9.figshare.14345960.v1. Our analyses relied on the following packages: 'MCMCglmm' (version 2.29) [95], 'vegan' (version 2.5-6) [93], 'climwin' (version1.2.3) [90], and 'stats' (version 4.0.3) [96].

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Author contributions

E.F.C. and B.C.S. conceived the study. C.E.R. and E.F.C. performed the analysis. E.F.C. and C.E.R. drafted the manuscript with input from B.C.S.

Competing Interests statement

The authors declare no competing interests.

Table 1. Parameter estimates from models examining the relationships between environmental predictors and the rate of laying date change at individual nest boxes. Fixed effect parameter estimates and credible intervals from a linear mixed effects model with the rate of change in laying date as the response, each environmental predictor, and the spatial similarity term as a random effect. Differences in the precision of laying date slope estimates from individual boxes was accounted for by weighting observations by the squared

standard error. Terms whose credible intervals do not overlap zero, and therefore were deemed to be statistically significant, are shown in bold.

Model term	Posterior mode	95% credible interval
Distance from woodland edge	$9.89 \times e^{-5}$	$-2.99 \times e^{-5} – 2.23 \times e^{-4}$
Number of oaks	$-3.02 \times e^{-4}$	$-8.06 \times e^{-4} – 2.62 \times e^{-4}$
Average oak dieback score	**0.022**	**0.004 – 0.041**
Mean territory area	$5.18 \times e^{-7}$	$-1.15 \times e^{-6} – 2.17 \times e^{-6}$
Altitude	$-1.40 \times e^{-5}$	$-7.50 \times e^{-4} – 8.45 \times e^{-4}$
Slope aspect	0.004	-0.015 – 0.027
Habitat type (18th/19th century plantation)	0.016	-0.030 - 0.060
Habitat type (secondary regenerated woodland)	0.034	-0.013 - 0.077
Habitat type (ancient semi-natural woodland)	0.016	-0.025 - 0.050

Figure legends:

Figure 1. **Great tit laying date has advanced as spring temperatures have warmed, allowing birds to track their caterpillar prey.** Changes over time in mean laying date of great tits (A), and half-fall date of winter moth caterpillars (B) at Wytham, near Oxford, UK, between 1961 and 2020, (C) early spring temperature (mean daily maximum temperature between 14th February and 1st May, Hadley Centre Central England Temperature dataset). Relationships between mean daily maximum temperature between 14th February and 1st May and annual mean laying date (D) and caterpillar half fall date (E). Points represent annual means (laying date and temperature) or annual measures (half fall date), error bars correspond to standard errors, lines correspond to fitted relationships from linear models.

Figure 2. The rate of change in laying date varies across Wytham Woods. (A) The spatial structure of laying date change in great tits across Wytham from 1961-2020. Arrows are plotted in the location of nest boxes occupied at least 10 times (n = 703). Note that we display boxes occupied 10 times as these are the boxes used in the analysis exploring predictors of the rate of laying date change. Arrow direction relative to 90˚ (and colour) indicates the direction of change (days/year) as estimated using a linear model with year as the single fixed effect; arrow length indicates the difference in laying date change relative to the population

mean of -0.27 days yr^{-1} (longer = larger difference); arrow thickness is inversely proportional to the box-level estimated standard error. (B) Rates of laying date change for boxes classified according to their laying date slopes (fast = lower 25%, slow = upper 25%, medium = remaining 50%). Fitted lines come from linear models with year as the only fixed effect, (C) Mantel correlogram showing the direction and strength of spatial autocorrelation between boxes in different distance classes. Open circles correspond to non-significant spatial autocorrelation whilst closed circles indicate significant positive or negative spatial autocorrelation.

