



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

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**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 in ameliorating challenges due to climate extremes.**

There is extensive evidence from a variety of biological systems for phenotypic responses to climate change, particularly with respect to phenological traits<sup>1–5</sup>. 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<sup>6–8</sup>. However, while some species and populations successfully track shifting climates, rates of change may vary, leading to disruption of the synchrony between trophic levels<sup>9</sup>. This has led to concerns that trophic mismatch may become widespread in some systems, leading to population decline and potential extinctions (for example, see refs. <sup>10–14</sup>).

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, such studies have provided evidence for climate-driven changes in the timing of migration and breeding in birds<sup>15,16</sup>, mammals<sup>17,18</sup>, amphibians<sup>19</sup> and fish<sup>20</sup>. Similarly, these studies have provided examples of phenological mismatch for a variety of species, such as the mismatch between seasonal coat-colour change in snowshoe hares and snow melt<sup>21</sup>, between the breeding time of barnacle geese and peak food quality for their offspring<sup>22</sup> and between the timing of bay-checkerspot-butterfly egg hatch and the senescence of their host plants<sup>23</sup>.

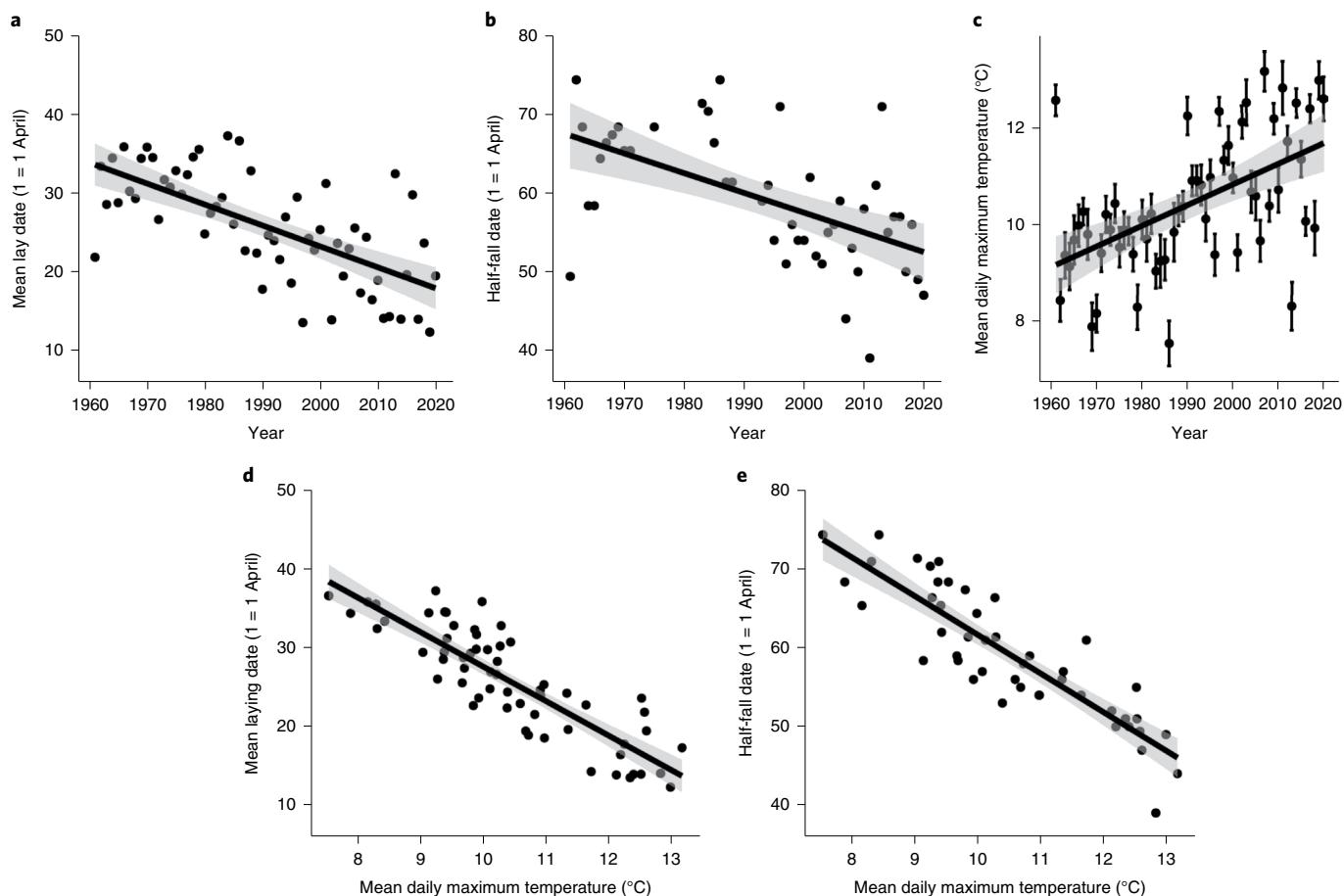
Population studies of the breeding phenology of birds have been a particularly important model both for characterizing the effects of climate change and for exploring the underlying mechanisms and constraints, chiefly because the behaviour of many individuals can be studied across time and space<sup>24,25</sup>. Of these, the tritrophic system of passerine songbirds (for example, the great tit, *Parus major*) feeding on caterpillars (for example, winter moth, *Opheroptera brumata*), which in turn feed on the newly emerged leaves of deciduous trees (for example, Oak, *Quercus robur*), has been especially influential<sup>4</sup>. 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<sup>26–28</sup>, often leading to greater mismatch between them and their prey<sup>29,30</sup> and to strong selection for earlier breeding<sup>15,29,31</sup>. 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<sup>15,29,32,33</sup>.

Although 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 characterizing 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 (for example, refs. <sup>18,34,35</sup>), 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 (for example, refs. <sup>15,35–37</sup>). Similarly, by neglecting other aspects of the environment that probably 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 (for example, refs. <sup>38–40</sup>).

