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Phenological shifts

Great tit response to climate change

Climate change induces earlier spring reproductive events in many wild species, as observed in a great tit population inhabiting the Wytham Woods near Oxford (UK). While earlier reproduction is expected to help cope with warmer springs, the health of oak trees seems to substantially influence bird's ability to modulate their breeding period according to the new climate conditions.

One of the main responses to climate change observed in wild organisms is phenological change¹ through phenotypic plasticity²⁻⁴, in which biological rhythms are shifted due to warmer temperature without genetic changes. Environmentally-induced modulation of life-history events may allow adaptive response to rapid climate change. However, the consequences of climate upheavals on the efficiency of plasticity in an altered habitat are still poorly understood⁵. Several facets of the environment – such as photoperiod, precipitation and temperature^{6,7} – influence bird phenology in a multi-dimensional way. By disrupting long-standing relationships between those environmental drivers, climate change may lead phenological plasticity to produce maladapted phenotypes in the new conditions. In addition to abiotic components, phenological changes in a given species may be driven by other species with which it interacts, inducing complex phenological entanglements through trophic levels⁸. Utilizing an exceptional long-term study in the Wytham Woods (UK), Ella F. Cole and collaborators⁹ explored the consequences of ecological interactions on bird ability to respond to climate change in the seminal tritrophic system: “great tit (*Parus major*) – caterpillar (e.g. the winter moth, *Opheroptera brumata*) – tree (e.g. oak, *Quercus robur*)”. The

authors used advanced statistical analyses applied on a longitudinal data set of sixty years to show how small-scale spatial variation of oak health influences the phenological changes in great tit over the years, and discussed how it is related to climate change.

Natural environments fluctuate, especially in temperate regions where organisms modulate their biological rhythms with the seasons. Every year, passerines (songbirds), must select the suitable period to breed, which varies due largely to among-year variation in spring temperatures. Caterpillars are the main nutritive resources to chicks. Therefore, the favourable period for reproduction will be the one synchronised with the caterpillar's peak of abundance; and both birds and caterpillars will lay and develop earlier in warmer spring. In line with previous studies of passerines in temperate forests (e.g. ^{1,10}), Cole and colleagues show that mean daily maximum temperature increased by 2.6°C in the Wytham Woods since 1961, inducing the great tit population to advance their laying date by about two weeks since the beginning of the study⁹. An older studies in the same great tit population suggested that this phenological change is mainly enabled by phenotypic plasticity¹¹, still allowing birds to track the earlier developmental period of their preys in this population⁹.

Because environmental cues used by birds to modulate their phenology vary at large but also at small spatio-temporal scales, and consequences of natural selection at the population level result from a sorting between individuals, it is crucial to study the influence of climate change at a local scale. Comparing bird phenological advancement among almost one thousand nest-boxes across 385-ha forest, Cole and colleagues highlighted that birds do not alter their reproductive period with to the same degree over the years, with earlier birds breeding two weeks and half before the latest ones. To understand this fine-spatial scale difference in bird phenology, the authors estimated the canopy health (i.e. percentage of

crown dieback) of 193 oaks and explored the relationship between bird laying date and oak dieback. They showed that birds breeding in nest-boxes surrounded by sick oaks advanced their laying date less through the years; with tree health explaining a fifth of the variation in bird phenology⁹. Since oak health was not related to the budburst phenology of the trees – which drives the timing of caterpillar development –, these findings show how fine-grained and spatially autocorrelated variation in response to climate change may emerge even from indirect species interactions⁹.

Canopy health may explain part of the variation in laying date rate of change in many ways. Phenotypic plasticity is assumed to be costly in resources, at least because it requires maintenance of the ability to perceive environmental variation and to produce new phenotypes accordingly¹². Therefore, if for example diseased oaks produce fewer leaves in the spring, resulting in a lower abundance of caterpillars than in healthier trees, then reproducing near sick oaks may constrain bird ability to modulate their phenology because the available nutritive resources are too low to afford the cost of plasticity. Alternatively, low caterpillar resources could induce bird diet to be more diversified and less dependent on the transient caterpillar peak date of abundance, selecting for lower plasticity. Moreover, competition for best territories may sort individuals according to their body condition, which could also explain the detected relationship between phenological change and tree health. Surely, the origin of spatial variation in phenological rate of change in this great tit population is highly multi-factorial. Further disentangling these non-exclusive hypotheses would require challenging experiments in natural environment spanning several trophic levels, which calls for other promising researches. Moreover, fitness advantages to modulate reproductive phenology according to climate also may depend on the oak health. Consequently, variation in oak dieback would induce fine-scale and autocorrelated spatial variation in natural

selection on laying date and its plasticity regarding temperature, which may have important consequences on population dynamics and adaptive potential, making such research very valuable in the context of rapid global changes.

This study is a great example of multi-dimensional phenotypic plasticity and shows how climate change may have tangled consequences on interacting organisms. Current environmental changes induce detrimental modifications in biological systems (e.g.¹⁰), and it is essential to understand the complexity of these changes in order to prevent the decline of wild populations¹³. This work by Ella E. Cole and colleagues⁹ is one of the numerous studies required to succeed.

Competing Interests

The authors declare no competing interests.

Figure

Great tit (*Parus major*).

In the Wytham Woods near Oxford (UK), the great tit population advanced its breeding period by about two weeks and half within sixty years because of spring temperatures increase of 2.6°C. Despite this average phenological advancement, variation in canopy health was linked to local differences in the phenological rate of change over the years. Hence, depending on the territory quality, authors observed substantial variations in bird response to climate change at a very fine-spatial scale. Photo by Stephan Tilló.

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