Figure 3. **Local oak health predicts the rate of laying date change.** The nestbox level rate of lay date change was related to the average oak dieback score within 75 m of a nestbox. Points show the raw data, with size corresponding to the standard error associated with the estimated box-level rate of laying date change

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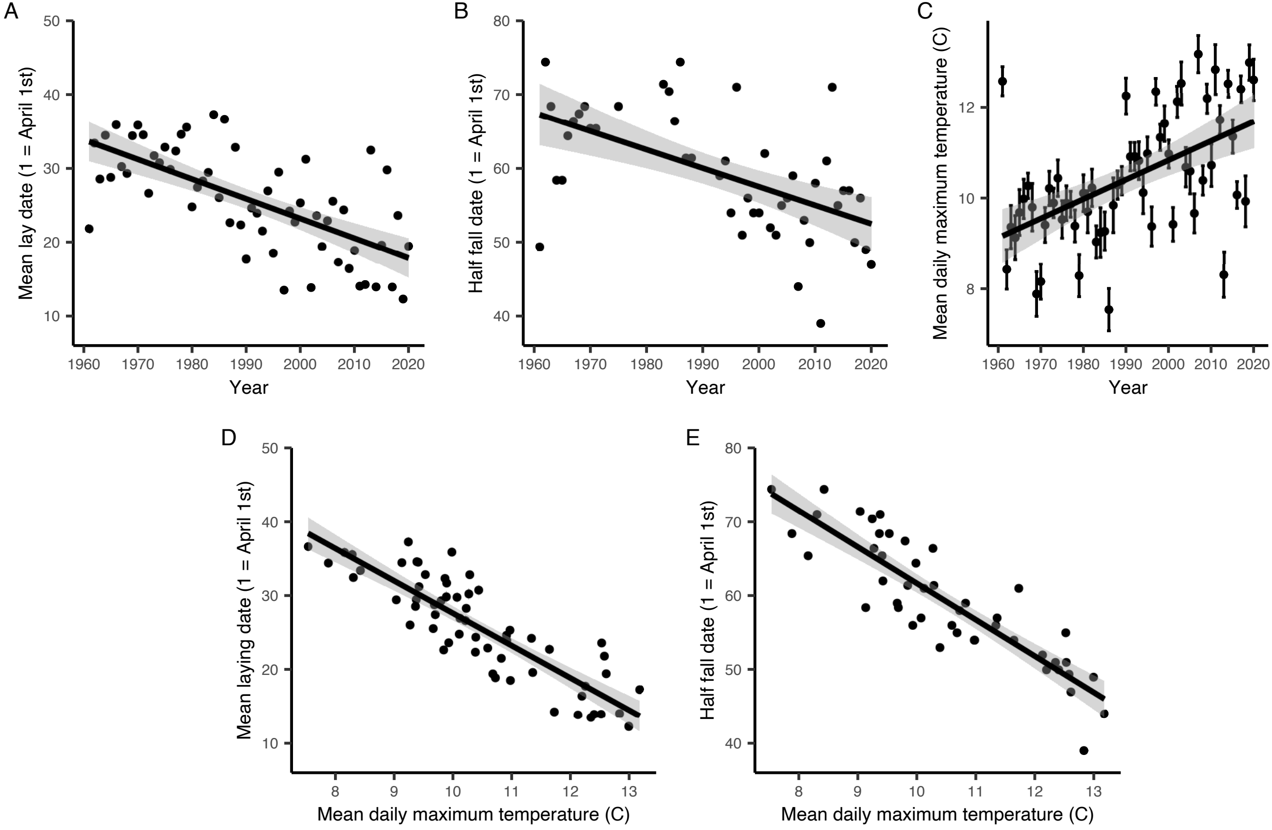