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 photo period<sup>41,42</sup>, temperature<sup>43,44</sup> and the local vegetation phenology<sup>40,45,46</sup>. These cues differ in the scales over which they act, from very large (photo period) to small spatial scales (local vegetation

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**Fig. 1 | Great tit laying date has advanced as spring temperatures have warmed, allowing birds to track their caterpillar prey. a–c.** 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, and early spring temperature (mean daily maximum temperature between 14 February and 1 May, Hadley Centre Central England Temperature dataset) (c). **d,e.** Relationships between mean daily maximum temperature between 14 February and 1 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.

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<sup>47</sup>. 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<sup>48</sup>. 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<sup>49</sup>.

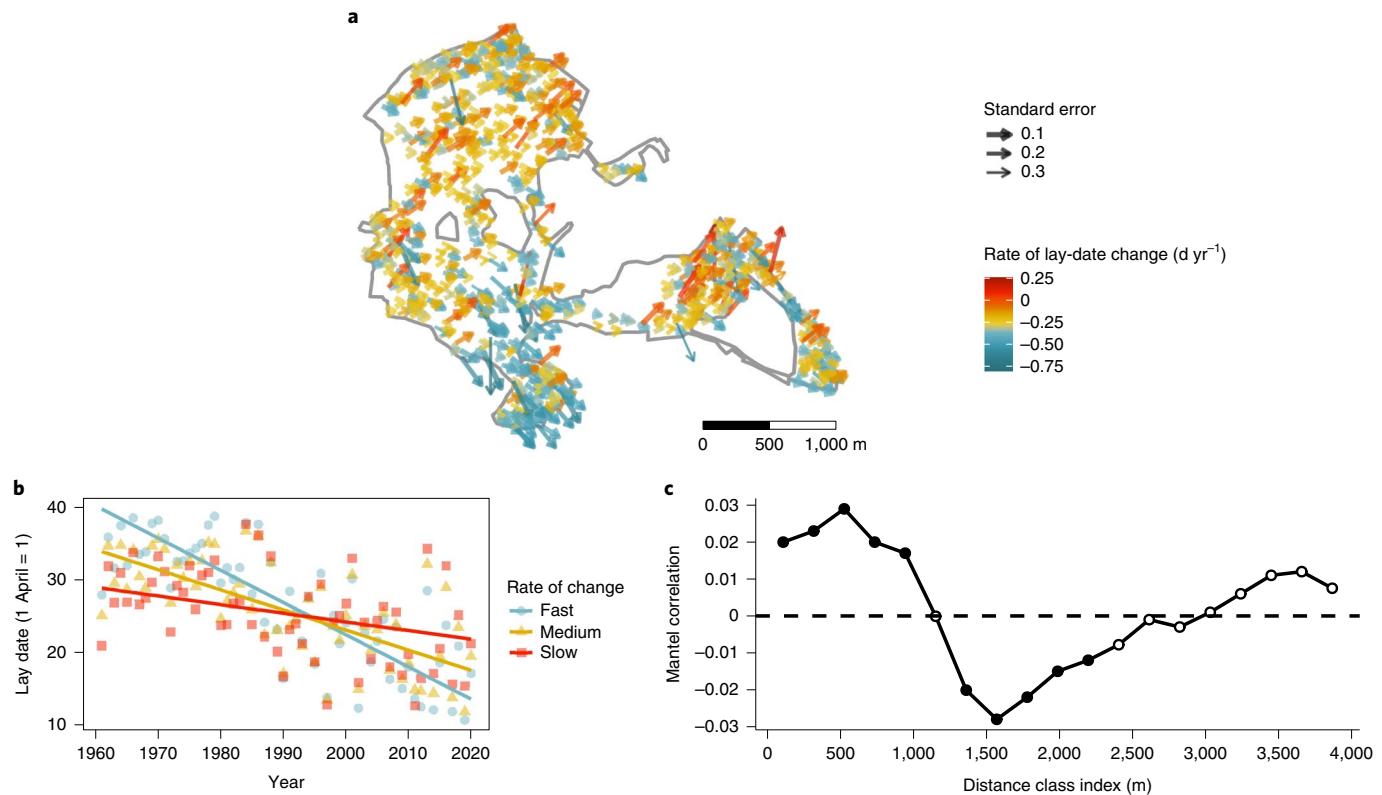
By considering small-scale spatial variability in climate–phenology relationships, we will gain an improved understanding of the limits on the ability of individual organisms to adjust to changing environments and therefore of the scope for populations to cope with climate change. For example, by ignoring 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<sup>50</sup>. 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 (1) quantify spatial structure in the rate at which the mean date of clutch initiation (laying date) has advanced over the study period and (2) 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: estimate (est.)  $\pm$  standard error



**Fig. 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 to 2020. Arrows are plotted in the locations of nestboxes occupied at least ten times ( $n=703$ ). We display boxes occupied ten times as these are the boxes used in the analysis exploring predictors of the rate of laying-date change. Arrow direction relative to  $90^\circ$  (and colour) indicates the direction of change (days per 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  $-0.27 \text{ d yr}^{-1}$  (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 while closed circles indicate significant positive or negative spatial autocorrelation.

(SE) =  $-0.27 \pm 0.04$ ,  $P < 0.0001$ ; caterpillars: est.  $\pm$  SE =  $-0.25 \pm 0.05$ ,  $P < 0.0001$ ; Fig. 1a,b). Both measures of phenology are strongly predicted by mean daily maximum temperature in early spring (Fig. 1d,e), which has shown an increase of  $2.6^\circ\text{C}$  over the past 60 years (est.  $\pm$  SE =  $0.04 \pm 0.009$ ,  $P < 0.0001$ ; Fig. 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<sup>51</sup>. Similarly, during breeding they spend 90% of their time within 45 m of their breeding site<sup>52,53</sup>. Given the study duration, and the short lifespan of individual great tits (mean generation time of 1.8 years<sup>54</sup>), 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 (Fig. 2a). For example, laying dates for females breeding in boxes whose rates of change fall in the upper quartile advanced at less than one-third the rate of those breeding in boxes whose rates of change lie in the lower quartile (Fig. 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 ~1 km of each other show more-similar rates of change than do those farther apart (Fig. 2c).

Various lines of evidence 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<sup>55</sup>, 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 (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 before 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<sup>56,57</sup>. Great tits breeding in oak-rich territories tend to breed earlier and have higher reproductive success<sup>58,59</sup>. A survey conducted in Wytham in 2011 revealed considerable spatial variation in the crown health of the 5,748 mature oak trees (Extended Data Fig. 1

**Table 1 | Parameter estimates from models examining the relationships between environmental predictors and the rate of laying-date change at individual nestboxes**

Model term	Posterior mode	95% credible interval
Distance from woodland edge	$9.89 \times 10^{-5}$	$-2.99 \times 10^{-5}$ to $2.23 \times 10^{-4}$
Number of oaks	$-3.02 \times 10^{-4}$	$-8.06 \times 10^{-4}$ to $2.62 \times 10^{-4}$
<b>Average oak-dieback score</b>	<b>0.022</b>	<b>0.004 to 0.041</b>
Mean territory area	$5.18 \times 10^{-7}$	$-1.15 \times 10^{-6}$ to $2.17 \times 10^{-6}$
Altitude	$-1.40 \times 10^{-5}$	$-7.50 \times 10^{-4}$ to $8.45 \times 10^{-4}$
Slope aspect	0.004	-0.015 to 0.027
Habitat type (eighteenth-/nineteenth-century plantation)	0.016	-0.030 to 0.060
Habitat type (secondary regenerated woodland)	0.034	-0.013 to 0.077
Habitat type (ancient semi-natural woodland)	0.016	-0.025 to 0.050

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 were 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.

and 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<sup>60</sup>. 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 (est. = -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 to -34.61; Extended Data Fig. 2; further details in Methods).

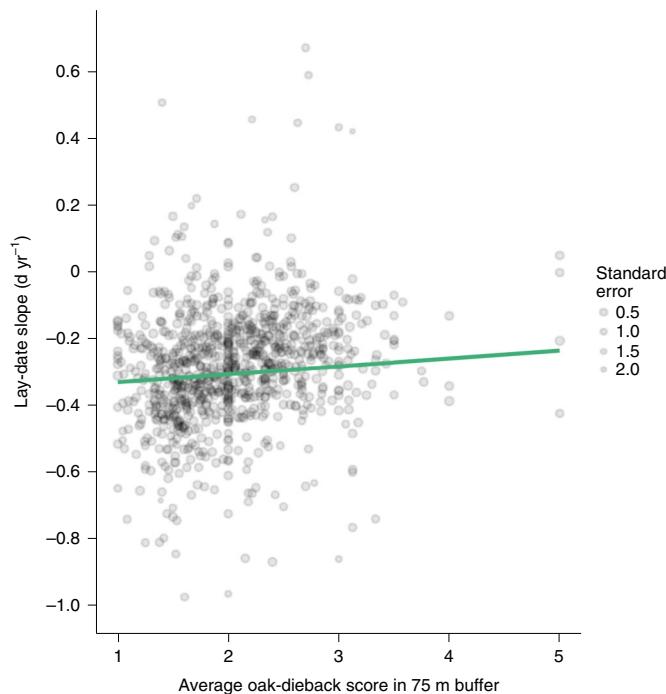
We tested whether spatial variation in local oak tree health explained variability in the rate of change in laying date while accounting for multiple environmental variables known to influence timing of breeding in our population. Of the environmental predictors considered (altitude, slope aspect, average territory size, number of oaks within a 75 m radius of the nestbox, distance to the edge of the woodland, habitat type and average oak-dieback score within a 75 m buffer around each box (see Extended Data Fig. 3 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, Fig. 3 and Table 1. See Extended Data Fig. 4 for posterior distributions). Birds breeding in boxes surrounded by healthy oaks (oaks within 75 m scoring an average crown dieback of one; Extended Data Fig. 5) advanced their laying by 0.34 days per year (95% CI = 0.47–0.21), while those nesting in areas with oaks in poor health (oaks within 75 m scoring an average crown dieback of five; Extended Data Fig. 5) advanced by only 0.25 days per 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 to 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: est. = -0.10, SE = 0.09, P = 0.24; measured in 2014: est. = -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 (Extended Data Fig. 6), 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 (for example, ref. <sup>61</sup>), 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<sup>62</sup>. 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<sup>63</sup> and local adaptation<sup>64</sup>, understanding the behavioural and fitness consequences of spatial environmental heterogeneity will probably 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<sup>65</sup>.

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<sup>6,24</sup>, but it has become clear that the role that phenotypic plasticity plays in facilitating responses to environmental change varies considerably between populations<sup>36,66</sup>. One potential reason for this is that plastic responses may be influenced or constrained by combinations of multiple environmental components<sup>6</sup>. For example, birds use a variety of cues when determining



**Fig. 3 | Local oak health predicts the rate of laying-date change.** The nestbox-level rate of laying-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.

when to breed, including temperature<sup>44</sup>, rainfall<sup>67</sup> and the social environment<sup>68</sup>. Therefore, plasticity in breeding timing is probably 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 ref. <sup>69</sup>). 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<sup>70</sup>, 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<sup>71</sup>, is a major way in which individuals adjust their exposure to environmental factors that influence fitness<sup>72</sup>. 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 maximize 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<sup>73,74</sup>. 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<sup>50,75</sup>. Despite this, little work has explored fine-scale spatial heterogeneity in climate change responses (but see refs. <sup>76,77</sup>), and thus studies examining changes in habitat selection behaviour in response to climate change, and its fitness consequences, are extremely rare (but see refs. <sup>78,79</sup>).

Our findings suggest that studying phenological change and resource utilization 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.

### Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-021-01140-4>.