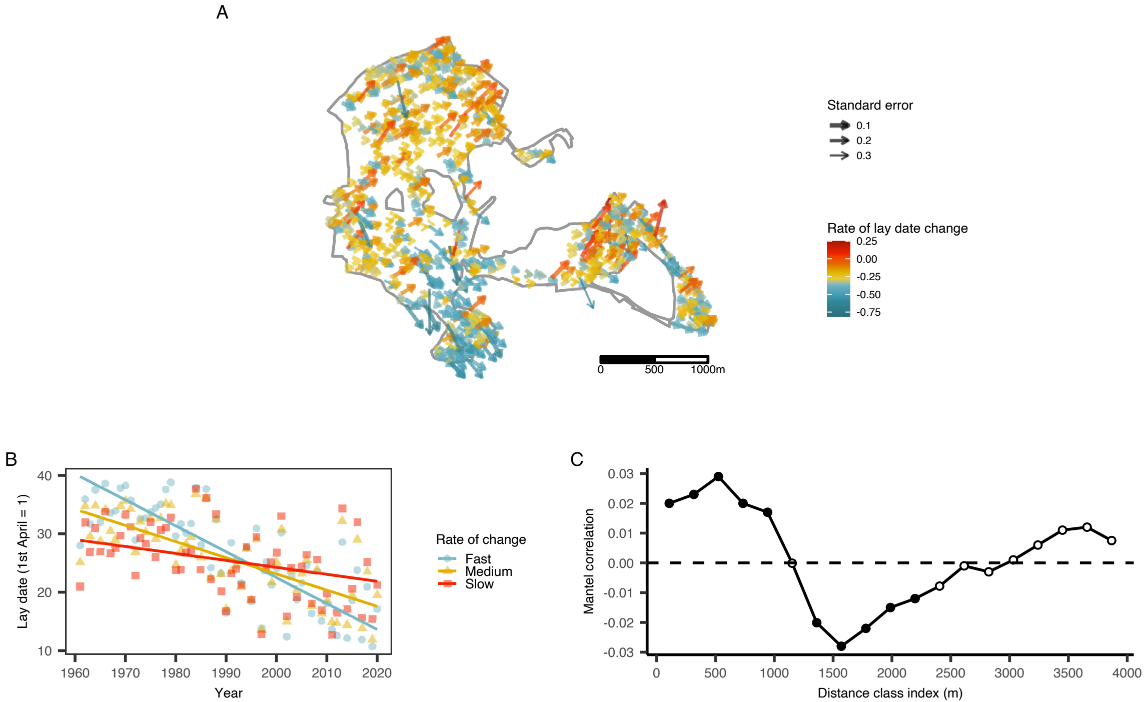
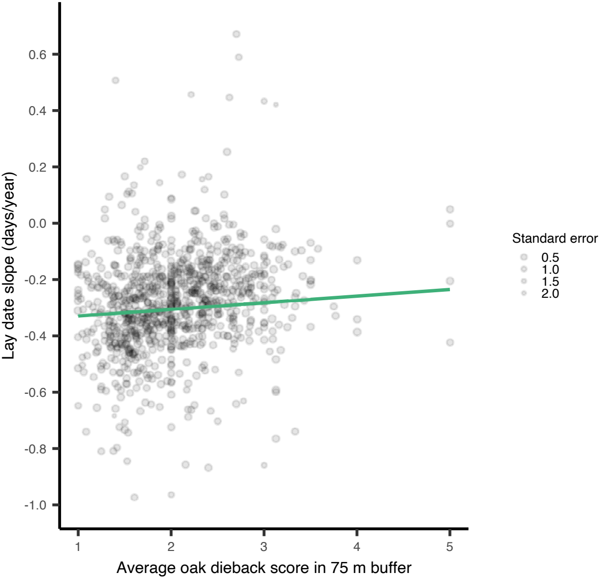
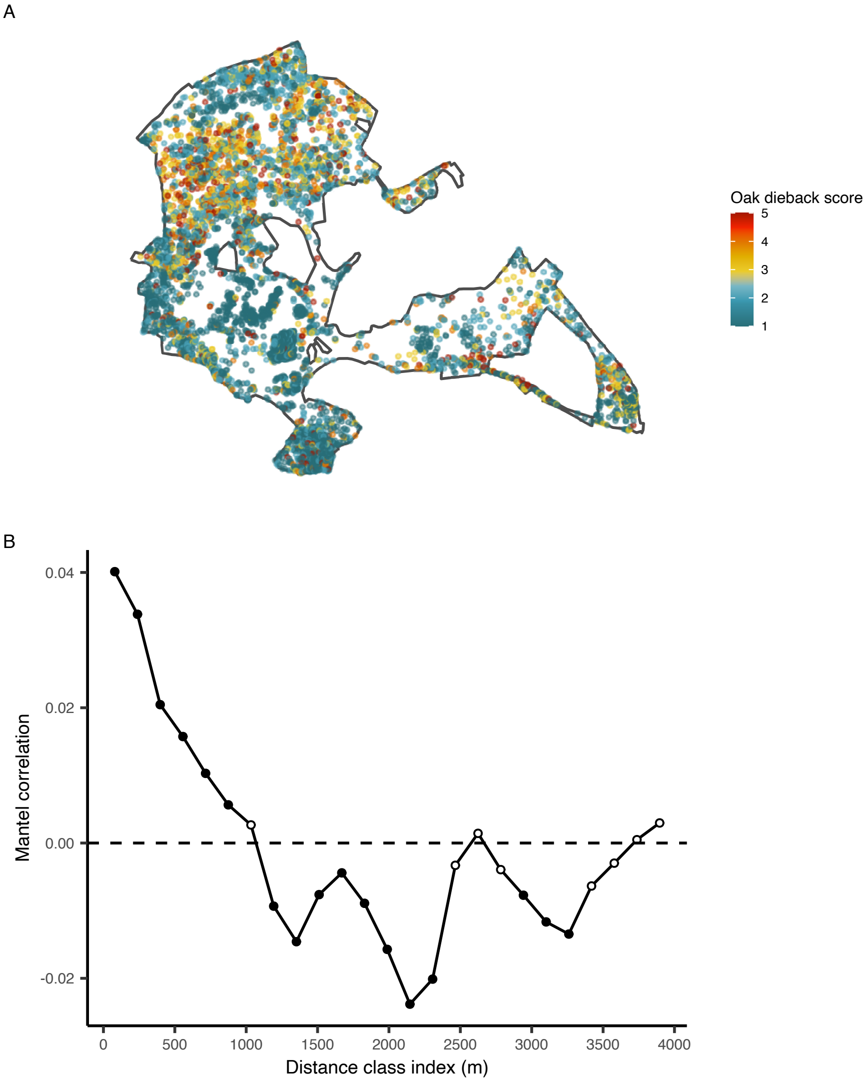
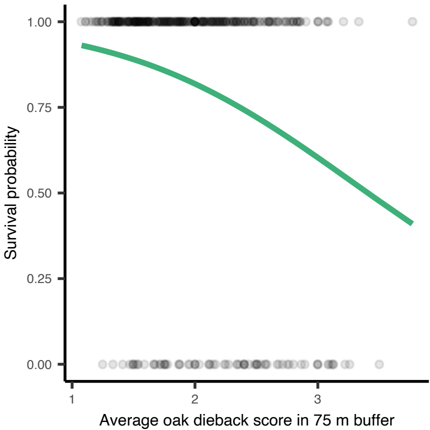
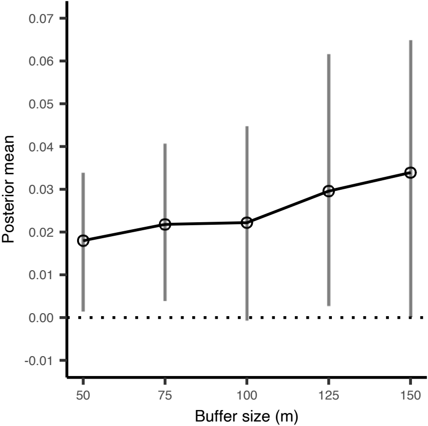