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### References

- Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42 (2003).
- Root, T. L. et al. Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60 (2003).
- Scheffers, B. R. et al. The broad footprint of climate change from genes to biomes to people. *Science* **354**, aaf7671 (2016).
- Cohen, J. M., Lajeunesse, M. J. & Rohr, J. R. A global synthesis of animal phenological responses to climate change. *Nat. Clim. Change* **8**, 224–228 (2018).
- Piao, S. et al. Plant phenology and global climate change: current progresses and challenges. *Glob. Change Biol.* **25**, 1922–1940 (2019).
- Merilä, J. & Hendry, A. P. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol. Appl.* **7**, 1–14 (2014).
- Chevin, L. M. & Hoffmann, A. A. Evolution of phenotypic plasticity in extreme environments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **372**, 20160138 (2017).
- Fox, R. J., Donelson, J. M., Schunter, C., Ravasi, T. & Gaitán-Espitia, J. D. Beyond buying time: the role of plasticity in phenotypic adaptation to rapid environmental change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **374**, 20180174 (2019).
- Thackeray, S. J. et al. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Change Biol.* **16**, 3304–3313 (2010).
- Kharouba, H. M. et al. Global shifts in the phenological synchrony of species interactions over recent decades. *Proc. Natl Acad. Sci. USA* **115**, 5211–5216 (2018).
- Radchuk, V. et al. Adaptive responses of animals to climate change are most likely insufficient. *Nat. Commun.* **10**, 3109 (2019).
- Visser, M. E. & Gienapp, P. Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879–885 (2019).
- Kharouba, H. M. & Wolkovich, E. M. Disconnects between ecological theory and data in phenological mismatch research. *Nat. Clim. Change* **10**, 406–415 (2020).
- Samplonius, J. M. et al. Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts. *Nat. Ecol. Evol.* **5**, 155–164 (2021).
- Charmantier, A. et al. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**, 800–803 (2008).
- Tomotani, B. M. et al. Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird. *Glob. Change Biol.* **24**, 823–835 (2018).

17. Moyes, K. et al. Advancing breeding phenology in response to environmental change in a wild red deer population. *Glob. Change Biol.* **17**, 2455–2469 (2011).
18. Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O. & Dobson, F. S. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature* **489**, 554–557 (2012).
19. Todd, B. D., Scott, D. E., Pechmann, J. H. K. & Whitfield Gibbons, J. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. *Proc. R. Soc. Lond. B Biol. Sci.* **278**, 2191–2197 (2011).
20. Taylor, S. G. Climate warming causes phenological shift in pink salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Glob. Change Biol.* **14**, 229–235 (2008).
21. Mills, L. S. et al. Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proc. Natl Acad. Sci. USA* **110**, 7360–7365 (2013).
22. Lameris, T. K. et al. Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Curr. Biol.* **28**, 2467–2473, e4 (2018).
23. Singer, M. C. & Parmesan, C. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3161–3176 (2010).
24. Charmantier, A. & Gienapp, P. Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evol. Appl.* **7**, 15–28 (2014).
25. Keegan, K. et al. Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nat. Clim. Change* **8**, 313–317 (2018).
26. Both, C. & Visser, M. E. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296–298 (2001).
27. Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B. & Visser, M. E. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* **78**, 73–83 (2009).
28. Cresswell, W. & McCleery, R. How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *J. Anim. Ecol.* **72**, 356–366 (2003).
29. Visser, M. E., Van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 1867–1870 (1998).
30. Sanz, J. J., Potti, J., Moreno, J., Merino, S. & Frías, O. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Glob. Change Biol.* **9**, 461–472 (2003).
31. Marrot, P., Charmantier, A., Blondel, J. & Garant, D. Current spring warming as a driver of selection on reproductive timing in a wild passerine. *J. Anim. Ecol.* **87**, 754–764 (2018).
32. Burgess, M. D. et al. Tritrophic phenological match–mismatch in space and time. *Nat. Ecol. Evol.* **2**, 970–975 (2018).
33. Visser, M. E., Holleman, L. J. M. & Gienapp, P. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**, 164–172 (2006).
34. Pearce-Higgins, J. W., Yalden, D. W. & Whittingham, M. J. Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* **143**, 470–476 (2005).
35. Nussey, D. H., Clutton-Brock, T. H., Elston, D. A., Albon, S. D. & Kruuk, L. E. B. Phenotypic plasticity in a maternal trait in red deer. *J. Anim. Ecol.* **74**, 387–396 (2005).
36. Husby, A. et al. Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. *Evolution* **64**, 2221–2237 (2010).
37. Matthysen, E., Adriaensen, F. & Dhondt, A. A. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). *Glob. Change Biol.* **17**, 1–16 (2011).
38. Fisher, J. I., Mustard, J. F. & Vadeboncoeur, M. A. Green leaf phenology at Landsat resolution: scaling from the field to the satellite. *Remote Sens. Environ.* **100**, 265–279 (2006).
39. Duparc, A. et al. Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. *Appl. Veg. Sci.* **16**, 305–316 (2013).
40. Hinks, A. E. et al. Scale-dependent phenological synchrony between songbirds and their caterpillar food source. *Am. Nat.* **186**, 84–97 (2015).
41. Lambrechts, M. M., Blondel, J., Maistre, M. & Perret, P. A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc. Natl Acad. Sci. USA* **94**, 5153–5155 (1997).
42. Dawson, A. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **363**, 1621–1633 (2008).
43. Visser, M. E. et al. Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3113–3127 (2010).
44. Caro, S. P., Schaper, S. V., Hut, R. A., Ball, G. F. & Visser, M. E. The case of the missing mechanism: how does temperature influence seasonal timing in endotherms? *PLoS Biol.* **11**, e1001517 (2013).
45. Bourgault, P., Thomas, D., Perret, P. & Blondel, J. Spring vegetation phenology is a robust predictor of breeding date across broad landscapes: a multi-site approach using the Corsican blue tit (*Cyanistes caeruleus*). *Oecologia* **162**, 885–892 (2010).
46. Bison, M. et al. Best environmental predictors of breeding phenology differ with elevation in a common woodland bird species. *Ecol. Evol.* **10**, 10219–10229 (2020).
47. Bernhardt, J. R., O'Connor, M. I., Sunday, J. M. & Gonzalez, A. Life in fluctuating environments. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **375**, 20190454 (2020).
48. Gienapp, P., Reed, T. E. & Visser, M. E. Why climate change will invariably alter selection pressures on phenology. *Proc. R. Soc. Lond. B Biol. Sci.* **281**, 20141611 (2014).
49. Lönstedt, O. M., McCormick, M. I., Chivers, D. P. & Ferrari, M. C. O. Habitat degradation is threatening reef replenishment by making fish fearless. *J. Anim. Ecol.* **83**, 1178–1185 (2014).
50. Pellerin, F., Cote, J., Bestion, E. & Aguilée, R. Matching habitat choice promotes species persistence under climate change. *Oikos* **128**, 221–234 (2019).
51. Firth, J. A., Verhelst, B. L., Crates, R. A., Garroway, C. J. & Sheldon, B. C. Spatial, temporal and individual-based differences in nest-site visits and subsequent reproductive success in wild great tits. *J. Avian Biol.* **49**, e01740 (2018).
52. Naef-Daenzer, B. & Keller, L. F. The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *J. Anim. Ecol.* **68**, 708–718 (1999).
53. Naef-Daenzer, B. Patch time allocation and patch sampling by foraging great and blue tits. *Anim. Behav.* **59**, 989–999 (2000).
54. Bouwhuis, S., Sheldon, B. C., Verhulst, S. & Charmantier, A. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 2769–2777 (2009).
55. Cole, E. F. & Sheldon, B. C. The shifting phenological landscape: within- and between-species variation in leaf emergence in a mixed-deciduous woodland. *Ecol. Evol.* **7**, 1135–1147 (2017).
56. Wint, W. The role of alternative host-plant species in the life of a polyphagous moth, *Operophtera brumata* (Lepidoptera: Geometridae). *J. Anim. Ecol.* **52**, 439–450 (1983).
57. Keller, L. F. & van Noordwijk, A. J. Effects of local environmental conditions on nestling growth in the great tit *Parus major*. *L. Ardea* **82**, 349–362 (1994).
58. Wilkin, T. A., Garant, D., Gosler, A. G. & Sheldon, B. C. Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. *J. Anim. Ecol.* **75**, 604–615 (2006).
59. Wilkin, T. A. & Sheldon, B. C. Sex differences in the persistence of natal environmental effects on life histories. *Curr. Biol.* **19**, 1998–2002 (2009).
60. Gagen, M. et al. The tree ring growth histories of UK native oaks as a tool for investigating chronic oak decline: an example from the Forest of Dean. *Dendrochronologia* **55**, 50–59 (2019).
61. Sturrock, R. N. et al. Climate change and forest diseases. *Plant Pathol.* **60**, 133–149 (2011).
62. MacColl, A. D. C. The ecological causes of evolution. *Trends Ecol. Evol.* **26**, 514–522 (2011).
63. Grant, P. R. & Price, T. D. Population variation in continuously varying traits as an ecological genetics problem. *Integr. Comp. Biol.* **21**, 795–811 (1981).
64. Hereford, J. A quantitative survey of local adaptation and fitness trade-offs. *Am. Nat.* **173**, 579–588 (2009).
65. Hadfield, J. D. The spatial scale of local adaptation in a stochastic environment. *Ecol. Lett.* **19**, 780–788 (2016).
66. Porlier, M. et al. Variation in phenotypic plasticity and selection patterns in blue tit breeding time: between- and within-population comparisons. *J. Anim. Ecol.* **81**, 1041–1051 (2012).
67. Hidalgo Aranzamendi, N., Hall, M. L., Kingma, S. A., van de Pol, M. & Peters, A. Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *J. Anim. Ecol.* **88**, 1799–1811 (2019).
68. Caro, S. P., Lambrechts, M. M., Balthazar, J. & Perret, P. Non-photoperiodic factors and timing of breeding in blue tits: impact of environmental and social influences in semi-natural conditions. *Behav. Process.* **75**, 1–7 (2007).
69. Bourret, A., Bélisle, M., Pelletier, F. & Garant, D. Multidimensional environmental influences on timing of breeding in a tree swallow population facing climate change. *Evol. Appl.* **8**, 933–944 (2015).
70. Nussey, D. H., Wilson, A. J. & Brommer, J. E. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**, 831–844 (2007).
71. Morris, D. W. Toward an ecological synthesis: a case for habitat selection. *Oecologia* **136**, 1–13 (2003).

72. Long, R. A. et al. Linking habitat selection to fitness-related traits in herbivores: the role of the energy landscape. *Oecologia* **181**, 709–720 (2016).
73. Morris, D. W. Spatial scale and the cost of density-dependent habitat selection. *Evol. Ecol.* **1**, 379–388 (1987).
74. Patten, M. A. & Kelly, J. F. Habitat selection and the perceptual trap. *Ecol. Appl.* **20**, 2148–2156 (2010).
75. Ponchon, A., Garnier, R., Grémillet, D. & Boulinier, T. Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. *Divers. Distrib.* **21**, 88–100 (2015).
76. Nilsson, A. L. K. et al. Hydrology influences breeding time in the white-throated dipper. *BMC Ecol.* **20**, 70 (2020).
77. Nilsson, A. L. K. et al. Location is everything, but climate gets a share: analyzing small-scale environmental influences on breeding success in the white-throated dipper. *Front. Ecol. Evol.* **8**, 542846 (2020).
78. Martin, R. O., Cunningham, S. J. & Hockey, P. A. R. Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich* **86**, 127–135 (2015).
79. Bailey, L. D. et al. Habitat selection can reduce effects of extreme climatic events in a long-lived shorebird. *J. Anim. Ecol.* **88**, 1474–1485 (2019).

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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*)<sup>80</sup>.

**Data collection. Bird phenology data.** The great tit population at Wytham Woods has been studied using standardized methods since 1947<sup>81</sup>. 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<sup>82</sup>. On average, 302 of these boxes are used by breeding great tits each year (1961–2020: mean = 302.4, s.d. = 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 (laying date). Tits generally lay one egg a day<sup>83</sup>, 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 for the periods 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 ref. <sup>15</sup>.

**Oak data.** In 2011, the location of every oak tree in Wytham Woods with a diameter at breast height greater than 30 cm ( $n=5,748$ ) was mapped using GPS. When this mapping was done, the diameter at breast height and crown health of each were also recorded. Health was scored on a scale from 1 to 5, where a score of 1 denotes a tree whose canopy has 0–25% dieback and a value of 5 denotes a tree that is dead. 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<sup>80</sup>. 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 ref. <sup>80</sup> 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 oak's 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 ref. <sup>55</sup>). Observations began when leaf buds started to swell and continued at three-day intervals until all shoots on the tree had developed small, unfolded leaves (see refs. <sup>55,84</sup>). 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 ref. <sup>40</sup>. 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<sup>58,59</sup>. 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 75 m 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 ref. <sup>82</sup> 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, and 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 unreasonable territory sizes (see ref. <sup>58</sup>). 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 twentieth-century plantations to areas of ancient semi-natural woodland<sup>85</sup>.