A
Mean lay date (1 = April 1st)
50
40
30
20
10
1960
1970
1980
1990
2000
2010
2020
Year
B
Half fall date (1 = April 1st)
80
70
60
50
40
1960
1970
1980
1990
2000
2010
2020
Year
C
Mean daily maximum temperature (C)
12
10
8
1960
1970
1980
1990
2000
2010
2020
Year
D
Mean laying date (1 = April 1st)
50
40
30
20
10
8
9
10
11
12
13
Mean daily maximum temperature (C)
E
Half fall date (1 = April 1st)
80
70
60
50
40
8
9
10
11
12
13
Mean daily maximum temperature (C)

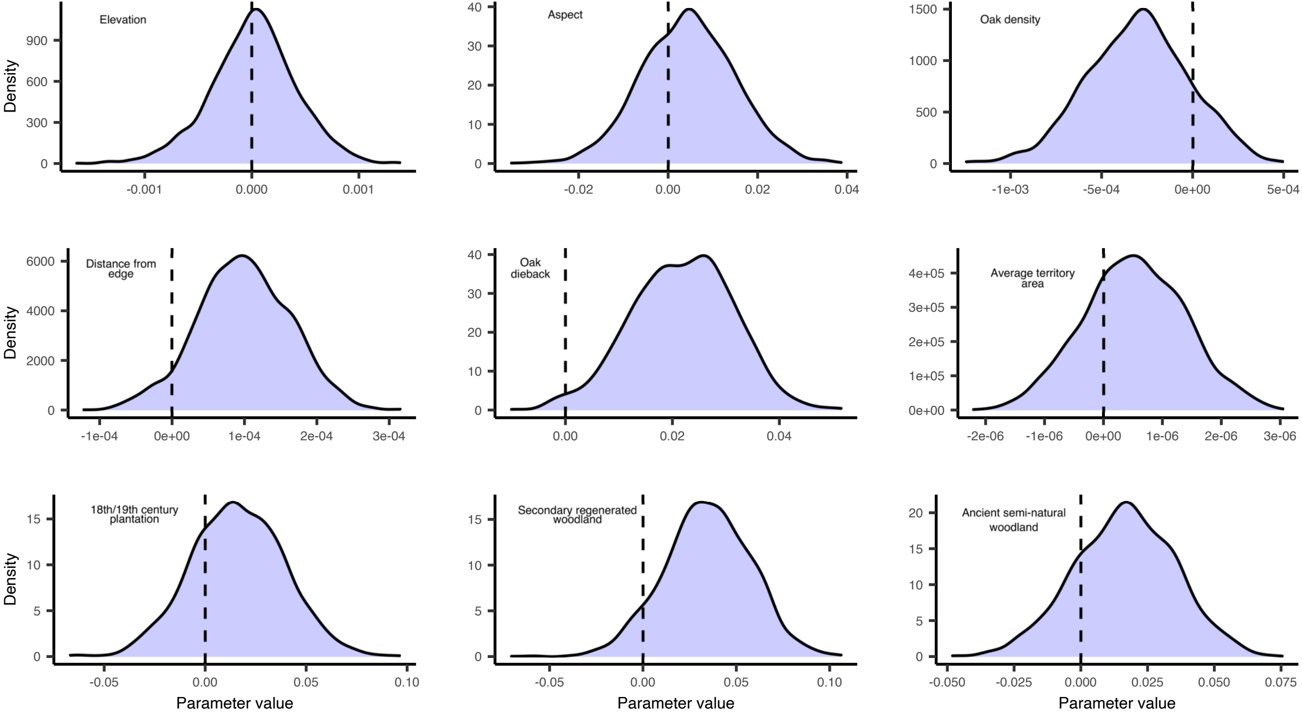

A
Standard error
0.1
0.2
0.3
Rate of lay date change
0.25
0.00
-0.25
-0.50
-0.75
0
500
1000m
B
Lay date (1st April = 1)
40
30
20
10
1960
1970
1980
1990
2000
2010
2020
Year
Rate of change
Fast
Medium
Slow
C
Mantel correlation
0.03
0.02
0.01
0.00
-0.01
-0.02
-0.03
0
500
1000
1500
2000
2500
3000
3500
4000
Distance class index (m)