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 the preceding), 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 mg per 100 g (for full survey details, see refs. <sup>86,87</sup>). Following ref. <sup>88</sup>, 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 ref. <sup>89</sup>). In each case, laying date was expressed relative to the first of April (that is, 1 April = 1). For the spring temperature analysis, we used the Hadley Centre Central England Temperature dataset (<https://www.metoffice.gov.uk/hadobs/hadcte>) to calculate the mean maximum daily temperature for the period of 14 March to 1 May in each year. This was the 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'<sup>90,91</sup>. In this analysis, we considered all possible windows spanning the day before the laying-date record to 365 days before the laying-date record. We used the corrected Akaike information criterion (AIC<sub>c</sub>) 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 on the basis of AIC<sub>c</sub>. It is important to note that sliding-window analyses have recently received some criticism<sup>77</sup>, and comparative work has shown that different sliding-window analysis methods may select markedly different time windows, with some methods producing biologically implausible results<sup>92</sup>. 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 before 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 excluded all clutches that had been subject to an experimental manipulation in a given year (1,824 of 18,200). 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'<sup>93</sup>. 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<sup>94</sup>.

**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 in the preceding) using a mixed-effects meta-analytic approach in MCMCglmm<sup>95</sup>. We considered multiple fixed effects: the average oak-dieback score within a 75 m buffer around each box (see Extended Data Fig. 3 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<sup>82</sup>. 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 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 (3,972 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; 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 reran 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 (1) the number of oaks within 75 m of a nestbox, (2) altitude, (3) distance from the woodland edge and (4) average territory size. These models were also carried out in MCMCglmm using the same model structure as the preceding 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 in the preceding). 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 1,000 iterations. These values were chosen to ensure low autocorrelation between successive samples and thus a good effective sample size. As in the preceding, the significance of fixed effects was determined on the basis of 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 in the preceding) that was associated with an oak identity random effect. Because we were unable to obtain spatial-similarity matrices for the full dataset of 4,483 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 used 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.

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

## 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 codes 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)<sup>95</sup>, 'vegan' (version 2.5-6)<sup>93</sup>, 'climwin' (version 1.2.3)<sup>90</sup> and 'stats' (version 4.0.3)<sup>96</sup>.

## References

80. Kirby, K. J. et al. Changes in the tree and shrub layer of Wytham Woods (southern England) 1974–2012: local and national trends compared. *Forestry* **87**, 663–673 (2014).
81. Perrins, C. & McCleery, R. Laying dates and clutch size in the great tit. *Wilson Bull.* **101**, 236–253 (1989).
82. Wilkin, T. A., Perrins, C. M. & Sheldon, B. C. The use of GIS in estimating spatial variation in habitat quality: a case study of lay-date in the great tit *Parus major*. *Ibis* **149**, 110–118 (2007).
83. Perrins, C. M. Population fluctuations and clutch-size in the great tit, *Parus major*. *J. Anim. Ecol.* **34**, 601–647 (1965).
84. Wesolowski, T. & Rowiński, P. Timing of bud burst and tree-leaf development in a multispecies temperate forest. *For. Ecol. Manage.* **237**, 387–393 (2006).
85. Gibson, C. W. D. in *Woodland Conservation and Research in the Clay Vale of Oxfordshire and Buckinghamshire* (eds Kirby, K. J. & Write, F. J.) 32–40 (JNCC, 1988).
86. Dawkin, H. C. & Field, D. R. B. *A Long-Term Surveillance System for British Woodland Vegetation*. Commonwealth Forestry Institute, Oxford, Occasional Paper No. 1. (1978).
87. Horsfall, A. S. & Kirby, K. J. *The Use of Permanent Quadrats to Record Changes in the Structure and Composition of Wytham Woods*, Oxfordshire Research and Survey in Nature Conservation No. 1 (JNCC, 1992).
88. Wilkin, T. A., King, L. E. & Sheldon, B. C. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. *J. Avian Biol.* **40**, 135–145 (2009).
89. Van Noordwijk, M. & Purnomasidhi, P. Root architecture in relation to tree-soil-crop interactions and shoot pruning in agroforestry. *Agrofor. Syst.* **30**, 161–173 (1995).
90. Bailey, L. D. & van de Pol, M. climwin: an R toolbox for climate window analysis. *PLoS ONE* **11**, e0167980 (2016).
91. van de Pol, M. et al. Identifying the best climatic predictors in ecology and evolution. *Methods Ecol. Evol.* **7**, 1246–1257 (2016).
92. Simmonds, E. G., Cole, E. F. & Sheldon, B. C. Cue identification in phenology: a case study of the predictive performance of current statistical tools. *J. Anim. Ecol.* **88**, 1428–1440 (2019).
93. Oksanen, J. et al. vegan: Community Ecology Package: R Package v.2.5-6 (2019); <https://CRAN.R-project.org/package=vegan>
94. Sturges, H. A. The choice of a class interval. *J. Am. Stat. Assoc.* **21**, 65–66 (1926).
95. Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* <https://doi.org/10.18637/jss.v033.i02> (2010).
96. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2020); <http://www.R-project.org/>

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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

The authors declare no competing interests.

## Additional information

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**Correspondence and requests for materials** should be addressed to Charlotte E. Regan or Ben C. Sheldon.