Lay date slope (days/year)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
1
2
3
4
5
Average oak dieback score in 75 m buffer
Standard error
0.5
1.0
1.5
2.0


A
Oak dieback score
5
4
3
2
1
B
Mantel correlation
0.04
0.02
0.00
-0.02
0
500
1000
1500
2000
2500
3000
3500
4000
Distance class index (m)


1.00
0.75
0.50
0.25
0.00
Survival probability
1
2
3
Average oak dieback score in 75 m buffer

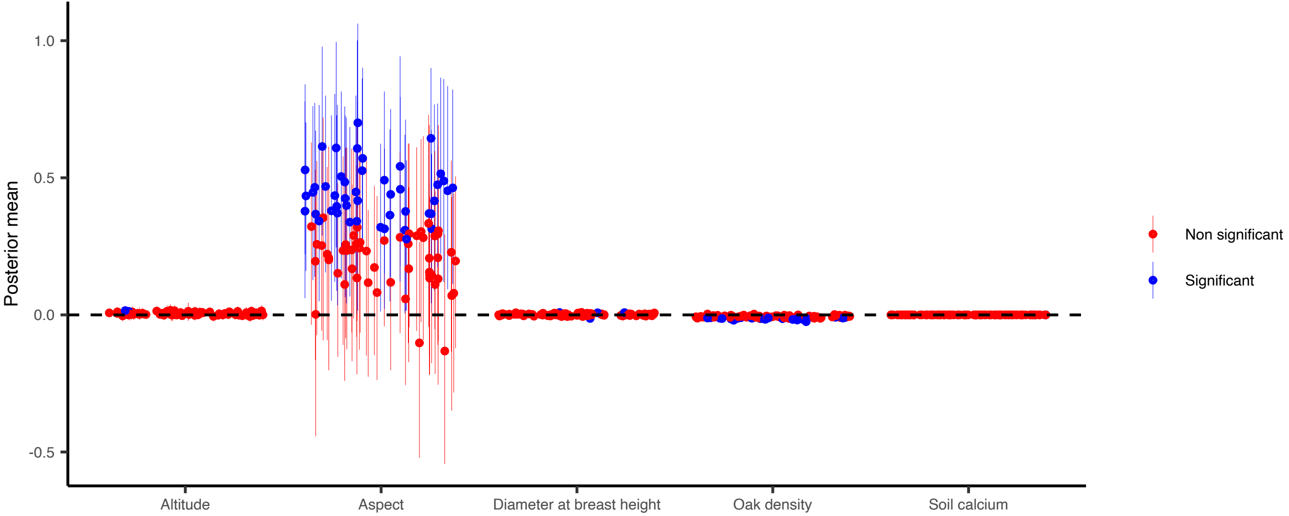

Posterior mean
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
Buffer size (m)
50
75
100
125
150



Elevation
Aspect
Oak density
Distance from edge
Oak dieback
Average territory area
18th/19th century plantation
Secondary regenerated woodland
Ancient semi-natural woodland
Density
Parameter value
0
300
600
900
-0.001
0.000
0.001
0
10
20
30
40
-0.02
0.00
0.02
0.04
0
500
1000
1500
-1e-03
-5e-04
0e+00
5e-04
0
2000
4000
6000
-1e-04
0e+00
1e-04
2e-04
3e-04
0
10
20
30
40
0.00
0.02
0.04
0e+00
1e+05
2e+05
3e+05
4e+05
-2e-06
-1e-06
0e+00
1e-06
2e-06
3e-06
0
5
10
15
-0.05
0.00
0.05
0.10
0
5
10
15
-0.05
0.00
0.05
0.10
0
5
10
15
20
-0.050
-0.025
0.000
0.025
0.050
0.075

1 2 3 4 5

Oak dieback score


Posterior mean
1.0
0.5
0.0
-0.5
Altitude
Aspect
Diameter at breast height
Oak density
Soil calcium
Non significant
Significant