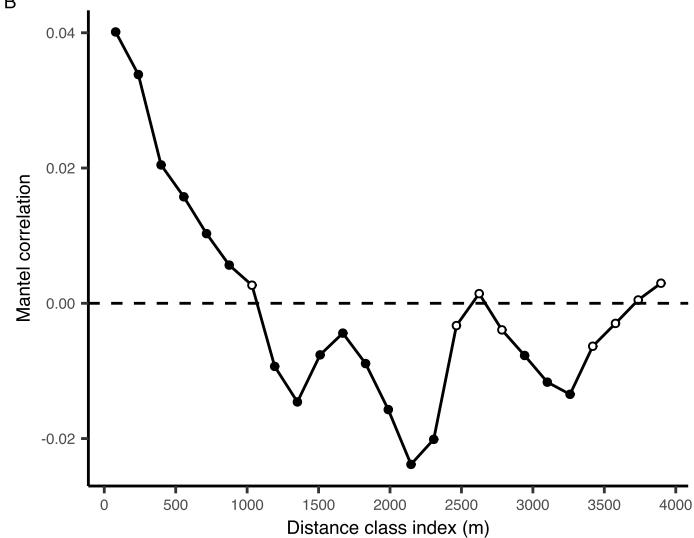
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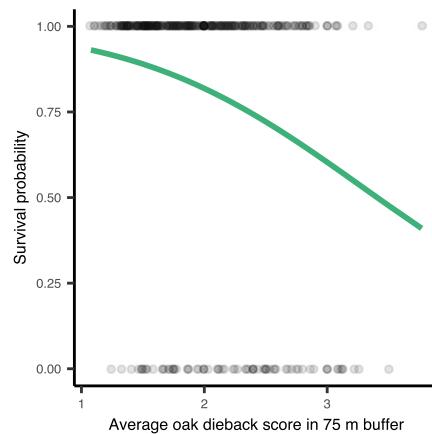
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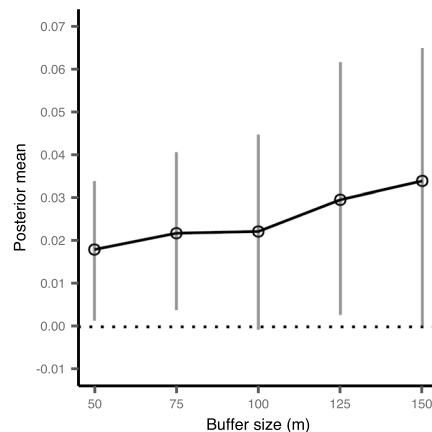
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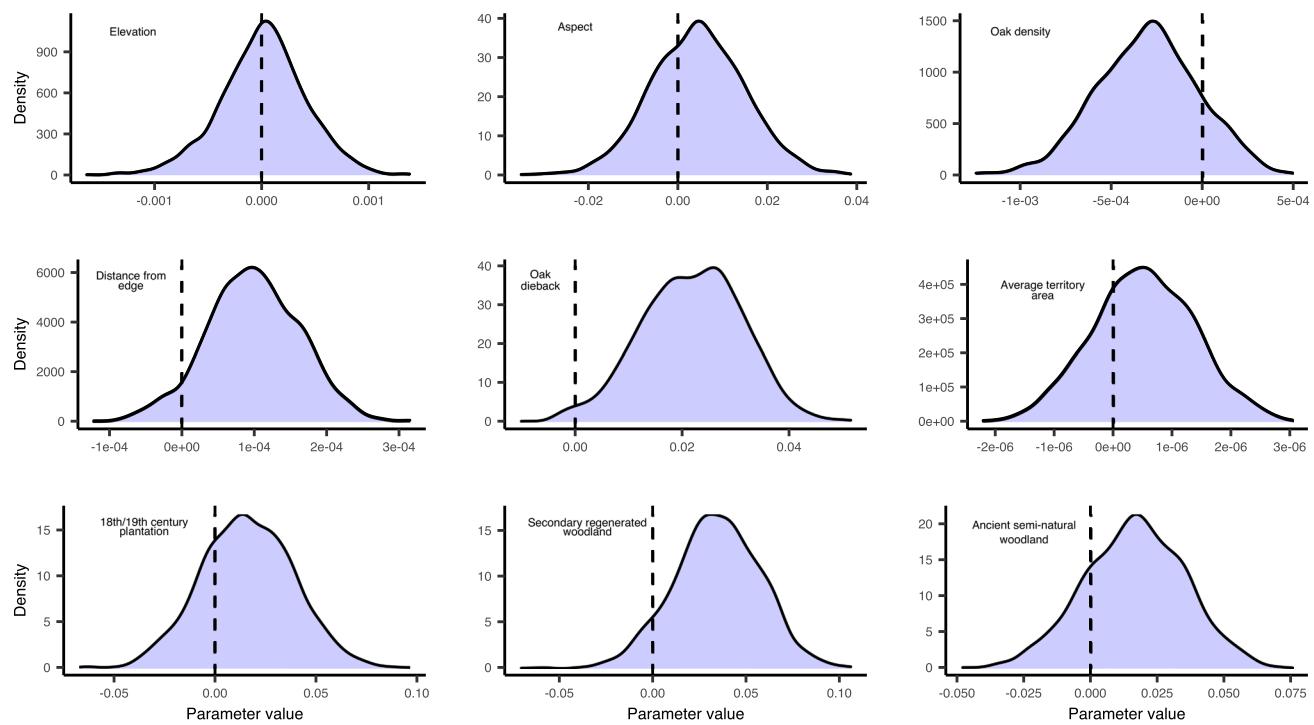
**Extended Data Fig. 1 | Oak health is non-randomly distributed across Wytham Woods.** (a) The spatial structure of oak crown dieback across Wytham. Shown are all 5,748 mature oak trees, coloured according to the amount of crown dieback (where a score of 1 denotes a tree whose canopy has 0 to 25 % dieback and a value of 5 denotes a tree that is dead) (b) Mantel correlogram showing the direction and strength of spatial autocorrelation in the dieback scores of oak trees in different distance classes.



**Extended Data Fig. 2 | An oak's survival probability is predicted by its dieback score.** Survival probability of 394 oaks over a 39-year period (1975–2014) in relation to the degree of local oak dieback.

**Extended Data Fig. 3 | The estimated relationship between oak dieback score and the rate of laying date change was consistent across buffer sizes.**

Shown are posterior means and credible intervals from models of the rate of laying date change with average oak dieback score calculated using buffers of different sizes.



**Extended Data Fig. 4 | Oak dieback was the only fixed effect whose 95% credible interval did not overlap zero.** Shown are fixed effect posterior distributions from the mixed effects model with rate of laying date change as the response, the fixed effects shown in the figure, a spatial similarity matrix, and each data point weighted according to its standard error.



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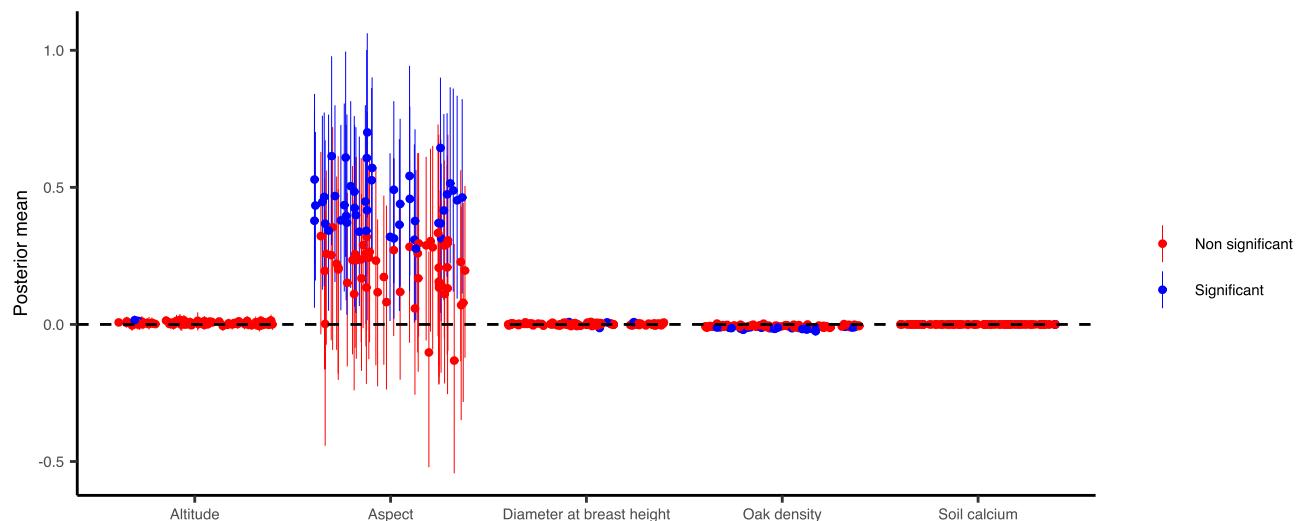
3

4

5

Oak dieback score

**Extended Data Fig. 5 | Oak canopy health was scored on a scale between 1 and 5.** A score of 1 corresponds to a tree with 0–25% dieback, 2 to a tree with 25%–50% dieback, 3 to a tree with 50%–75% dieback, 4 to a tree with 75% to 100% dieback, and 5 to a tree that is dead.



**Extended Data Fig. 6 | There were no consistent effects of environmental explanatory variables on oak dieback score.** Shown are posterior means and 95% credible intervals from the 100 models exploring the relationships between local environmental factors and oak dieback scores for random samples of 200 trees. Each model included a spatial similarity matrix to account for potential spatial autocorrelation in dieback scores.

## Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

### Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
  - Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted
  - Give  $P$  values as exact values whenever suitable.*
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection No software were used explicitly for data collection.

Data analysis All analyses were performed in R 4.0.3 in packages MCMCglmm 2.29, vegan 2.5-6, climwin 1.2.3, and stats 4.0.3

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

### Data

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All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on 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>

# Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences       Behavioural & social sciences       Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://nature.com/documents/nr-reporting-summary-flat.pdf)

## Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used data from a long-term individual based study of a wild great tit population to explore the effect of spatial environmental variation on the rate of change in laying date at 1021 nest boxes.
Research sample	We used breeding records from the Wytham woods great tit ( <i>Parus major</i> ) population spanning 1965 - 2020 to characterise nestbox-level rates of laying date change across the woodland.
Sampling strategy	We used all breeding data from broods that were not part of experimental manipulations and that were in nestboxes where we had information on characteristics of the surrounding environment.
Data collection	Data have been collected following a standardised protocol each spring since 1965.
Timing and spatial scale	The data used span from 1965 to 2020 and cover the breeding population in Wytham woods each year.
Data exclusions	We excluded broods part of experimental manipulations to avoid effects of manipulations on laying date. We also used broods from 1965 onwards as the standardised data collection protocol commenced at this time. We also excluded broods from nestboxes where environmental data were not available as this was key to the questions being asked in the study.
Reproducibility	We checked the robustness of our results to different decisions such as the buffer used to quantify environmental components and model structure.
Randomization	As this study relies on the monitoring of a breeding population of wild birds where all nestboxes are monitored each year, no randomisation was necessary.
Blinding	Blinding was not relevant to this study given that it is based on longitudinal data collected over many decades.

Did the study involve field work?  Yes  No

## Field work, collection and transport

Field conditions	The study used data collected during the breeding season in each year (March - June)
Location	Wytham woods, Oxford, UK (51.77190, -1.3376981).
Access & import/export	All birds were captured under BTO licenses.
Disturbance	Visits to nests may have caused low levels of disturbance to the birds but these visits are timed to minimise these effects and are always carried out as quickly as possible.

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

**Materials & experimental systems**

n/a	Involved in the study
<input checked="" type="checkbox"/>	Antibodies
<input checked="" type="checkbox"/>	Eukaryotic cell lines
<input checked="" type="checkbox"/>	Palaeontology and archaeology
<input type="checkbox"/>	Animals and other organisms
<input checked="" type="checkbox"/>	Human research participants
<input checked="" type="checkbox"/>	Clinical data
<input checked="" type="checkbox"/>	Dual use research of concern

**Methods**

n/a	Involved in the study
<input checked="" type="checkbox"/>	ChIP-seq
<input checked="" type="checkbox"/>	Flow cytometry
<input checked="" type="checkbox"/>	MRI-based neuroimaging

**Animals and other organisms**

Policy information about [studies involving animals; ARRIVE guidelines](#) recommended for reporting animal research

## Laboratory animals

The study did not involve laboratory animals.

## Wild animals

The study used data from wild great tits (*Parus major*) aged 1 year and older. Birds were never transported but were captured at the nest to enable individual identification. All catching was done under appropriate licenses from the British Trust for Ornithology.

## Field-collected samples

The study did not involve samples collected from the field.

## Ethics oversight

All birds were captured by fieldworkers with British Trust for Ornithology licenses.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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